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DARTMOUTH STUDIES IN TROPICAL ECOLOGY

Dartmouth College runs an annual 9-10 week ecological field research program in Costa Rica and the Caribbean. Manuscripts from the research projects in this program have been published in the annual volume "Dartmouth Studies in Tropical Ecology" since 1989. Copies are held in the Dartmouth library and in Costa Rica at the San Jose office of the Organization for Tropical Studies (OTS/OET), at the OTS field stations at Palo Verde, Las Cruces and La Selva, at the Sirena Station of the Corcovado National Park, and at the Monteverde Biological Station. On Little Cayman Island, there are copies at the marine laboratory of the Little Cayman Research Center.

Dartmouth faculty from the Department of Biological Sciences, along with two Ph.D. students from Dartmouth's Environmental and Evolutionary Biology graduate program, advise ca. 15 advanced undergraduate students on this program. The first few projects are designed by the advisors, but undergraduates soon begin conceiving and designing their own projects.

The order of authorship on each paper was chosen randomly, in keeping with the style of the program, which emphasizes a cooperative and egalitarian relationship among undergraduates in each project. Where faculty or graduate student mentors have pre-designed a project, this is indicated after the author listing at the head of the paper. For each paper there is a faculty editor (also indicated after the author listing), who takes responsibility for defining the required revisions, and decides on the acceptability of manuscripts for publication. On each paper, at least one faculty member and one graduate student are heavily involved as mentors at every stage, from project design to final manuscript. However, it is our policy that faculty and graduate students are not included as authors for undergraduate projects. Our annual books do include a few projects initiated and conducted by graduate students; these tend to be rare, due to the heavy research advising commitments of Ph.D. students on the program. Spanish abstracts (and in a few cases, complete articles) were translated from English by Ernesto Ruelas Inzunza.

We would like to thank the Costa Rican Ministry of the Environment and Energy (MINAE) for permission to conduct research in Costa Rica's extraordinary national parks. The Organization for Tropical Studies (OTS/OET) has provided critical support for our program for over 30 years, taking care of most of our logistical needs in Costa Rica, always to high standards of quality and reliability. We thank OTS staff at the Palo Verde and La Selva Biological Stations, and at the Wilson Botanical Garden at Las Cruces, for all their services rendered efficiently, politely and in good spirit. Staff at the Santa Rosa and Corcovado National Parks have also been gracious in accommodating and assisting us. We are grateful to the staff of the Monteverde Biological Station for access to their wonderful facilities, and for making us so comfortable when we arrive

late, dirty, hungry and tired from Santa Rosa.

On Little Cayman Island, the Little Cayman Research Center (LCRC), operated by the Central Caribbean Marine Institute, is our base for the entire coral reef ecology segment of the program. Expert LCRC staff run the lab, provide accommodations and food, operate research vessels and take care of SCUBA diving logistics and safety. On the Dartmouth campus, the Off Campus Programs Office, under the Associate Dean of International and Interdisciplinary Studies, deals with administration and emergency services and provides an essential lifeline to remote locations in rare times of need.

If you have questions about this volume or the program, contact the Biological Sciences Department at Dartmouth College, Hanover New Hampshire, USA. Currently, the Biology Foreign Studies Program Director is David Peart at david.peart@dartmouth.edu and the administrative assistant is Mary Poulson at mary.poulson@dartmouth.edu.

A NOTE ON SPANISH ABSTRACTS:

This is the first time that the *Dartmouth Studies in Tropical Biology* volume contains abstracts in Spanish for all the papers written during our course's stay in Costa Rica. Translating abstracts of scientific reports (or any other text) can be challenging and some adjustments need to be made to make them readable to Spanish speakers.

A few comments are necessary to explain some decisions made in these translations. First, the abstracts in Spanish are not direct translations, as the grammatical structure and other narrative constructions do not perform well in the other language. I opted for translating the intended meaning of the sentence while keeping its grammar and style as literal as possible.

Many terms that are well established in the (English language) literature do not have a direct translation or read awkwardly when translated (e.g. how do you translate "lottery hypothesis," or "fungal rhizomorph"?), so the reader will find some cases where a concept/word is described more extensively in the Spanish translation.

Students often write titles and colloquial phrases that are entertaining or make sense in English but do not translate well in Spanish. In order to convey the meaning of the title intended by the authors, I read each paper and consulted with them on the strict meaning of these phrases and titles.

The English common names of most groups of animals, plants, fungi, and other organisms do not have an equivalent in Spanish, although attempts have been made by several authors to impose a standardized nomenclature. I am an advocate of preserving local names as an element of cultural richness across the countries and people that speak Spanish. I opt for the use of scientific names to attain the desired precision. I use a "generic" common name only if it is well-established across Spanish-speaking languages, (e.g. "higuera" for "fig" and "abeja" for "bee"); the scientific name follows these common names. Last, I couldn't help but use my Mexican Spanish, although I tried to make it as standard as possible.

Ernesto Ruelas Inzunza
Little Cayman Island, 11 March 2009.

FSP 2009 SCHEDULE

		Morning	Afternoon	Evening
6 Jan	To San Jose	Travel	Travel	Arrive in evening, group meeting
7 Jan	In San Jose	OTS, InBIO	Free	Group dinner in SJ, Group meeting
8 Jan	To Palo Verde	Travel	Orientation	Lec: Intro trop ecol
9 Jan	Palo Verde	Orientation	Research questions	Lec: Primate ecol
10 Jan	Palo Verde	FP-1	Stats lab	Data analysis/synthesis
11 Jan	Palo Verde	MN[c]; CP[d]	Insect lab; Anal/writing	FP-1 seminars. FP 1 ms due
12 Jan	Palo Verde	MN; CP	Vert lab; Lec Avian I	Lec: Species coex
13 Jan	Palo Verde	MN; SIFP[e] plan	Plt lab & Lec: Poll Ecol	Data anal & writing
14 Jan	Palo Verde	SIFP-1	SIFP-1	CP seminars; Anal/writing
15 Jan	Palo Verde	SIFP-1	Data analysis & writing.	Lec: PV mgmt (Dr. Sasa?)
16 Jan	Palo Verde	River trip	Writing. SIFP-1 seminars	Writing. SIFP-1 ms due.
17 Jan	Santa Rosa	Travel/walk	Orientation; Lec: Sea turtles	Field: Sea turtle nesting
18 Jan	Santa Rosa	Lec: Mangrove	Exploration[f]	Field: Sea turtle nesting
19 Jan	To Monteverde	Walk/Travel	Orientation	Lec: Stream Ecol.
20 Jan	Monteverde	Orientation	SIFP-2 planning	Gst Lec: Amphibs (A Pounds)
21 Jan	Monteverde	CP	SIFP-2 pilot /props.	Lec: Social Insects
22 Jan	Monteverde	SIFP-2	SIFP-2	Analysis and writing
23 Jan	Monteverde	SIFP-2	SIFP-2	Analysis and writing
24 Jan	Monteverde	SIFP-2 sem	Bat Jungle (R. Laval)	Bats. Writing. SIFP-2 due.
25 Jan	At MV, to SJ	free [lnch@MV]	Travel to SJ	free
26 Jan	In SJ	830 to Serp	free	free
27 Jan	To Cuerici	Travel	Orientation	Lec: For Cns Mgt
28 Jan	Cuerici	CP;MN;SIFP-3	SIFP-3 plan	Lec: For Dyn
29 Jan	Cuerici	Trip to Paramo	SIFP-3	Lec: Herbivory
30 Jan	Cuerici	SIFP-3	SIFP-3	Anal & writing; SIFP2 rev due
31 Jan	Cuerici	SIFP-3	SIFP-3	Anal & writing. SIFP2 FIN due
1 Feb	Cuerici	SIFP-3 seminars	Writing	Writing: SIFP-3 ms due
2 Feb	Cuerici/travel	Exploration	Travel to La Palma	free
3 Feb	To Corcovado	Walk/orient	Walk/orientation	Discussion
4 Feb	Corcovado	Orientation	Orientation	Lec: Avian Ecol.II
5 Feb	Corcovado	MN; CP; SIFP	SIFP-4 plan/proposals	Lec: Seed disp pred
6 Feb	Corcovado	SIFP-4	SIFP-4	Writing/night walk
7 Feb	Corcovado	SIFP-4	SIFP-4	Lec: ConsBiol
8 Feb	Corcovado	Exploration	Anal/writing: SIFP4 sem.	Writing: SIFP4 ms due
9 Feb	To Las Cruces	Walk	Travel	Guest lec Zak Zahawi. Disc.
10 Feb	Las Cruces	Plant lab.	Writing. SIFP4 rev due	Lec: Soil/Biogeoch
11 Feb	Las Cruces	Bird lab/quiz	Pl.lab&quiz. Writing	Writing. SIFP3 FIN due
12 Feb	To SJ	Travel to SJ	Free	Free
13 Feb	To La Selva	Travel	Orientation	Guest lec (Clarks) Writing
14 Feb	La Selva	Orientation	SIFP planning/pilot	Writ. SIFP4 FIN due
15 Feb	La Selva	MN;CP; SIFP	SIFP-5	Guest lec (Clarks?) Anal CP
16 Feb	La Selva	SIFP-5	SIFP-5	CP seminar. Writing: CP due
17 Feb	La Selva	SIFP-5	Agroecol. field trip	Writing; SIFP5 mss due
18 Feb	La Selva	Writing	Writing	*All final CR revisions due*
19 Feb	La Selva, to SJ	Exploration	Travel	Group dinner in SJ
20 Feb Depart for Little Cayman, leave LC 12 Mar				

[a] Orientation = learning new site/ecosystem/organisms [b] FP = field problems (staff initiated)

[c] MN = Mist netting [d] CP = Comparative project

[e] SIFP = student initiated field problems [f] Explor. = Time to explore site

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http://cayman.com.ky/about-cayman/island-information/cayman-islands-map.html

NICARAGUA

PANAMA

LITTLE CAYMAN

Save the babies: Preferential defensive recruitment
of *Pseudomyrmex spinicola* to *Acacia collinsii* thorns

Jeremy H. M. Chan, Eben E. B. Bein, Marguerite N. Dashevsky,
Keng-Lou Hung, and Brianna L. Wilkinson

Project Design: Rebecca E. Irwin. Faculty Editor: Rebecca E. Irwin

Abstract: We investigated whether *Pseudomyrmex spinicola* would preferentially protect some *Acacia collinsii* thorns over others. Because the number of ant offspring per thorn is correlated with thorn size, we predicted that ants would defend larger thorns more than smaller thorns. To test this prediction, we simultaneously tapped large and small thorns on the same tree to simulate predatory activity. We counted the number of ants that recruited to each thorn and then dissected the thorns to determine the number of larvae and pupae inside. Our results supported our prediction: more ants recruited to defend the larger thorns. Increased defensive recruitment to larger thorns could be a viable mechanism to increase the fitness of the colony.

Key words: resource allocation, predation, mutualism

Defensa preferencial de *Pseudomyrmex spinicola*
a espinas grandes de *Acacia collinsii*

Resumen: Investigamos si la hormiga *Pseudomyrmex spinicola* tiene preferencias al proteger unas u otras espinas del cornezuelo *Acacia collinsii*. Debido a que el número de huevos y larvas de hormigas está correlacionada positivamente con el tamaño de las espinas, nuestra predicción es que las hormigas defenderán más a las espinas grandes que a las pequeñas. Para probar esta predicción, dimos pequeños golpes en espinas pequeñas y grandes en el mismo árbol para simular actividad de depredadores. Contamos el número de hormigas que respondieron a la perturbación de cada espina y posteriormente diseccionamos las espinas para cuantificar el número de larvas y pupas en su interior. Nuestros resultados dan soporte a nuestra predicción: más hormigas acudieron a defender espinas grandes y este puede ser un mecanismo para incrementar el potencial reproductivo de la colonia.

Palabras clave: designación de recursos, depredación, mutualismo

Introduction

One way for an organism to increase its fitness is to invest in defense, either of itself or of relatives that carry similar genes. Evolutionary theory predicts that organisms should allocate defensive resources optimally to maximize their fitness (Steiner 2007). Many different strategies of defense have arisen in insects, making them excellent study organisms to test this hypothesis. Here, we tested whether *Pseudomyrmex spinicola* optimally defended their progeny.

Pseudomyrmex spinicola are plant ants that form an obligate mutualism with the plant *Acacia collinsii*. *Pseudomyrmex spinicola* protects *A. collinsii* from herbivores and competing vegetation (Camacho and

Lindquist 2007). In exchange, *A. collinsii* provides the resident ants with nectar and lipid-rich Beltian bodies. In addition, *A. collinsii* provides *P. spinicola* with swollen thorns for shelter and protection from predators. Thorn size is especially important to *P. spinicola* because it dictates the amount of offspring that they can harbor; Isbey et al. (2007) found that *P. spinicola* keep more larvae and pupae in larger thorns than in smaller thorns. Because loss of offspring in social Hymenoptera often reduces the colony's reproductive capacity (Smith 2006), we predicted that *P. spinicola* will preferentially defend larger thorns to increase the overall fitness of the colony. Specifically, we predicted that if we simultaneously simulated predator activity at two thorns, more ants would recruit to defend the larger thorn over the smaller thorn.

METHODS

Our study site was located in the tropical dry forest of Palo Verde National Park in the Guanacaste region of Costa Rica. The semideciduous forest has only two strata of trees, shrubs often have thorns or spines, and the ground layer is sparse except in forest gaps (Janzen 1983). The study area was located less than 1 km southeast of the Palo Verde Organization for Tropical Studies (OTS) Field Station on the morning of 10 January 2009, at the beginning of the six-month dry season.

We observed the behavioral response of *P. spinicola* to simulated predation on
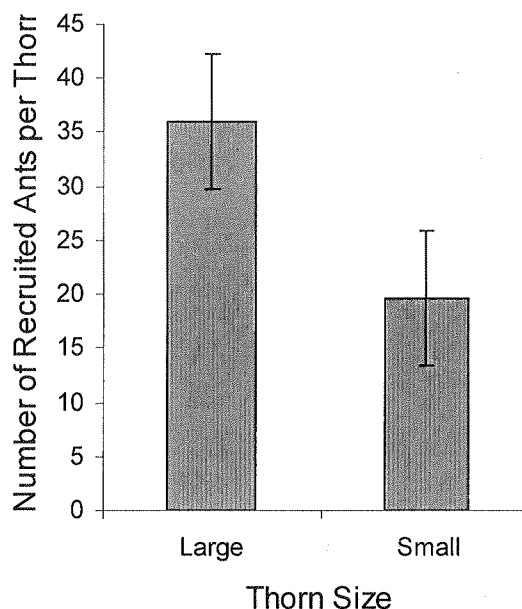
FIG. 1. Number of *Pseudomyrmex spinicola* individuals recruited to large and small thorns of *Acacia collinsii* when tapped. The study took place in Palo Verde National Park, Costa Rica. More *P. spinicola* recruited to larger thorns than to smaller thorns. Bars are means ± 1 S.E.

ten *A. collinsii*. We selected two thorns no higher than 2 m from the ground that differed substantially in size by eye. These thorns were located either on the tree's trunk or at the base of a branch and were within 0.75 m of each other. We tapped the thorns simultaneously with a metal rod 30 times each to simulate a predator, such as another ant or bird. For 60 seconds, observers counted the ants that came within three centimeters of the thorn as recruits. We then removed the thorns and measured the length of each half, as well as the width where the two halves met. Length measurements were averaged and multiplied by width to estimate thorn area. The average areas of large and small thorns were 460.0 mm²

and 286.8 mm² respectively (one-tailed, paired t-test: t_8 = -6.58, P < 0.001). Finally, we counted the number of ant offspring (larvae and pupae) contained within each thorn.

We used a one-tailed paired t-test to test the prediction that ants would preferentially recruit to defend large thorns more than small thorns. In addition, we used a one-tailed paired t-test to test the assumption that larger thorns harbored more ant larvae and pupae. The statistical analyses were performed in JMP 7.0 (SAS Institute, Inc. 2007).

RESULTS

There was a significant difference between the response of *P. spinicola* to the disturbance of large thorns versus small thorns (one-tailed, paired t-test: t_9 = -2.60,
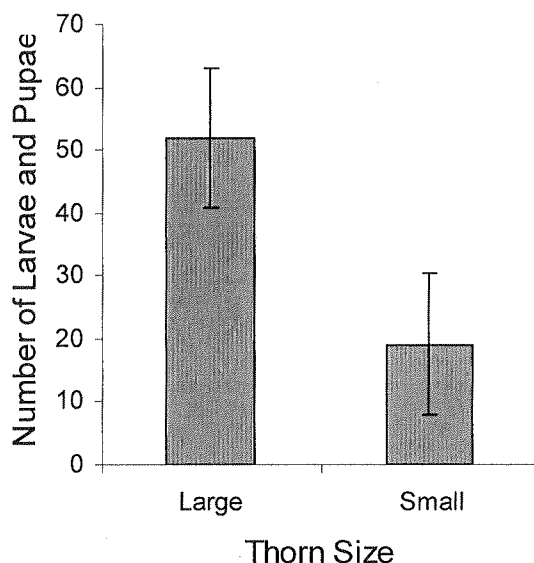
FIG. 2. Number of *Pseudomyrmex spinicola* larvae and pupae present in large and small thorns of *Acacia collinsii* in Palo Verde National Park, Costa Rica. Larger *A. collinsii* thorns harbor more larvae and pupae of *P. spinicola* than smaller thorns. Bars are means ± 1 S.E.

P = 0.0144; Fig. 1). There were 1.8 times more ants that recruited to the large thorns than to the small thorns. Furthermore, there were 2.7 times more ant offspring in the larger thorns (paired-t_6 = -2.95, P = 0.013; Fig. 2).

DISCUSSION

Our results indicate that ants recruit more to larger thorns than smaller thorns on the same tree after predator simulation. An ant colony's fitness is measured by the number of reproductive individuals it produces. Preferential recruitment to larger thorns with more larvae and pupae may protect more offspring, leading to a larger colony size, and larger colonies may produce more reproductive individuals. Thus, if ants successfully defend their larvae and pupae from a predator, they may increase the fitness of the colony.

We assumed that ants that recruited to the thorns were indeed providing protection to the larvae and pupae. We think this assumption is supported by ant behavior. As we experienced, ants recruiting to the thorn stung and bit us painfully. We can assume that ants that recruit to the thorn will defend the thorn where their larvae and pupae are stored.

One potential caveat to the interpretation of our study is that Iwamoto et al. (2003) showed that there is higher baseline ant activity on branches with more resources, such as extra-floral nectaries, Beltian bodies, and thorns. This higher baseline activity may have influenced the number of recruits found at larger

3

thorns. However, Iwamoto et al. (2003) also found that, when they disturbed the branches, there was no difference in the recruitment to high- versus low-resource branches. Therefore, our data probably were not skewed by baseline numbers of ants on the branches with large vs. small thorns.

To further understand how ants allocate defenses, another study could investigate the number of defenders originally allocated to a thorn before a threat is presented. A possible outcome could be that there are more ants inside the larger thorns to begin with, in addition to the greater number of recruited ants. This would support our conclusion that ants increase colony fitness by preferentially defending thorns with more larvae and pupae inside. We also do not know whether the ants would differentiate between herbivory and predation. If *P. spinicola* prioritize their own fitness over the fitness of *A. collinsii*, they might allocate more defenders to the site of a predatory threat than to that of an herbivorous threat. A future study could compare *P. spinicola*'s reaction to a simulated herbivore threat with the reaction to a simulated predator threat. Finally, studies that investigate the mechanism by which *P. spinicola* allocate defense would provide additional ecological insight. Communication of a threat is the key component of this mechanism. Wood and Wood (2004) found that crushed *A. collinsii* leaves release volatile compounds, which attract ants to the damaged area. However, the ants themselves are also known to use alarm pheromones when the colony is threatened (Yamagata et al. 2007). Future studies should clarify whether either of these mechanisms is involved in *P. spinicola*'s preferential defensive response.

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NOT ALL MUTUALISMS ARE CREATED EQUAL: DIFFERENCES BETWEEN TWO *PSEUDOMYRMEX* SPP. INHABITING *ACACIA COLLINSII*

KARL GRUNSEICH, REBECCA D. DAVIDSON WOLF, ROBIN M. MEYERS, DANIEL L. SUSMAN, AND JONATHAN M. WACHTER

Project Design: Ernesto Ruelas Inzunza. Faculty Editor: Rebecca E. Irwin

Abstract: In an obligate mutualism, swollen-thorn acacias (*Acacia collinsii*) provide nutrients and protective thorns to ants (*Pseudomyrmex* spp.) in return for defense from herbivores and competition from other plants. Two *A. collinsii* mutualists, *Pseudomyrmex spinicola* and *P. flavicornis*, differ in their aggressiveness. We investigated whether this difference in aggressiveness affected the extent to which the ants reduce interspecific competition through clearing neighboring plants. We also looked at difference in thorn size as a way of measuring *A. collinsii* investment in its mutualists. The more aggressive ant, *P. spinicola*, more effectively cleared non-*A. collinsii* stems within a 2 m radius than *P. flavicornis*. Because of the difference in plant-clearing ability of the ant species, we predicted that *A. collinsii* inhabited by *P. spinicola* would be more successful than those inhabited by *P. flavicornis*. One way in which *A. collinsii* could respond to this difference in success is through a greater investment in thorn size for the ants. We found that *A. collinsii* with *P. flavicornis* had thorn sizes that did not vary with tree size class, while among *A. collinsii* with *P. spinicola*, medium-sized trees produced the largest thorns. The stark increase in clearing of other stems under *P. spinicola* trees may influence succession in forests with *A. collinsii*.

Key words: plant defense, costs, competition, ants

NO TODOS LOS MUTUALISMOS SON IGUALES: DIFERENCIAS ENTRE DOS ESPECIES DE *PSEUDOMYRMEX* SPP. QUE HABITAN EN *ACACIA COLLINSII*

Resumen: En un mutualismo obligado, las acacias *Acacia collinsii* proveen nutrientes y espinas protectoras a las hormigas del género *Pseudomyrmex* a cambio de defensa de herbívoros y competencia con otras plantas. Dos mutualistas de *A. collinsii*, *Pseudomyrmex spinicola* y *P. flavicornis* difieren en agresividad. Investigamos si esta diferencia en agresividad afecta en qué medida las hormigas reducen la competencia interespecífica por plantas vecinas. También observamos la diferencia en el tamaño de las espinas como indicador de la inversión en su mutualista. La hormiga más agresiva, *P. spinicola*, elimina de manera más efectiva los tallos de plantas diferentes a *A. collinsii* en un radio de 2 m que su congénere *P. flavicornis*. Debido a esta diferencia en su capacidad para eliminar plantas por parte de las hormigas, las *A. collinsii* habitadas por *P. spinicola* debieran ser más exitosas que las habitadas por *P. flavicornis*. Una manera en que *A. collinsii* podría responder a esta diferencia de capacidades es a través de una mayor inversión, reflejada en el tamaño de las espinas disponibles para las hormigas. Encontramos que *A. collinsii* con *P. flavicornis* tenía espinas que no varían de acuerdo al tamaño de los árboles, mientras que entre *A. collinsii* con *P. spinicola* los árboles medianos producen las espinas más grandes. El notorio incremento en la capacidad de eliminar vegetación competidora en árboles ocupados por *P. spinicola* puede tener una influencia importante en el proceso de sucesión en bosques con *A. collinsii*.

Palabras clave: defensa de plantas, costos, competencia, hormigas

INTRODUCTION

Mutualisms, interactions between two species in which both have a net benefit in fitness, are vital for some organisms' survival (Bronstein 2001). An important example of obligate mutualism in the tropics is the relationship between the tree *Acacia collinsii* and some species of *Pseudomyrmex* ants (Ward 1993).

Janzen (1966) provided the first detailed documentation of this relationship. *Acacia collinsii* attracts mutualist ant colonies by providing swollen thorns to be hollowed out by the ants as shelter, as well as food for the ants in the form of nectar secretions and lipid-rich Beltian bodies. In return, *Pseudomyrmex* spp. attack possible herbivores of their host *A. collinsii*, such as insects, mammals, and birds, while eliminating vegetation in close proximity to their host.

Mutualisms entail costs as well as benefits for both organisms, and investment in the relationship will be minimized wherever possible (Bronstein 2001). Janzen (1966) previously observed that the more aggressive *P. spinicola* offers more protection to its host *A. collinsii* than does *P. flavicornis*, but did not provide empirical support.

In this study we focused on two species of *Pseudomyrmex* that are obligate *A. collinsii* mutualists commonly found in the tropical dry forests of Costa Rica: *P. spinicola* and *P. flavicornis* (previously *P. beltis*) (Ward 1993). We examined how these two ant species differentially reduced interspecific competition for their host *A. collinsii* and how the *A. collinsii* respond to these differences with investment in the relationship.

Based on Janzen's (1966) observations, we first predicted that *A. collinsii* colonized by *P. spinicola* would have less surrounding vegetation than *A. collinsii* colonized by *P. flavicornis*. Second, we predicted that *A. collinsii* occupied by *P. spinicola* would have larger thorns than those occupied by *P. flavicornis* as a result of the better protection given by *P. spinicola*. This assumes that *A. collinsii* can modify thorn size based on ant activity and available resources.

METHODS

We performed our study on 10 January 2009 at four sites along the entrance road 100 to 500 m east of the Organization of Tropical Studies Field Station at Palo Verde National Park, Guanacaste Province, Costa Rica. Sites were at least 50 m apart and included both sides of the access road. We chose *A. collinsii* of three size classes based on height: small (0-1.5 m), medium (1.5-3 m) and large (3-4.5 m). At each site, we chose one member of each size class colonized by *P. spinicola* and one by *P. flavicornis*. Each *A. collinsii* included in our sample was at least 4 m apart from other sampled *A. collinsii* to avoid counting the same stems twice for competing vegetation data, detailed below.

We used two methods to investigate the behavior of the ant species in clearing away competing vegetation under their tree. First, we counted the number of

stems of all living plants, both het-erospecifics and conspecifics, within 2 m of each *A. collinsii*. Second, we counted the number of branches of foreign plants making contact with each *A. collinsii*, either continuously or intermittently in the wind.

We estimated mean thorn length for each *A. collinsii* by measuring five thorns from the lower half of the tree and five from the upper half. Thorns are found in pairs; we measured the length of only one thorn of the pair from tip to base, measuring the larger of the two thorns if there was a size discrepancy. This proce-

FIG. 1. There were fewer non-*Acacia collinsii* stems surrounding trees inhabited by *Pseudomyrmex spinicola* than trees inhabited by *P. flavicornis* (N = 24 trees) at Palo Verde National Park, Costa Rica. Bars are means ± S.E.

dure was not always feasible due to a lack of thorns or the top half of the tree being out of reach. In the latter case, thorns from the bottom half of the tree were measured instead.

To test whether the ant species dif-fered in their ability to clear away competing vegetation, we used paired t-tests with mean number of stems as the response variable. We used one-way ANOVAs to compare mean number of stems across size classes, separated by ant species. We used one-way ANOVAs to compare mean thorn size, using *A. collinsii* size classes as the predictor. We used paired t-tests to compare thorn size within *A. collinsii* size classes for plants with *P. spinicola* and *P. flavicornis*. All statistical analyses were performed using JMP 7.0 (SAS Institute, Inc. 2007).

RESULTS

Acacia collinsii with *P. spinicola* had 73% fewer non-*A. collinsii* stems within 2 m of them than *A. collinsi* with *P. flavicornis* did (paired-t_{22} = 5.69, $P < 0.01$; Fig. 1). There was no difference in the number of other *A. collinsii* stems within 2 m of the selected plants (paired-t_{22} = 0.516, P = 0.61). We observed no difference in number of branches touching *A. collinsii* with either ant species (paired-t_{22} = 0.28, P = 0.78). There was no significant difference in number of heterospecific stems between different *A. collinsii* size classes for *P. spinicola* ($F_{2,9}$ = 0.35, P = 0.71) and *P. flavicornis* ($F_{2,9}$ = 0.03, P = 0.97).

We also found a significant difference in *A. collinsii* thorn size based on tree size class and ant species. While *A. collinsii* with *P. flavicornis* had similar sized thorns through all size classes ($F_{2,109}$ = 0.74, P = 0.48), plants defended by *P. spinicola* had different thorn sizes based on their age ($F_{2,110}$ = 26.25, $P < 0.01$;

Fig. 2).

We also compared thorn sizes within each *A. collinsii* size class for the two ant species. For the Small size class, thorn size was 17% larger for *A. collinsii* inhabited by *P. flavicornis* than for *A. collinsii* inhabited by *P. spinicola* (paired-t_{63} = 3.84, $P < 0.01$). For Medium and Large size classes, thorn size did not differ between *A. collinsii* inhabited by the different ant species (Medium paired-t_{78} = 1.79, P= 0.08; Large paired-t_{78} = 0.06, P = 0.95).

DISCUSSION

Our results show that *P. spinicola* is more effective at clearing stems of non-*A. collinsii* plants within 2 m of the plant's base than is *P. flavicornis* (Fig. 1). This result agrees with the predictions of Suarez et al. (1998) that more aggressive ants will clear more vegetation from the base of their host *A. collinsii* than less aggressive ants will. Our findings give empirical support to Janzen's foundational paper (1966), in which he observes that *P. spinicola* is a more effective defender of its host than *P. flavicornis* in central Costa Rica. Similarly, we observed that there was more damage to non-*A. collinsii* stems near *A. collinsii* with *P. spinicola* than to stems near *A. collinsii* with *P. flavicornis*. For both ant species, there was no difference in clearing across size classes. In a broader context, these results suggest that *P. spinicola* is more effective at clearing potentially competitive plants away from the base of its host *A. collinsii* than is *P. flavicornis*.

We predicted that there would be fewer branches touching *A. collinsii* with the more aggressive *P. spinicola* because they would be more effective in eliminating this competing vegetation. However, we found no significant difference in the number of foreign branches touching the *A. collinsii* colonized by the two ant species. There are two possible explanations for this result. First, it was not always clear which branches were touching the *A. collinsii* and which were not, due to
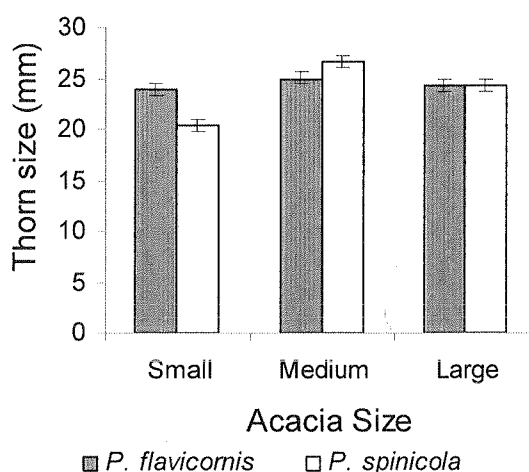
FIG. 2. Thorn size was not significantly different among age classes of *Acacia collinsii* defended by *Pseudomyrmex flavicornis*, while thorn sizes of each age class were significantly different from each other for *A. collinsii* defended by *P. spinicola* at Palo Verde National Park, Costa Rica. Bars are means ± S.E.

occasional wind. It was difficult to maintain a standard for counting the number of touching branches across different trees. Second, this measurement may not be a good measure of the ants' elimination of vegetative competitors. Ants can only eat away branches when they are in actual contact with the plant. Also, foreign branches that have been partly at-

tacked by ants but still touch the plant may have been included in our measurements. A better estimate of ant defense may be the proportion of foreign branches that have been attacked.

We found some significant differences in thorn size between size classes and between ant species. First, small *A. collinsii* with *P. spinicola* had significantly smaller thorns than small *A. collinsii* with *P. flavicornis* (Fig. 2). This result is difficult to interpret, as we would expect small *A. collinsii* with more aggressive *P. spinicola* to be more successful and therefore be "rewarded" with larger thorns, although there has been no research to back up this assumption. Furthermore, this result is likely skewed by the fact that several of the small *A. collinsii* measured had fewer than 10 thorns, which might reduce the reliability of the thorn size measurement. More research must be done on the subject to determine the factors affecting thorn sizes in *A. collinsii.*

The second significant result is that thorn size was statistically the same across all size classes for *A. collinsii* with *P. flavicornis*, while thorn size was significantly different between the size classes for *A. collinsii* with *P. spinicola*. Thorns on small *A. collinsii* with *P. spinicola* are significantly smaller than the other size classes (Fig. 2). This result could be explained by the fact that smaller plants simply cannot grow thorns as large as those on larger trees, or it may be confounded by the previously mentioned shortcoming in thorn numbers on small plants. Thorn size peaks in medium-sized trees, and decreases in large trees. A possible explanation for this trend is that larger trees may need less protection from herbivores and competitors than medium sized trees and therefore do not invest as much in producing large thorns to encourage large ant populations. It is also possible that thorn size at the midsection of a tree is not indicative of thorn size overall, or that our inability to reach parts of the higher trees skewed the data.

Our study design has at least two important shortcomings. First, the sample size was small. While we did find significant and meaningful trends, a larger sample size may greatly improve our confidence in results and possibly reveal more trends in thorn size across size classes and ant species. Second, *A. collinsii* with *P. spinicola* were more abundant than *A. collinsii* with *P. flavicornis*. The easiest method for finding *A. collinsii* with *P. flavicornis* was to search for areas that had more ground cover. Thus, our results could be biased because we searched more heavily for *P. flavicornis* in more heavily vegetated areas.

Our results may have significant consequences for understanding the broader forest structure. *P. spinicola* may clear so much surrounding vegetation to ensure the success of their host *A. collinsii* that it alters the path of succession, even delaying or preventing certain secondary succession species from colonizing. More long-term studies should be carried out to determine how succession occurs with and without *P. spinicola.* Longitudinal

studies should also examine how the abundance and dispersion of *P. spinicola* and *P. flavicornis* vary over time. Such an approach could answer questions about how *P. flavicornis* persists even though it appears to provide inferior protection to *A. collinsii*. It is possible that in times of plant stress, such as drought or extreme temperatures, *A. collinsii* provide fewer resources to ants and that *P. flavicornis* could cope better with fewer resources. Such a study may also clarify the role competition plays in abundance of *P. spinicola* over other ant species.

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"Wren"ting an Acacia:
Differential Response of Acacia Ants to Bird Nest Material

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Project Design: Thomas A. Morrison. Faculty Editor: Rebecca E. Irwin

Abstract: Despite the aggressive behavior of the acacia-dwelling ant, *Pseudomyrmex spinicola,* several bird species, including the Rufus-naped Wren (*Campylorhynchus rufinucha*) and the Streaked-backed Oriole (*Icterus pustulatus*), are able to build nests in acacia trees (*Acacia collinsii*). In this study we compared the response of *P. spinicola* to the different nesting materials used by the two bird species; the wrens use straw and rootlets while orioles use fungal rhizomorphs. There was no significant difference in the amount of time it took for *P. spinicola* to react to the different nesting materials. However, on average, individual ants spent significantly more time interacting with the fungal rhizomorph than with the straw. This result suggests that the ants are more tolerant of the wren's nest material than the oriole's nesting material.

Key words: behavior, Acacia collinsii, Pseudomyrmex spinicola, *oriole, wren*

Respuesta diferencial de las hormigas de acacia a material de nidos de aves

Resumen: Pese al comportamiento agresivo de la hormiga de acacia *Pseudomyrmex spinicola,* varias especies de aves, incluida la matraca *Campylorhynchus rufinucha* y la calandria *Icterus pustulatus* son capaces de construir nidos en árboles de acacia o cornezuelo (*Acacia collinsii*). En este estudio, comparamos la respuesta de *P.spinicola* a diferentes materiales de nido utilizados por dos especies de aves: las matracas usan paja y rizomas, mientras que las calandrias usan micelios rizomorfos. No encontramos diferencias significativas entre el tiempo de reacción de *P. spinicola* a los diferentes materiales colocados en las acacias que defienden. Sin embargo, las hormigas pasaron más tiempo en promedio interactuando con los micelios rizomorfos que con la paja. Este resultado sugiere que las hormigas son más tolerantes con el material de nido de las matracas que con el de las calandrias.

Palabras clave: comportamiento, Pseudomyrmex spinicola, Acacia collinsii, *matraca, calandria*

Introduction

Aggressive colonies of the ant *Pseudomyrmex spinicola* have a well-documented mutualism with the acacia tree *Acacia collinsii.* The ants inhabit the acacia thorns and feed on Beltian bodies produced by the tree, which are rich in lipids and proteins (Janzen 1983). They defend the tree from herbivores and sometimes reduce the abundance of the tree's competitors by removing vegetation from around the base of the tree (Janzen 1983). Despite the aggressive protection provided by ant species such as *P. spinicola,* several bird species build nests in acacia trees and may benefit indirectly from the ants' protection. The Rufus-naped Wren (*Campylorhynchus rufinucha*) prefers aca-

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cias with aggressive ant species (Young et al. 1990), presumably due to the protection such sites provide. Streak-backed orioles (*Icterus sclateri*) also nest in acacia trees but do not show the strong preference attributed to wrens (Young et al. 1990). Nest material differs substantially between bird species: orioles use finely woven black fungal rhizomorphs while the wrens build with straws and rootlets (Stiles and Skutch 1989).

In this study, we investigated the differential response of *P. spinicola* to the introduction of wren and oriole nesting materials to host *A. collinsi* individuals. We measured the time spent by *P. spinicola* individuals examining or trying to remove each nest material. We predicted that the ants would spend more time in-

teracting with the oriole nest material than the wren nest material.

METHODS

Study system

Our study took place in the lowland dry forest of Palo Verde National Park, in northwestern Costa Rica, on the morning of 10 January 2009. We sampled *A. collinsii* individuals found in the forest several hundred yards east from the biological station, located next to the road. We sampled trees between 3 and 5 m in height, that were inhabited by *P. spinicola* and looked healthy. We observed 30 trees total, 15 with each type of bird nest material.

Field Methods

We used strands of fungal rhizomorph from an abandoned oriole nest acquired in the field to simulate oriole nest material and strands of dry hay to simulate wren nest material. Small amounts of nest material (ca. 0.5 g) were placed on the tree near a branch junction along the main trunk at breast height. One person tapped near the material until ants arrived and we observed the ant response to the nest material for 5 minutes. Timing began the moment the nesting material was securely placed and continued until the material was removed by the ants or the five minute trial ended. We recorded the elapsed time from placement to discovery of the material. Each timer selected a focal ant individual heading towards the material and kept track of the amount of time that the
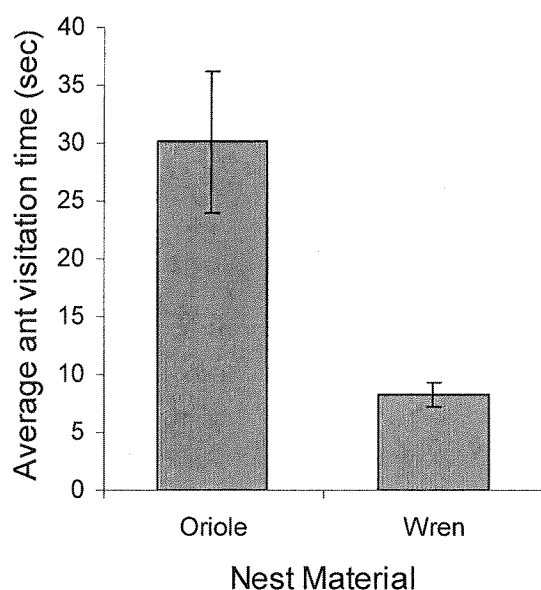
FIG. 1. *Pseudomyrmex spinicola* spent significantly more time interacting with the Streaked-backed Oriole (*Icterus pustulatus*) nest material than with the Rufous-naped Wren (*Campylorhynchus rufinucha*) nest material. Bars are means ± 1 SE. N = 15 trees per nest material.

ant spent within a one inch radius of the nest material. Once a focal ant left the radius, the timer watched a new individual. The recorder catalogued the entering and leaving times for each ant and noted the presence or absence of a previous nest in the tree.

Data Analysis

We calculated an average amount of time the ants spent interacting with the nest material for each tree and used this as the unit of replication for comparing ant response to nest material. We used a t-test to compare ant response to the two nest materials. We also recorded the time of first ant arrival and log-transformed this data to run another two-sample t-test to compare the arrival times to the two nest materials. All statistical analyses were performed in JMP 7.0 (SAS Institute, Inc. 2007).

RESULTS

We found that *P. spinicola* spent ca. four times longer interacting with the oriole nest material than with the wren nest material ($t_{14.5} = -3.66$, $P = 0.002$; Fig. 1). Within the 5 minute trial, the ants succeeded in removing the oriole material in 53% of trials (8 of 15) and succeeded in removing the wren material in 0% of trials (0 of 15). We found that there was no significant difference between the amount of time it took the ants to reach the different type of nest materials ($t_{24.7} = 0.02$, $P = 0.98$).

DISCUSSION

In accordance with our initial predic-tion, *P. spinicola* spent more time investigating the oriole nest material than the wren nest material. In addition to differences in examination time, we observed that the ants attacked the oriole nest material more vigorously than the wren nest material and often expelled the introduced oriole nest material from the tree. These data suggest that the ants are more tolerant of the wren nest material than of the oriole nest material. We suspect this tolerance may be because the wrens construct nests of woody, herbaceous materials that are more similar to the acacia tree's makeup or debris that may be wind-dispersed and lodged harmlessly on the acacia. Since some fungi grow on trees as parasites, the oriole's fungal nest material may be interpreted as a threat to the acacia. This may cause the ants to react more aggressively to the oriole nest than to the wren nest. Knowing whether the ants view the fungi as potentially harmful to the tree would aid in understanding the ants' behavior.

We recorded examination time for several individual ants, but we did not record the total number of ants that visited the substrate during the 5-minute trial. This might be an interesting factor to examine in the future to understand colony response to the different materials. Total number of ants recruited to the site may be a better measure of ant response than mean time spent on nest substrate. Also, we were unable to effectively replicate either bird's nest building habits. In creating their nests, the two species probably cause a different

amount of disturbance in the tree. Their nests are also placed in different locations within the tree, which may also play a role in affecting differential response by ants.

A study in Palo Verde National Park observed higher rates of predation on artificial bird nests by Rufous-naped Wrens in acacia trees than in non-acacia trees through pecking by these wrens (Young et al 1990). The higher predation rates demonstrated that wrens may protect nesting sites by destroying the eggs of other species trying to nest in acacia trees. Whether the wrens or acacia benefit from this association is unclear. Wiley (1983) found that ants habituate to the presence of the wren nest, and may even protect it from climbing predators, like snakes and monkeys.

Our study shows that *P. spinicola* has a differential response to oriole and wren nest material. The fact that the wren nest material does not elicit as strong an agonistic response from the ants could suggest that the ants' tolerance may be the result of an indirect benefit they derive from the wrens' tendency to protect their nesting site. Such a hypothesis warrants further investigation.

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The effect of three plant species on the abundance and diversity of freshwater macroinvertebrates in Palo Verde, Costa Rica

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Faculty Editor: Rebecca E. Irwin

Abstract: Macroinvertebrates in wetlands are used as indicators of water quality and play an important role as a food source, particularly for fish and birds. In this study, we examined the abundance and diversity of freshwater invertebrate communities found under three dominant plant species, cattail (*Typha dominguensis*), water hyacinth (*Eichornia crassipes*), and sedge (*Oxycaryum cubense*), in the marshlands of Palo Verde National Park, Costa Rica. We took standardized samples from each plant type and counted the number of invertebrates contained within the root system and the underlying water column. We found that hyacinth had a significantly more abundant and diverse macroinvertebrate assemblage than sedge, and sedge had a significantly more abundant and diverse macroinvertebrate assemblage than cattail. Furthermore, dissolved oxygen was significantly higher in the hyacinth than the sedge and in the sedge than the cattail. These differences in dissolved oxygen may explain the differences in invertebrate community structure among the plant species. Aquatic invertebrates have an important effect on all trophic levels of the marsh. We conclude that if Palo Verde's goal is to maintain bird habitat and food sources, it is a good strategy to eliminate cattail and allow hyacinth and sedge to grow in the marsh, thereby increasing the abundance and diversity of macroinvertebrates.

Key words: wetland, birds, Typha dominguensis, *water hyacinth,* Eichornia crassipes, Oxycaryum cubense

El efecto de tres especies de plantas en la abundancia y diversidad de macroinvertebrados dulceacuícolas en Palo Verde, Costa Rica

Resumen: Los macroinvertebrados son utilizados como indicadores de calidad del agua en humedales y juegan un papel importante como fuente de alimento, particularmente para peces y aves. En este estudio, examinamos la abundancia y diversidad de comunidades de invertebrados dulceacuícolas encontrados bajo tres especies de plantas dominantes, el junco *Typha dominguensis*, el lirio acuático *Eichornia crassipes* y la juncia *Oxycarium cubense*, en los humedales del Parque Nacional Palo Verde, Costa Rica. Colectamos muestra estandarizadas de cada tipo de planta y contamos el número de invertebrados que se encontraban en sus raíces y la columna de agua subyacente. Encontramos que el lirio acuático tenía un ensamble de macroinvertebrados significativamente mayor en el número de individuos y diversidad de especies que el de la juncia y ésta a su vez un ensamble de especies mayor al del junco. De igual manera, el oxigeno disuelto fue significativamente mayor en el lirio acuático que en la juncia y esta a su vez mayor que la del junco. Estas diferencias en oxigeno disuelto podrían explicar los cambios en la estructura de la comunidad de invertebrados entre especies de plantas. Los invertebrados acuáticos tienen un efecto importante el todos los niveles tróficos de humedal, incluidos peces y aves. Con esto concluimos que si la meta del humedal de Palo Verde es la manutención de hábitat y fuentes de alimento para aves, eliminar el junco y permitir el lirio y la juncia en el humedal son una buena estrategia dado que estos aumentan la diversidad de macroinvertebrados.

Palabras clave: humedal, aves, Typha dominguensis; *lirio acuático,* Eichornia crassipes; Oxycarium cubense

INTRODUCTION

Aquatic macroinvertebrates make up a critical component of many aquatic bird diets, supplying high quality protein necessary for their development, reproduction and survival (Anderson and Smith 1998). Numerous studies have shown the distribution of aquatic invertebrates to significantly influence the use of wetlands by migratory birds (Voigts 1976, Andrei et al. 2008). In turn, aquatic plants directly influence the invertebrate communities by chemical (e.g., dissolved oxygen levels, acidity) and physical (e.g., root systems, protection) means (Olson et al. 1999). Although numerous studies discuss the relationship between aquatic plants and invertebrate communities, findings generally do not extend to different climatic and geological settings (Davis and Bidwell 2008). Therefore, it is important to determine the relationship between aquatic plant and macroinvertebrate communities for specific wetland ecosystems.

Palo Verde National Park, Guanacaste County, Costa Rica protects an important marshland for birds and manages the highly invasive cattail population (Trama 2005). The majority of birds do not prefer cattail as habitat; the lack of both solid physical structure and easy access to the water in cattail may explain this (Trama 2005). We propose that birds also reject cattail as habitat due to the different community of macroinvertebrates found there (Voigts 1976).

A previous study in Palo Verde National Park found higher abundance and diversity of macroinvertebrates under grasses and sedges in the marsh than under cattail and observed that sedges and grasses have more exposed water around them, creating a more diverse and oxygen-rich habitat for macroinvertebrates to grow (Brosnahan et al. 2002). Moreover, a recent study by Kostecke et al. (2005) supports the finding that cattail supports lower numbers and diversity of invertebrates than most other aquatic plants, such as sedge. Toft et al. (2003) explain that the structurally complex root canopy of water hyacinth encourages higher invertebrate density and diversity than the functionally equivalent native pennywort (*Hydrocotyle umbellata*).

Our study examined the abundance and diversity of aquatic macroinvertebrate communities found under three of the dominant marsh plants in Palo Verde: water hyacinth, cattail, and sedge. We predicted that invertebrate communities would be both more diverse and more abundant under sedge and hyacinth than under cattail.

METHODS

This study was conducted at the Rio Tempisque marshland in Palo Verde National Park, Costa Rica. Water hyacinth (*Eichornia crassipes*, Pontederiaceae), cattail (*Typha dominguensis*, Typhaceae), and sedge (*Oxycaryum cubense*, Cyperaceae) dominate the marsh vegetation. For each of these species we haphazardly chose four sites that were within 2 m of open water and which were at least 10 m from

shore. The sites ranged in depth from 0.5-0.75 m and the water temperature and pH did not vary considerably across sites (Table 1). At each site, we measured dissolved oxygen levels (mg/L) at 0.15 m depth three times. We also removed a 0.15 m² area of vegetation and shook it vigorously in 10% ethanol solution to dislodge macroinvertebrates associated with the roots (as in Toft et al. 2003). Immediately after removing the plant biomass from the water, we swept the water column with a net for 10 seconds to get any invertebrates that detached from the roots during removal. For each sample, we counted 50 macroinvertebrates and calculated abundance (per m² of plant cover). Due to time constraints, we only identified each macroinvertebrate to order and excluded non-aquatic invertebrates from our results. As a measure of richness, we counted the total number of orders in each sample.

For each vegetation type, we tested whether there was a difference in dissolved oxygen levels across vegetation types using an ANOVA and Tukey's HSD test. We also performed an ANOVA to test whether there was a difference in mean macroinvertebrate abundance and diversity across vegetation types. We set up linear contrasts with the hypothesis that hyacinth and sedge would have higher macroinvertebrate abundance than cattail. All statistical analyses were conducted using JMP version 4.02 (SAS Institute, Inc. 1989-2000).

RESULTS

We found a significant difference in the abundance of macroinvertebrates among vegetation types ($F_{2,9}$ = 4.04, P = 0.004, Fig. 1). As we predicted from our linear contrasts, we found that macroin-
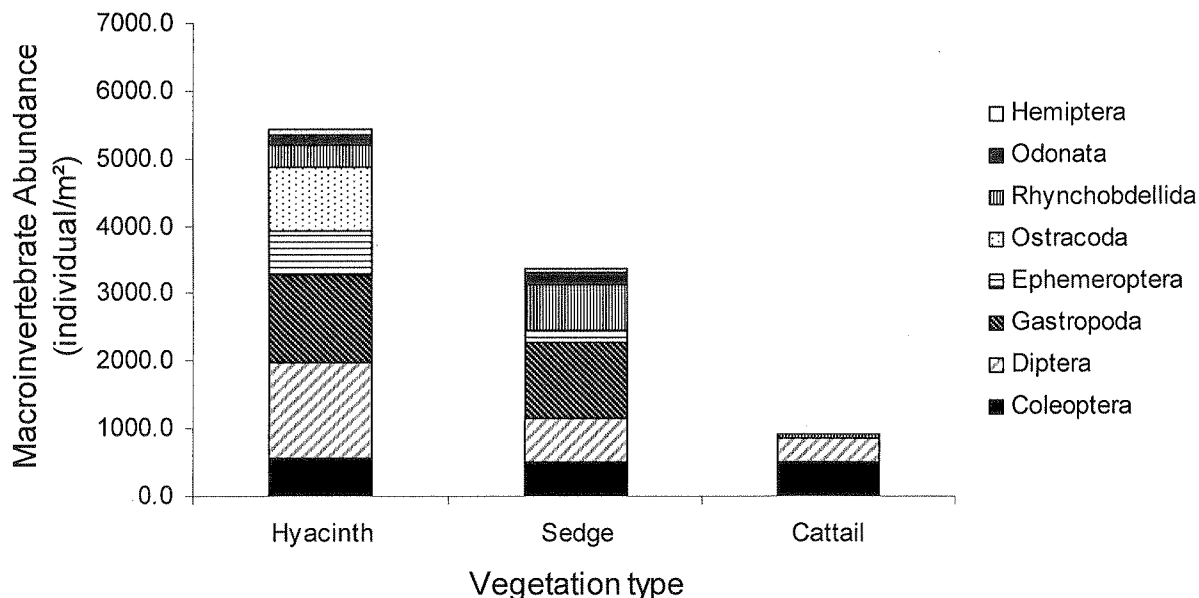
FIG. 1. Macroinvertebrate abundance across different taxa among each vegetation type. Different letters above each bar signify that means are significantly different at α = 0.05 based on Tukey' HSD test. Bars are means $\pm$ S.E.

vertebrate abundance in both hyacinth and sedge were significantly greater than in cattail (t_9 = 4.58, P = 0.001 and t_9 = 6.27, P = 0.033, respectively; Fig. 1). In addition, we found that Order richness significantly varied across types, with nine Orders of macroinvertebrates found in hyacinth and sedge and only two in cattail ($F_{2,9}$ = 70.2, P < 0.001; Fig. 1). We also found that DO levels were significantly different across all vegetation types ($F_{2,6}$ = 212.07, P < .001) with DO levels close to five times greater in hyacinth than in cattail and more than two times greater in sedge than in cattail (Fig. 2).

DISCUSSION

We found that hyacinth, cattail and sedge each hosted significantly different abundances and diversities of aquatic macroinvertebrates, and furthermore that dissolved oxygen levels differed significantly among the three plants.

We confirmed the results of a prior study that macroinvertebrate abundance

TABLE 1. The mean and standard error (in parentheses) of temperature and pH across three vegetation types, cattail, sedge, and water hyacinth, in Palo Verde marsh.

Vegetation Type	Temperature (C°)	pH
Cattail	24.47 (0.07)	6.88 (0.03)
Sedge	24.73 (0.15)	7.13 (0.02)
Hyacinth	24.87 (0.06)	7.30 (0.04)

in sedge was significantly different than in cattail in Palo Verde marsh (Brosnahan et al. 2002). We also demonstrated that macroinvertebrate abundance in hyacinth was over five times greater than in cattail (Fig. 1). As new management regimes have begun successfully clearing cattail from the marsh and allowing hyacinth and sedge to dominate, our results examine fundamental questions about how these changes affect the entire marsh ecosystem. Since macroinvertebrates are the basal food resource for fish and birds, a cattail dominated marsh may provide inferior food resources to that of one dominated by hyacinth or sedge.

The differing vegetation types probably influences the DO levels in their respective patches. Similar to our findings, one study found that water surrounding hyacinth consistently has a DO level of ca. 5 mg/l (Toft et al. 2003). Sedges have been shown to significantly lower DO, though not to anaerobic levels (Battle and Golladay 2001), and cattail is often associated with extremely low DO levels (Kostecke et al. 2005).

DO levels are important determinants for invertebrate communities (Toft et al. 2003). In close to anoxic conditions, much

FIG. 2. Dissolved oxygen varied significantly among all vegetation types. Different letters above bars note significant differences in dissolved oxygen at α = 0.05. Bars are means ± 1 SE.

like those in the cattail, very few organisms that require oxygen can survive (Irving et al. 2004). It is likely that the increasing abundance and diversity of invertebrates from cattail to hyacinth is due in part to these increasing DO levels.

Although we infer that DO levels explain the trends we see in the variation between macroinvertebrate abundance and diversity, it could be that there are also other concurrent explanations for this variation. For example, many areas of hyacinth had many open patches of water that allow light into the marsh, allowing phytoplankton, algae, and other primary producers to grow better in those areas. Since this primary production can be an important food source for macroinvertebrates, denser vegetation could seriously limit their growth. Alternatively, macroinvertebrate groups such as gastropods (which were very abundant in the hyacinth and sedge patches) are not found in cattails due to their inability to digest its cellulosic structure. Finally, insects such as damselflies and dragonflies may not be able to use cattail habitats as a resource because they are unable to oviposit in the cellulosic cattail shoots.

To account for the weaknesses of our study, future investigators should include a much larger sample size for each vegetation type, with samples drawn randomly from a much larger area around the marsh and from deeper within vegetation patches. Also, invertebrates should then be identified to a lower taxonomic level to gain a better

resolution of taxonomic diversity.

Based on our results, it is likely that controlling cattail populations within the marsh will have a positive influence on bird populations. Cattail has been found to exclude birds both by physically limiting their access to the water surface and also by reducing the diversity and abundance of a major food source—aquatic invertebrates. Therefore, we recommend that further action be taken to exclude cattail from the marsh in order to support a more productive food web for fish and birds. However, monitoring of the effects of hyacinth and sedge on the marsh ecosystem should continue, as these species are fast-growing and could also have deleterious impacts on the marsh ecosystem.

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Hide and seek: Spatial and temporal predator avoidance among fish of the Palo Verde marshland

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Faculty Editor: Rebecca E. Irwin

Abstract: We investigated the effect of water hyacinth (*Eichhornia crassipes*) on the distribution of fish species. We predicted a difference in the spatial and temporal abundance of marsh fish in open water vs. water near *E. crassipes*, due to top-down control by piscivorous birds. Spatially, we predicted that there would be more fish near *E. crassipes* than in the open water. We predicted that the density of fish near *E. crassipes* would be positively correlated with the number of aerial predators foraging. *Poecilia gillii* was significantly more abundant near *E. crassipes* than in open water and was also more abundant in the morning compared to the afternoon, for the open water plot. However, we did not find significant temporal or spatial variation in aerial foraging on the marsh. Thus, we did not find support for a top-down effect of aerial predation on *P. gillii* abundance in space or time.

Key words: Poecilia gillii, Eichhornia crassipes, *molly, water hyacinth*

Evasión espacio-temporal de depredadores en los peces del humedal de Palo Verde

Resumen: Investigamos el efecto de *Eichhornia crassipes* en la distribución de especies de peces. Nuestra predicción es que la diferencia en la abundancia espacio-temporal de peces del humedal en aguas abiertas y en aguas adyacentes a *E. crassipes* es debida a control arriba-abajo por aves piscívoras. Espacialmente, nuestra predicción es que habría más peces cerca de *E. crassipes* que en aguas abiertas. Predecimos que la densidad de peces cerca de *E. crassipes* estaría positivamente correlacionada con el número de depredadores aéreos forrajeando. *Poecilia gillii* fue significativamente más abundante cerca de *E. crassipes* que en aguas abiertas y también más abundante en la mañana que en la tarde en esta misma área. Sin embargo, no encontramos variación espacial o temporal en el forrajeo aéreo en el humedal, por tanto no encontramos soporte para efectos por depredación aérea arriba-abajo en *P. gillii* y su abundancia en espacio y tiempo.

Palabras clave: Poecilia gillii, Eichhornia crassipes, *guppy, lirio acuático*

Introduction

Predation can greatly affect the distribution of prey species. Some aquatic habitats vary spatially and temporally in predation risk, and many prey species are capable of assessing these risks and adjusting their behavior to avoid predation (Werner et al. 1983). The specific predator-avoidance behavior depends upon the species of fish (Savino and Stein 1989). The marshlands of Palo Verde National Park provide a range of aquatic habitats to study predator-avoidance behavior in fish. We evaluated habitat choice between open water and areas near water hyacinth (*Eichhornia crassipes*;

Pontederiaceae).

We hypothesized that fish abundance would be negatively correlated with the frequency of visitation by foraging piscivorous birds within each habitat. We predicted that fish would be more abundant near water hyacinth than in open water during assumed peak predation hours (0800, 1100, 1500). We also predicted that piscivorous birds would forage in the open water plots more in the afternoon, when glare off the water would be minimal.

METHODS

Study system

The marshlands adjacent to the Tempisque River, 200 m south of the Palo Verde Organization of Tropical Studies Field Station in the Guanacaste region of Costa Rica, contain a diverse mixture of plants, birds, invertebrates, and fish. The dynamics of the marsh have been changed by several invasive aquatic plants; we focused on water hyacinth. Water hyacinth shelters small animals from predation (Brendonck et al. 2003) and provides a substrate for birds to land. The marsh includes the following fish species: *Poecilia gillii* (Poeciliidae), *Parachromis dovii* (Cichlidae), *Parachromis managuensis* (Cichlidae), *Astyanax aeneus* (Characidae), *Dormitator latifrons* (Eleotridae), *Herotilapia multispinosa* (Cichlidae), and *Rhamdia guatemalensis* (Heptapteridae). We also saw and caught large predatory cichlids, and freshwater eels have been reported to live in the marsh (Craig Layne, pers. comm.).

Field methods

We laid out eight 5 m x 20 m plots within a 300 m² study area. Four were along the edge (just outside) of the water hyacinth. We were unable to sample directly under the hyacinth, which may have limited our capacity to detect the extent to which prey fish use the hyacinth as a refuge. The other four plots were paired with the edge plots and set ca. 20 m into open water. The plots were sampled using a 5 m seine pulled through 20 m. At the same time, we moved a large stick back and forth to create a disturbance at the far end of the plot to scare fish towards the net. On 14 January 2009, we sampled three plot pairs at 0730 and all four plot pairs at 1430.

At 0730, each catch was placed into its own bucket and counted on shore. In the afternoon, we identified and counted fish on the boat immediately after seining a

FIG. 1. In the marsh at Palo Verde, Costa Rica, *Poecilia gillii* was more abundant near the water hyacinth (*Eichhornia crassipes*) than in the open water. Bars are means ± 1 S.E.

plot. For each species we recorded the length of five fish, to calculate average length, and abundance. For *P. gillii*, which had a wide range of sizes, we calculated average length for two size classes (n = 5 for each). We seined on only one day due to many crocodile sightings.

On 15 January 2009, we recorded the presence of all piscivorous birds that appeared to be foraging in or above our plots; those present were Anhinga (*Anhinga anhinga*), Royal Tern (*Sterna maxima*) and the Common Tern (*Sterna hirundo*). We recorded this information at 0800, 1100, and 1500 for 30 minutes each. Other piscivorous birds that occur in the marsh include Osprey (*Pandion haliaetus*), Snowy Egret (*Egretta thula*), Great Egret (*Casmerodius albus*), and Little Blue Heron (*Egretta caerulea*).

For all pairwise tests, there was a significant difference in variances, so we ran t-tests with unequal variances. We used JMP v. 7.0 (SAS Institute 2007) for all analyses.

<div align="center">RESULTS</div>

Of the seven fish species we caught, *P. gillii* accounted for more than 50% of
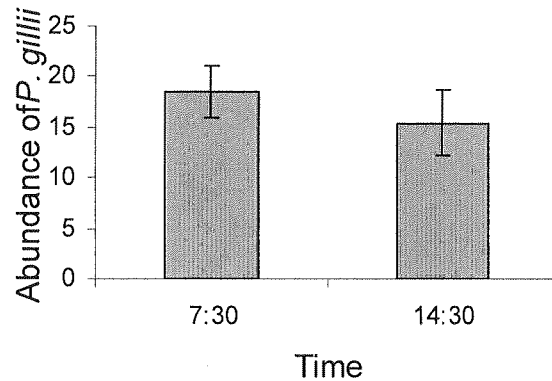
FIG. 2. In open water in the marsh at Palo Verde, *Poecilia gillii* was more abundant in the morning (0730) than the afternoon (1430). Bars are means ± 1 S. E.

the overall catch (Table 1). *Poecilia gillii* were 30% more abundant near the water hyacinth than in the open water ($t_{8.909}$ = -2.46, P = 0.036; Fig. 1). In open water, *P. gillii* were nearly twice as abundant in the morning as in the afternoon ($t_{3.774}$ = 2.77, P = 0.054; Fig. 2). However, *P. gillii* abundance near the hyacinth did not change over time ($t_{9.81}$ = -0.11, P = 0.91). *Astyanax aeneus*, which accounted for 42% of the catch, had no apparent preference for either habitat ($t_{7.11}$ = -0.33, P = 0.75), nor did its abundance change over time ($t_{9.89}$ = 1.29, P = 0.23).

TABLE 1. Fish caught in Palo Verde marsh in open water and near water hyacinth.

Species	Open Water	Hyacinth
Astyanax aeneus	163	158
Dormitator latifrons	1	3
Herotilapia multispinosa	1	0
Parachromis dovii	1	4
Parachromis managuensis	11	20
Poecilia gillii	174	227
Rhamdia guatemalensis	2	3
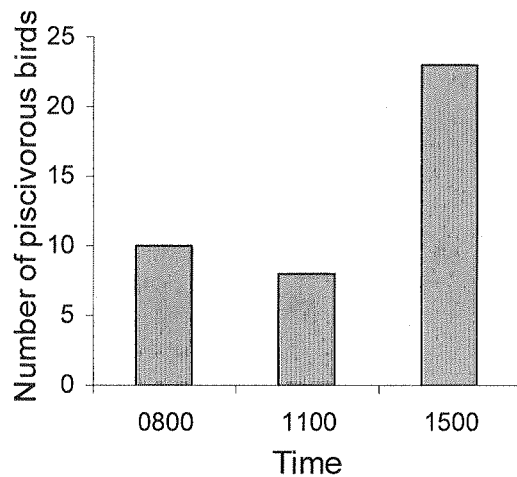
FIG. 3. In the marsh at Palo Verde, more piscivorous birds foraged during the afternoon than during the morning or mid-day, but this difference was not statistically significant.

The frequency of foraging piscivorous birds did not vary with time ($\chi^2_4 = 6.59$, $P = 0.16$; Fig. 3) or between habitats ($\chi^2_1 = 2.77$, $P = 0.096$).

DISCUSSION

Due to the small sample of visits by foraging birds, we did not have enough power to test whether the presence of piscivorous birds influenced the trends we observed in *P. gillii*. *Poecilia* sp. stops foraging and takes cover in the presence of an imitation bird (Davidson Wolf, unpublished; Templeton and Shriner 2004). Templeton and Shriner (2004) also found that the presence of aerial predators elicited a stronger response in *Poecilia* spp. than did aquatic predators. Therefore, if top-down control on *P. gillii* local distribution occurs, aerial predators are more likely to be the cause.

The lack of significant trends for species other than *P. gillii* may be due to low sample sizes and/or differences in species behaviors (e.g. *R. guatemalensis* forages near the bottom and may not respond to water hyacinth cover). Furthermore, *A. aeneus*, a visual predator, may prefer to forage in the well-lit open water than under water hyacinth cover. It is also a quick swimmer that may be at low risk from bird predation.

In spite of these limitations, our results suggest that *P. gillii* uses water hyacinth as a refuge from aerial predators.

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PARTITIONING OF RESOURCES IN SPACE AND TIME BY BIRDS IN LAGUNA PALO VERDE

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Abstract: Similar species can partition resources to alleviate interspecific competition for food by segregating themselves either spatially or temporally. In Laguna Palo Verde, there are many bird species living together whose food resources overlap. We chose four pairs of species (Osprey/Anhinga, Black-bellied Whistling-Duck/Black-necked Stilt, Snail Kite/Glossy Ibis, Snowy Egret/Great Egret) that share food resources in the marsh. We observed their foraging behaviors in several habitats within a large study plot over the course of two days. Three of the pairs differed in their foraging location, showing spatial segregation, while the fourth pair (Osprey/Anhinga) showed a temporal difference in foraging throughout the day. Our data support our initial prediction that spatial and temporal separation exist, and that these segregations can alleviate food competition in the marsh. Our research suggests that no pair of species exploiting the same food resource can overlap in space and time.

Key words: marsh birds, niche overlap, Palo Verde, resource partitioning

REPARTO DE RECURSOS EN ESPACIO Y TIEMPO EN LAS AVES DE LA LAGUNA PALO VERDE

Resumen: Las especies similares pueden repartir recursos alimenticios para disminuir la competencia interespecífica segregándose espacial o temporalmente. En la laguna Palo Verde hay muchas especies de aves que coexisten y cuyos recursos alimenticios se traslapan. Escogimos cuatro pares de especies: águila pescadora (*Pandion haliaetus*)/pato aguja (*Anhinga anhinga*); pijije (*Dendrocygna autumnalis*)/cigüeñuela (*Himantopus mexicanus*); gavilán caracolero (*Rostrhamus sociabilis*)/ibis (*Plegadis falcinellus*), y dos especies de garza (*Egretta thula* y *Casmerodius albus*) que comparten recursos alimenticios en el humedal. Observamos su comportamiento de forrajeo en varios hábitats dentro de un área de estudio mayor durante dos días. Tres de los pares de especies difieren en sitio específico de forrajeo, mostrando segregación espacial, mientras el par restante (águila pescadora/pato aguja) mostró diferencias en la temporalidad de forrajeo a lo largo del día. Los datos que obtuvimos dan soporte a nuestra predicción inicial de que la separación espacial y temporal existe, y que esa segregación puede reducir la competencia en el humedal. Nuestra investigación sugiere que ningún par de especies que explota el mismo recurso alimenticio puede traslaparse en espacio y en tiempo.

Palabras clave: aves del humedal, traslape de nicho, Palo Verde, reparto de recursos

INTRODUCTION

Niche theory states that two species may not occupy the same niche in an ecosystem. However, coexisting organisms often utilize the same or similar resources within an environment without excluding each other. Niche specialization allows for high species diversity in a community with potentially limiting resources, and the partitioning of resources

in time and space may alleviate conflicts unresolved by life history differences.

The study of resource partitioning in avian communities examines the physical and temporal distribution of species in an ecosystem and asks how species with overlapping food sources may resolve potential resource conflicts (Ehrlich et al. 1988). Important determinants of species richness in a given ecosystem include habitat complexity, competitive interactions, and productivity (Terborgh 1977).

The habitat diversity and productivity at Laguna Palo Verde supports an avian community that includes species with potential resource conflicts. Our study focuses on how species with food overlaps resolve these conflicts by partitioning marsh resources in space and time. We postulate that the array of species found in the marsh is not a chance assemblage of species but that the composition of the community is the result of biological interactions which determine exclusion or inclusion of members (Ehrlich et al. 1988). In this study, we ask how species in four potentially competing pairs of birds resolve resource conflicts in space and time. We hypothesized that the members of each pair would resolve resource conflicts through "optimal foraging" with respect to one another. We define optimal foraging as the process in which focal pairs avoid or reduce overlap in three parameters: space (specific habitat utilization in the marsh), time, and food resource.

METHODS

Study System

Our study took place in the Palo Verde National Park in the Guanacaste region of northwestern Costa Rica, from 13-15 January 2009. As a representative microcosm of the Tempisque river marshland, we selected a 1 ha. plot divided into 12 equally sized quadrants distinguished by several pre-existing landmarks (Fig. 1). To the east was a picket fence with several large bushes; to the north was a row of three distinguishable trees. Within the plot, we found three types of habitats: mud, water hyacinth (*Eichornia crassipes*), and open water. We observed the same species returning to our focal plot each day, so our plot
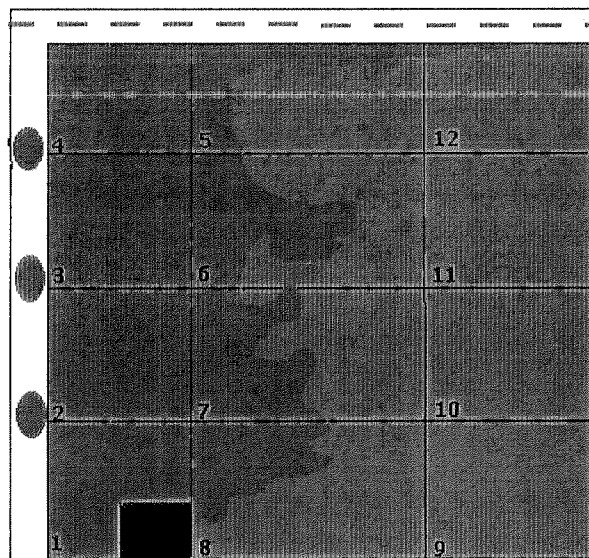
FIG. 1. Tempisque River marshland study plot (10,000m^2). The solid black box in quadrant 1 represents the position of the observation tower. The brown represents the mud habitat; the green represents the hyacinth habitat; the blue represents the open water habitat. The divisions of our study site were determined by pre-existing landmarks. The green dots represent three large trees; the brown dotted line represents a fence. Even though the real boundaries were not perfectly demarcated as shown, each quadrant was of equal area.

likely constituted an established avian community.

We studied four pairs of potential bird competitors: Osprey/Anhinga (OSPR/ANHI), Black-bellied Whistling-Duck/Black-necked Stilt (BBWD/BNST), Snail Kite/Glossy Ibis (SNKI/GLIB), and Snowy Egret/Great Egret (SNEG/GREG). We selected our pairs based on the assumption that they were competing for food resources (Stiles and Skutch 1989, Garrigues and Dean 2007).

In order to reliably observe a pattern of temporal or spatial separation of competitors, each of these pairs was chosen based on their overlap in food resource. The Osprey (*Pandion haliaetus*) maintains a fishing territory and feeds primarily on fish and occasionally lizards while the Anhinga (*Anhinga anhinga*) feeds on fish, snakes, and sometimes young caiman. The Black-bellied Whistling-Duck (*Dendrocygna autumnalis*) and the Black-necked Stilt (*Himantopus mexicanus*) both eat aquatic insects as well as crustaceans and mollusks. The Snail Kite (*Rostrhamus sociabilis*) and the Glossy Ibis (*Plegadis falcinellus*) feed primarily on apple snails while the ibis occasionally takes aquatic insects as well. The Snowy Egret (*Egretta thula*) and the Great Egret (*Casmerodius albus*) eat small fish and frogs (Janzen 1983).

Field Methods

During 14 observation periods spanning two days, we watched the birds and recorded their behavior (foraging, not foraging, aggression), location, or absence. At two-hour intervals between 0530 and 1730 from 13-15 January 2009, we observed species pairs from the lookout tower 6 m above the marsh. For five minutes, we scanned the study area to locate individuals of each species. We then spent five minutes observing each species of our competitive pairs separately. The order of observation was determined randomly. The five-minute trials were split into ten 30-second segments of focal observation. We treated each 30-second interval as a single foraging event, termed a "state of foraging" in Altmann's (1974) description of behavioral observation sampling methods. If we found ten or more individuals of a species present in the plot, we observed one individual during each 30-second interval. When less than 10 individuals of a species were present in the plot, we observed each individual for a proportional number of 30-second segments (e.g., two Anhingas, each observed for five 30-second segments). If the number of species did not divide evenly into ten, we observed each individual for a 30 second period, rotating randomly among the individuals until the 5-minute focal period ended.

Statistical Analyses

To compare the percent of each bird species foraging in each habitat across a whole day and at three times of day across habitats, we used the Wilcoxon test (data were not normally distributed and no transformations improved the distribution). For each pair of species, separate Wilcoxon tests were used. We made the same comparisons using Wil-

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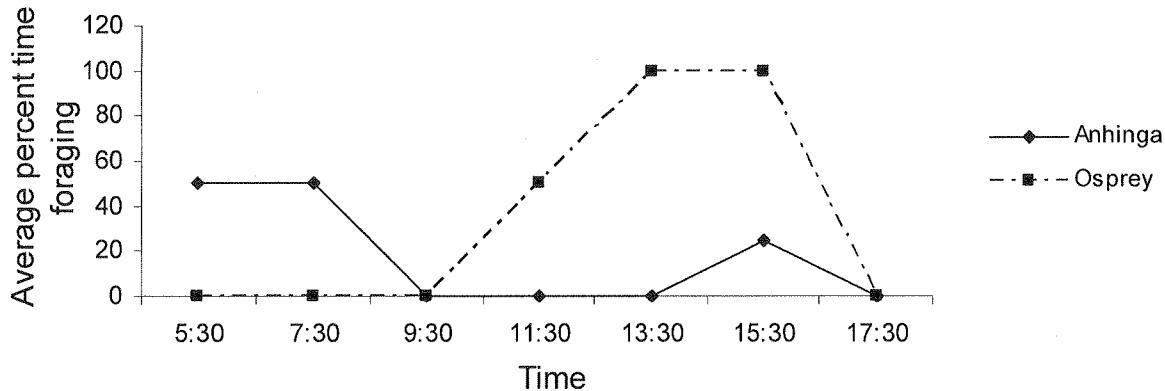
FIG. 2. The average percent of time foraging for the Osprey/Anhinga competitive pair over the course of the day, showing that the two species segregate their foraging habits temporally.

coxon tests on proportional abundance data.

RESULTS

One pair of species partitioned the use of a similar food resource temporally. Anhingas had higher proportional abundance in the morning than the Osprey, which was not present during this time

TABLE 1. For each competitive pair, a Wilcoxon test was used to compare the proportion of times observed between species at a particular time of day or in each habitat. Means (standard error), chi-square and p-values are shown; those that are significant are in bold. (Values indicate frequency of each species observed in each habitat (or time of day) ÷ total number of observations attempted.)

	Habitat			Time of Day		
	Mud	Hyacinth	Open	Morning	Midday	Afternoon
BNST	0.43 (0.14)	0 (0)	0 (0)	0.33 (0.14)	0 (0)	0.17 (0.11)
BBWD	0.05 (0.02)	0.95 (0.02)	0 (0)	0.33 (0.13)	0.33 (0.11)	0.33 (0.12)
X^2	1.33	24.06	0.00	0.07	7.00	2.54
P value	0.25	**0.0001**	1	0.79	**0.0082**	0.11
SNEG	0.29 (0.13)	0.07 (0.07)	0 (0)	0.08 (0.08)	0.11 (0.08)	0.17 (0.11)
GREG	0.11 (0.08)	0.75 (0.11)	0 (0)	0.17 (0.11)	0.33 (0.11)	0.33 (0.14)
X^2	1.06	13.53	0.00	0.37	3.24	0.85
P value	0.30f	**0.0002**	1.00	0.55	0.07	0.36
OSPR	0 (0)	0 (0)	0.36 (0.13)	0 (0)	0.17 (0.09)	0.17 (0.11)
ANHI	0 (0)	0.43 (0.12)	0.36 (0.11)	0.33 (0.14)	0.28 (0.08)	0.17 (0.09)
X^2	0.00	10.50	0.04	4.60	1.97	0.11
P value	1.00	**0.0012**	0.84	**0.032**	0.16	0.74
SNKI	0 (0)	0.11 (0.08)	0.89 (0.08)	0.33 (0.14)	0.28 (0.11)	0.33 (0.14)
GLIB	0.38 (0.13)	0.41 (0.13)	0 (0)	0.17 (0.10)	0.33 (0.11)	0.33 (0.19)
X^2	7.34	3.14	22.75	0.52	0.13	0.02
P value	**0.0069**	0.08	**0.0001**	0.47	0.72	0.89

period (Table 1). We found no significant difference in proportional abundance of the two bird species during the midday and afternoon hours. A close examination of percent of time foraging for this species pair across a day showed a lack of overlap in the time of day during which the birds forage (Fig. 2).

Three pairs of species showed spatial segregation patterns. The Black-bellied Whistling-Duck had both higher proportional abundance and higher percent foraging in the hyacinth than Black-necked Stilts (stilts were not present in this second habitat type; Tables 1 and 2). Additionally, Black-bellied Whistling-Ducks had higher proportional abundance than

stilts at midday (Table 1). The Glossy Ibis foraged more in the mud and hyacinth while the Snail Kite foraged more in open water (Table 2). Also, the Glossy Ibis had greater proportional abundance in the mud while the Snail Kite had a greater proportional abundance in open water (Table 1).

The Great Egret had approximately 10 times greater proportional abundance in the hyacinth than did the Snowy Egret (Table 1). The Great Egret also had a higher percent foraging rate in the hyacinth than Snowy Egrets because the Snowy Egrets did not forage there (Table 2).

It is important to note that compari-

TABLE 2. For each competitive pair, a Wilcoxon test was used to compare the proportion of foraging observations made in each habitat or at a particular time of day. Means (standard error), chi-square and p-values are shown; those that are significant are in bold. (Values indicate frequency of foraging observations ÷ number of attempted observations).

	Habitat			Time of Day		
	Mud	Hyacinth	Open	Morning	Midday	Afternoon
BNST	0.21 (0.10)	0 (0)	0 (0)	0.16 (0.10)	0 (0)	0.08 (0.08)
BBWD	0.01 (0.01)	0.12 (0.05)	0 (0)	0.07 (0.04)	0.02 (0.02)	0.05 (0.04)
X^2	1.33	7.23	0.00	0.01	2.06	0.25
P value	0.2491	**0.0072**	1.00	0.94	0.15	0.62
SNEG	0.16 (0.09)	0 (0)	0 (0)	0 (0)	0.07 (0.05)	0.08 (0.08)
GREG	0.03 (0.03)	0.48 (0.13)	0 (0)	0.08 (0.08)	0.11 (0.06)	0.33 (0.14)
X^2	1.37	12.28	0.00	1.00	1.21	2.18
P value	0.24	**0.0005**	1.00	0.32	0.27	0.14
OSPR	0 (0)	0 (0)	0.36 (0.133)	0 (0)	0.17 (0.09)	0.17 (0.11)
ANHI	0 (0)	0.07 (0.07)	0.11 (0.08)	0.17 (0.11)	0 (0)	0.04 (0.04)
X^2	0.00	1.00	2.05	2.09	3.18	0.49
P value	1.00	0.32	0.15	0.15	0.07	0.48
SNKI	0 (0)	0 (0)	0.19 (0.07)	0.13 (0.07)	0.03 (0.03)	0.05 (0.05)
GLIB	0.23 (0.11)	0.38 (0.12)	0 (0)	0.08 (0.06)	0.26 (0.10)	0.24 (0.13)
X^2	4.47	7.27	7.23	0.24	2.15	1.44
P value	**0.0345**	**0.007**	**0.0072**	0.63	0.14	0.23

sons are made using mean proportional abundances and mean percent total birds foraging despite the lack of normality of the data. No other measure (median or mode) provides useful information due to the high number of true zeros in the data. Because many pairwise tests were done on the same data set, p-values only slightly less than 0.05 should be considered marginal.

DISCUSSION

Our data suggest that pairs of competing species (species with overlapping niches) resolve potential resource conflicts by foraging at different times or in different parts of the Tempisque marsh.

The Osprey and the Anhinga appear to partition their resources temporally. The temporal separation may occur because they cannot separate their common resources of fish and open water spatially. Because of these species' territoriality (Stiles and Skutch 1989) they may differentiate temporally to reduce overlap.

The other three pairs appeared to partition their resources spatially. The ducks and stilts utilized different habitats while foraging. Further exploration could exclude stilts to study the effect on duck foraging in time and space. The ibis and kite separated themselves spatially to resolve their snail resource conflict. The spatial separation indicates a possible divergence of habitat use even though snails can be acquired in both habitats and the birds are sufficiently mobile to exploit them in either habitat.

Our results indicate that the Snowy Egret and Great Egret may prefer to forage solitarily in different habitats to alleviate their resource conflict. Divergent phylogenetic traits do not account for the separation due to shared family classification. Therefore the pair's spatial avoidance may be a strategy utilized by solitary individuals. Further study of this pair in isolation would provide insight into foraging interactions between large wading birds with similar hunting strategies.

We have a complex data set and our study attempts to synthesize many interactions and interpret pairwise conflict resolutions as components of a larger ecosystem model. Our data may have been confounded by several factors. Other researchers occasionally entered our study site and frightened the birds, especially those foraging in the mud habitat such as the Snowy Egrets. Crocodiles in our plot affected the ducks' and wading birds' behavior for at least one data point, and possibly more. Bottom-up effects regulating resource allocation in space should be analyzed by studying distribution of specific resources as another proximate explanation for the patterns observed.

Overall our results are consistent with previous studies (Buskirk 1976, Emmons 1980) which demonstrate the tendency for organisms to partition resources in space and time in order to alleviate resource conflicts within an ecosystem. We confirmed our hypothesis that no focal pair would overlap in both space and

time. Our data demonstrate possible solutions reached by a diverse community of tropical avifauna.

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Extended parental care of adult male Northern Jaçanas (*Jacana spinosa*) limits their food resource use

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Abstract: The territorial males of the polyandrous Northern Jaçana (*Jacana spinosa*) perform all incubating and brooding parental responsibilities, and as a consequence have reduced foraging rates during this period. In this study, I examined how the association with juveniles affects foraging rates in adult males and females during an extended parental care period. I found that the association with juveniles reduced adult male feeding rates by 48.3% compared to males without associated juveniles. Females showed no difference between foraging rates with and without associated juveniles. Small males and fewer adults per juvenile reduce parent-offspring competition for food resources, a highly adaptive strategy if food is the primary limit to jaçana fitness. This study supports the hypothesis that food resources are limiting for offspring, driving the evolution of reversed sexual size dimorphism and polyandrous social organization.

Key words: reversed sexual size dimorphism, polyandry, territory

Extender el cuidado parental limita el uso de recursos alimenticios en machos adultos de la jaçana (*Jacana spinosa*)

Resumen: Los machos territoriales de la jaçana (*Jacana spinosa*), una especie poliandra, están encargados de las actividades de incubación y cuidado parental de la nidada y como consecuencia reduce sus tasas de forrajeo durante este periodo. En este estudio, examiné cómo la asociación con juveniles reducen la tasa de forrajeo de los machos adultos en un 48.3% comparado con los machos sin juveniles asociados. Las hembras no mostraron diferencias entre tasas de forrajeo con o sin juveniles asociados. Machos pequeños y menos adultos por juvenil reducen la competencia por recursos alimenticios, una estrategia altamente adaptativa si la principal limitación al potencial reproductivo de las jaçanas es el alimento. Este estudio da soporte a la hipótesis de que las limitaciones de alimentos para la progenie dirigen la evolución del dimorfismo sexual revertido y la organización social poliandra.

Palabras clave: dimorfismo sexual revertido, poliandria, territorio

Introduction

The Northern Jaçana (*Jacana spinosa*) is a polyandrous bird (Jenni and Collier 1972) that exhibits sex-role reversal (Miller 1931, in Jenni and Collier 1972). The jaçana inhabits ponds and marshes of Costa Rica, using its elongated toes to walk on floating vegetation while foraging primarily on insects (Jenni and Collier 1972). Females, plumaged the same as males but up to 75% larger, hold a super-territory containing the territories of one to four males (Jenni and Collier 1972). Males perform all incubation and brooding duties, while the female, freed from these responsibilities, is able to in-

vest in the defense of resources, such as territory (Alcock 1979). Jaçanas will defend their territory aggressively, with loud calls, showy displays of the yellow-green underside of their wings, and even by swooping towards the intruder. Adults show interspecific aggression as well, particularly against potential predators (Stephens 1984).

Betts and Jenni (1991) provided quantitative time-budget data for adult Northern Jaçanas through different stages of their reproductive cycle. Adult males' time-budget, although similar to the females' before she lays the clutch, greatly diverged from that of the female once eggs and chicks were present, reducing foraging behavior by up to a third, to tend to incubation and brooding responsibilities (Betts and Jenni 1991).

Brooding behaviors begin declining 5 weeks after hatching, and end at 10 weeks (Jenni and Betts 1978). However, Betts and Jenni (1991) made no observations beyond 10 weeks, even though juveniles may remain in their natal area for up to 12 months after hatching (Jenni and Mace 1999). Past studies of Northern Jaçanas have suggested, though without quantitative support, a uniparental care hypothesis suggesting that the limiting food resources may be driving the evolution of the jaçana polyandrous social organization by reducing parent-offspring competition for food (Jenni and Collier 1972). The small size of males, while it reduces competition for food resources between the two sexes, may also be explained by reducing resource use and competition with offspring (Jenni and Collier 1972). Other studies have rejected this hypothesis but did not study jaçana juveniles older than 10 weeks of age (Betts and Jenni 1991).

In this study, I look at the effects of association with juveniles older than 10 weeks on the foraging rates of adult male and female Northern Jaçanas. For the purpose of this paper, I call this an "extended parental care" period. These juveniles are no longer brooding and no longer experiencing a heightened threat of predation compared to an adult since they are now roughly the same size. I predicted that this extended association will continue to limit adult male food resource use, even though males no longer have to include incubation, brooding, or vigilance against predation in their time budget. This continued decrease in foraging rate would reduce parent-offspring competition for food resources. Based on past studies, I also predicted that female feeding rates should remain unaffected, since female associations with juveniles are less frequent (Jenni and Collier 1972). This study may provide additional evidence to elucidate the mechanisms jaçanas use to resolve food availability limitation and their unique social organization system.

METHODS

I performed this study at Laguna Palo Verde, just south of the Organization of Tropical Studies Field Station at Palo Verde, Guanacaste Province, Costa Rica. I worked in a plot that was bordered on

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the west by the boardwalk, on the east by the fence posts running out into the marsh approximately 350 m from the boardwalk, and to the north by the edge of the marsh. The southern border of the plot varied across the marsh, either confined by the range of my 8x42 binoculars, or the edge of appropriate habitat (not open water) for the jaçana. I estimated that this boundary, averaged across the length of the plot, was 40 m from the northern border, giving an estimated plot area of 1.4 ha. The aquatic vegetation of this habitat mainly consisted of water hyacinth (*Eichhornia crassipes*), water lilies (*Nymphaea pulchella*), and sedges (*Eleocharis mutata*).

On 15 and 16 January 2009, I made repeated observational surveys of this plot from 0700 to 1600 every 1.5 hours, for a total of 14 surveys. I took the same route along the northern and western border of the plot for each survey, starting at the northeastern corner of the plot, and ending at the southwestern corner (the end of the boardwalk). Along this path, I marked eight sampling locations. To standardize my sampling effort, at each sampling location I scanned the visible area of the plot back and forth once, searching for adult jaçanas. I recorded the number of male and females and how many of each were associated with juveniles. Individuals already sampled during the survey, or those that could be better viewed from a subsequent sampling location, were not included in the counts. The jaçana population inhabiting this plot was small enough that during a sur-

vey each individual could be easily kept track of and was sampled only once per survey. If an individual could not be positively identified as male or female, due to distance or being obscured by vegetation, I did not include it in the sample. For males, association with juveniles was determined based on proximity and associational behaviors, such as walking in the same general direction as the juveniles, foraging alongside them, etc. I used a different decision rule for female association with juveniles, which was based merely on proximity (unless the female showed aggression towards the juveniles) because female association with juveniles is rare and, in past studies, has seemed only fortuitous (Jenni and Collier 1972).

I focally observed each adult jaçana for two minutes and counted the number of foraging attempts, while also noting
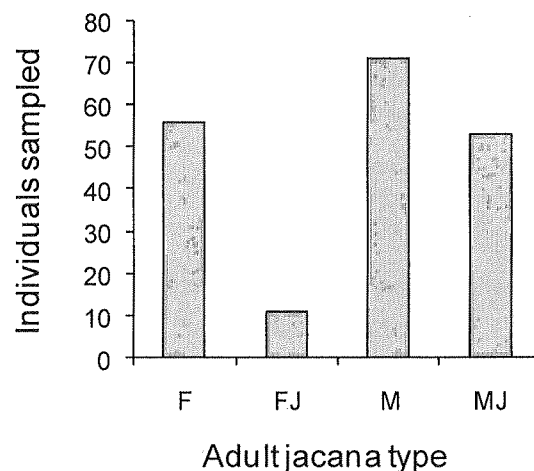
FIG. 1. Total numbers of adult jaçana types sampled during 14 surveys of the Palo Verde Marsh (n = 191). F = females without association to juveniles, FJ = females with association to juveniles, M = males without associations to juveniles, MJ = males with associations to juveniles.
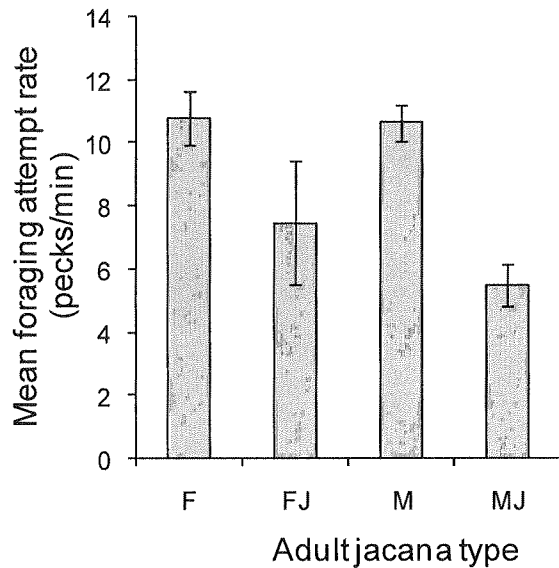
FIG. 2. Mean foraging attempts per minute with standard error bars as a function of sex and association with juveniles. F, FJ, M, and MJ are as in Fig. 1 N = 191 jaçanas. There was no significant difference in foraging rate between females with and without juveniles; however, males with juveniles foraged significantly less than males without juveniles.

other behaviors, such as aggression and brooding. A foraging attempt was defined as a peck at water, substrate, or vegetation. Occasionally, the jaçana's head would become obscured during the two-minute focal observation. In these instances, if the jaçana was in an obvious foraging position—head down, tail up—I would tally a foraging attempt every three seconds based on previous observations of maximum foraging rates. I then calculated foraging attempt rate (pecks/minute). Before leaving a sampling location, I made a second back-and-forth scan of the visible area of the plot, to make sure I had not missed any adults, and would add any I had missed to the counts and perform a two minute focal observation on them as well.

Since jaçanas are territorial, it is likely that across each survey of the plot I sampled many of the same individuals, but each focal observation was treated as an independent data point. Mean foraging attempt rates were calculated across all focal observations. I used a two-way ANOVA to determine the effects of sex, juvenile-association, and their interaction on foraging attempt rate. I used a paired t-test to compare differences in mean foraging attempt rates between females with associated juveniles and females without associated juveniles. I used a second paired t-test to compare differences in mean foraging attempt rates between males with associated juveniles and males without associated juveniles. All statistical analyses were performed using JMP 7.0 (SAS Institute, Inc. 2007).

RESULTS

Over the 14 total surveys, I took 191 focal samples, many of which may have been the same individuals but were treated as individual samples. I observed a total of 124 males, 53 associated with juveniles and 71 without, and 67 females, 11 associated with juveniles and 56 without (Fig. 1). I observed 11 to 16 total individuals per survey. In each survey, adult males ranged from seven to 11 individuals, and adult females from four to six individuals. A two-way ANOVA testing for the effects of sex and association with juveniles on foraging attempt rate showed a significant effect of the whole model ($F_{3,187} = 11.48$, $P < 0.001$). I found no effect of sex on foraging attempt rates

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across associated and unassociated adults ($F_{1,187} = 1.04$, $P = 0.31$). Adults associated with juveniles foraged at a significantly lower rate than those unassociated ($F_{1,187} = 16.67$, $P < 0.0001$). There was no significant interaction between sex and association with juveniles on foraging attempt rates ($F_{1,187} = 0.77$, $P = 0.38$).

The greatest number of females associated with juveniles sampled in one survey was two, while there were as many as seven males associated with juveniles. There was no difference between mean foraging attempt rates of females associated with juveniles and those not (paired t-test, $t_{65} = 1.56$, $P = 0.12$; Fig. 2). There was, however, a strongly significant effect of association with juveniles on the foraging attempt rates of males, reducing male feeding rate by 48.3% (paired t-test, $t_{122} = 5.74$, $P < 0.0001$; Fig. 2).

DISCUSSION

I found a significant reduction in the feeding rates of adult males associated with juveniles during the extended care period compared to adult males unassociated with juveniles. Previous studies have shown that male Northern Jaçanas reduce their foraging rates during the incubating and brooding periods when they are associated with juveniles (Jenni and Betts 1978). My results matched my predictions that male foraging rates would remain reduced during the extended parental care period, while female foraging rates would remain unchanged.

Other observations of my study corre-spond to those of previous researchers. My observed male to female ratio of 1.8:1 was close to Jenni and Collier's (1972) observed ratio of 1.7:1 in 1970. I did not attempt to determine which adults were territorial and which were non-territorial; however, in 1970 Jenni and Collier (1972) observed a territorial to non-territorial ratio of 1.4:1 for males and 1:1 for females. I observed at most 11 males and six females on the plot at any given time (indicating at least this many individuals in the population). Taking the territorial and non-territorial ratios into account, of 11 males, about six should be territorial and five nonterritorial. Of six females, three should be territorial and three non-territorial. Jenni and Collier (1972) found average territory size of 0.15 and 0.36 ha for males and females, respectively. This roughly calculates to 0.90 ha of male-territorialized area contained within 1.08 ha of female-territorialized area, out of the 1.4 ha total of my plot. In Northern Jaçana populations, there is some area not held as territory (Jenni and Collier 1972), and all male territory must also be defended by a female (Alcock 1979). Thus, the agreement between my approximated territorialized areas (based on Jenni and Collier 1972) and the area of the whole plot show that my data collection was comparable to Jenni and Collier's (1972) year-long study, as I only missed members of the population when they were out of view or had moved beyond the boundaries that I established for the plot.

All but one group of juveniles were

similarly sized to the adults and had already developed yellow-green undersides of their wings and the conspicuous yellow shield on the forehead. These juveniles were clearly older than 10 weeks of age, and therefore in the extended care period. I observed neither any incubating nor brooding activity. Over the course of 9 days at the field station, no Purple Gallinules (*Gallinula chloropus*), the largest predation threat to jaçana eggs and chicks, were observed by any member of a team of eighteen researchers, who often partook in bird-watching activities by the marsh. Moreover, I did not observe any other threat of interspecific predation on the jaçana juveniles or interspecific aggression by jaçana adults.

Past studies of jaçanas suggest that food for juveniles may be a limiting resource, based on observations of decreased male foraging rates and incidents of juvenile starvations (Jenni and Collier 1972). Males presumably limit their own food resource use to reduce parent-offspring competition. The data of my study during the extended parental care period also supports this hypothesis. By continuing to keep foraging rates low, male jaçanas, relieved of direct parental care but still associated with juveniles, may improve their offspring's fitness.

Two caveats are important to the interpretation of this study. First, more definitive predation studies on Northern Jaçana juveniles at the Laguna Palo Verde site are required to draw stronger conclusions about the time-budgets of the adult males and to show if vigilance against predators is important at this stage in juvenile development or not . Second, further studies in jaçana habitat quality and food availability would provide greater insight into what factors are driving the evolution of the jaçana polyandrous mating system.

My data show that adult male Northern Jaçanas continue to limit their food resource use during the extended parental care period. These results may illuminate the adaptive value of the sexual size dimorphism and polyandrous social organization of jaçanas by reducing parent-offspring competition. The role that food availability and other factors play in the unusual morphology and behavior of Northern Jaçanas should be a topic of future studies.

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A Pride of Antlions? Examining the Aggregating Behavior of *Myrmeleon* sp. and its Relation to Foraging Efficiency

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Abstract: To maximize fitness, organisms must achieve a density that maximizes the benefits and minimizes the costs of living near conspecifics. We investigated the aggregating behavior of *Myrmeleon* sp. larvae with the prediction that they would actively position themselves at preferred distances from their neighbors, presumably optimal for limiting competition and maximizing the benefits of high density. For example, we predicted that larvae in clusters would encounter prey at a higher rate than do solitary larvae. To test the first prediction, we placed antlions in experimental plots at distances greater, the same as, and less than average distances we observed in the field. We then compared the average distances at which individuals in each group actually constructed their pits. To test the second prediction, we built experimental enclosures and compared the prey encounter rate of clustered larvae to that of individual larvae. Our results supported our first hypothesis that *Myrmeleon* sp. actively aggregate to optimally dispersed clusters, but not our second hypothesis that clustered individuals have a higher per capita encounter rate with prey. The aggregation behavior may thus serve other functions, such as predator swamping or synergistic modification of their environment that facilitates pit construction.

Key words: intraspecific interactions, density dependence, dispersion, local migration, habitat choice

Un examen del comportamiento gregario de *Myrmeleon* sp. y su relación con eficiencia de forrajeo.

Resumen: Para maximizar su potencial reproductivo, los organismos deben alcanzar una densidad que maximice los beneficios y minimice los costos de vivir cerca de sus conspecíficos. Investigamos el comportamiento gregario de las larvas de hormigas león *Myrmeleon* spp. con la predicción de que se posicionarían activamente a distancias preferidas respecto a sus vecinos, presumiblemente las óptimas para limitar la competencia y maximizar los beneficios de altas densidades. Por ejemplo, predecimos que las larvas agrupadas encontrarían presas a tasas más altas que las larvas solitarias. Para probar la primera predicción, colocamos hormigas león en parcelas experimentales a distancias mayores, iguales o menores que las observadas en el campo. A continuación, comparamos las distancias promedio reales a las que los individuos de de cada grupo construían sus fosos. Para probar la segunda predicción, construimos encierros experimentales y comparamos la tasa de encuentro de presas de las larvas agrupadas respecto a la larva solitaria. Nuestros resultados dan soporte a nuestra primera hipótesis de que *Mymeleon* se asocia activamente en grupos óptimamente dispersos, pero no a nuestra segunda hipótesis de que los individuos agrupados tienen una mayor tasa per cápita de encuentro de presas. El comportamiento gregario puede servir otras funciones, como la saturación de depredadores o la modificación en sinergia de su ambiente para facilitar la construcción de fosos.

Palabras clave: interacciones interespecíficas, dependiente de la densidad, migración local, elección de hábitat

INTRODUCTION

For members of the same species, there are both advantages and disadvantages to living close together. At high density, individuals are better able to co-operate, swamp predators, mate, etc., but they must also compete with one another for the same resources (Berryman 2002). Evolutionary theory predicts that mobile organisms will disperse themselves to maximize their fitness by balancing the positive and negative aspects of living near conspecifics (Kent et al 2003).

The antlion *Myrmeleon* sp. is an excellent organism to study how species disperse to maximize fitness. The larvae of *Myrmeleon* select small patches of sandy soil in which they construct sloping pits, where they lay in wait for their prey to fall in. This behavior makes it very easy to measure the exact distance between one antlion and its conspecifics.

Past research has suggested many variables that may contribute to the *Myrmeleon's* choice of location. For example, the density of *Myrmeleon* larvae increases where there is more available prey per larva (Brayce et al. 1999). *Myrmeleon* sp. has also been shown to prefer fine-grained substrate and has the ability to relocate in search of ideal soil (Grace et al. 2001). In addition, *Myrmeleon* distribute themselves evenly when crowded together in small enclosures, presumably to alleviate intraspecific competition (Ermentrout et al. 2003). We noted, however, that in regions of relatively even substrate quality and prey abundance,

Myrmeleon have a tendency to form visible clusters, with few individuals located more than 30 cm from their closest neighbor. In light of this observation, we hypothesized that *Myrmeleon* larvae are able to detect the presence of nearby conspecifics and aggregate to form clusters in which individuals are optimally distributed (based on the field observations of closest neighbors). Further, we hypothesized that forming optimally dispersed clusters increases the overall foraging efficiency of each individual in the cluster. Thus, we had two predictions: (1) larvae removed from their pits would position themselves to form a cluster that is optimally dispersed to balance any costs of being either too clumped together or too far apart, and (2) a cluster of larvae would encounter more prey per larva than would a solitary larva, given identical patch dimensions and prey abundance.

METHODS

Study system

Our study was conducted in the tropical dry forest of Palo Verde National Park in the Guanacaste region of Costa Rica from 14-16 January 2009, at the beginning of the six-month dry season. We made observations and set up field experiments 1.2 km west of the Palo Verde Organization for Tropical Studies (OTS) Field Station. The shaded but open stretch of ground on the side of the road already contained many clusters of antlion pits.

Myrmeleon sp. belongs to the family

Myrmeleontidae in the order Neuroptera and are close relatives to lacewings, mantidflies, and owlflies. The adults are winged and slender-bodied; females oviposit in patches of sand or soil (Borror et al. 1989). *Myrmeleon* larvae are known for conical pits with which they trap ants and other small insects. Sometimes referred to as doodlebugs, *Myrmeleon* can leave scribbled paths on the ground as they search for the ideal substrate for pit-building. They have strong, flexible necks and large mandibles which they use both to toss sand from their pits and to inject their prey with digestive enzymes.

Field methods

First, we took measurements in the field to approximate the average distance between antlions in a cluster. We defined a cluster as an area of 0.5 m² containing at least 5 antlion pits; each cluster usually contained approximately 7 pits. In 15 haphazardly chosen clusters, we randomly picked 5 pits and measured the distances between them and their two nearest neighbors. We then took the average of these measurements as an approximation for *Myrmeleon*'s optimally dispersed distance in nature. The average distance was 11 ± 0.50 cm.

We then investigated whether the larvae prefer to have holes at this particular distance. We removed *Myrmeleon* from 6 circular plots, 0.5 m in diameter, at haphazardly chosen sites in the field. We shoveled, sifted, and spread the dirt in these plots to limit the effects of substrate preference. We then placed 10 larvae

(abdomen length of approximately 4 mm) in each plot at various distances from one another. We placed larvae at 11 cm from one another ("normally dispersed") in two of the plots, at 20 cm from one another ("overdispersed") in another two plots, and at 5 cm from one another ("underdispersed") in the remaining two plots. After they had finished choosing sites and constructing pits, we counted the number of larvae that ended up in the plot and approximated the average distance between pits as we did in the field (i.e., we picked five pits at random, measured the distance between them and their two closest neighbors and took the average of those distances). Then, we removed the larvae, resifted the plots and added new sets of larvae for a total of 12 replicates (4 replicates per treatment). We rotated which plots we used for each initial distance to control for any potential plot effects.

We used one-tailed, paired t-tests to test the prediction that underdispersed *Myrmeleon* larvae would reposition themselves farther apart from one another and that overdispersed larvae would reposition themselves closer together, and a two-tailed, paired t-test to test the prediction that normally dispersed larvae would not significantly change their average distance from their nearest neighbors. We also used a one-way ANOVA to test the prediction that the three dispersion treatments would converge to the optimal distance of 11 cm.

Finally, we tested if ant prey would encounter *Myrmeleon* pits more often per

larva if the pits were closer together. We filled four boxes (19 x 30 x 8 cm each) with 4 cm of finely sifted sand. We put five larvae in two of the boxes and one larva in the other two and allowed them to construct their pits. To test prey encounter rates, we placed two newly collected ants of the same species in each box for 5 minutes and counted the number of times an ant fell into a pit, replacing ants as they fell. For each replicate, we completed two trials per box and averaged the results. Then, we reset the boxes with new larvae and ants. We conducted a total of 10 replicates, 5 with one antlion and 5 with five antlions. We then compared the average encounter rate per larva at each density. We used a one-tailed, paired t-test to test the prediction that *Myrmeleon* larvae in clusters would have a higher per-individual encounter rate with prey than would solitary larvae. All statistical analyses were performed in JMP 4 (SAS Institute, Inc. 1989-2000).

RESULTS

The underdispersed *Myrmeleon* larvae increased their average distance from their nearest neighbors to 16.43 cm (paired-t_3 = 14.37, P = 0.0004; Fig.1), while the overdispersed larvae decreased their average distance to 14.08 cm (paired-t_3 = -9.23, P = 0.0013; Fig.1). The normally dispersed larvae did not change their average distance from their nearest neighbors (paired-t_3 = 2.16, P = 0.12; Fig.1).

Myrmeleon in the three dispersion patterns differed in their final average dis-
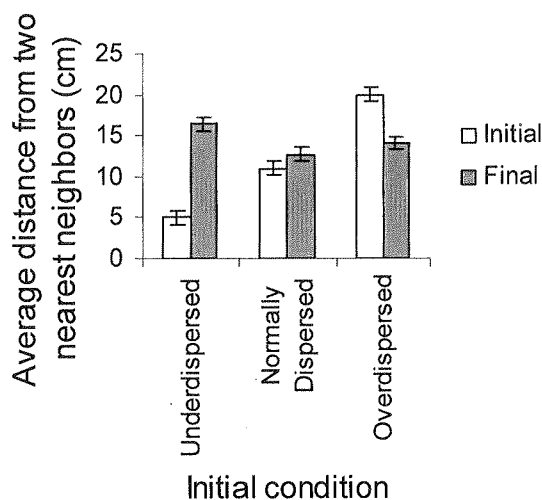
FIG.1. Underdispersed *Myrmeleon* sp. at Palo Verde National Park, Costa Rica repositioned themselves to increase their average distance from their nearest neighbors. Overdispersed individuals decreased their average distance from nearest neighbors. Normally dispersed individuals did not change their average distance from nearest neighbors. Bars are mean ± SE.

tances ($F_{2,9}$ = 6.39, P = 0.019; Fig.2). In particular, the Tukey-Kramer HSD test showed that the average distance between an individual and its two closest neighbors was greater for underdispersed individuals than for normally dispersed individuals.

Solitary *Myrmeleon* and those placed in clusters of five individuals did not differ significantly in their average per-larva encounter rate with prey (paired-t_4 = 0.88, P = 0.21; Fig. 3).

DISCUSSION

Our data supported our first prediction that *Myrmeleon* would cluster at a specific optimal density, approximately 11 cm from their two nearest neighbors. When placed at this distance, they did not move significantly farther away from or towards each other. However, when

we placed them at twice this distance, they moved closer to one another. This result suggests that *Myrmeleon* do have a mechanism for sensing how far they are from their neighbors and that they actively seek out this optimal distance.

As previous research also shows (Ermentrout et al. 2003), we found that when we crowded *Myrmeleon* at 5 cm from one another, they responded by spreading out. Interestingly, they spread out to an average distance of 16.43 cm, significantly beyond the observed average field distance of 11 cm. One interpretation of this result is that the larvae over-compensate in their attempt to disperse from the overly crowded area. This may additionally suggest that the cost of being too close (e.g., having one's neighbors throw sand into one's pit) may
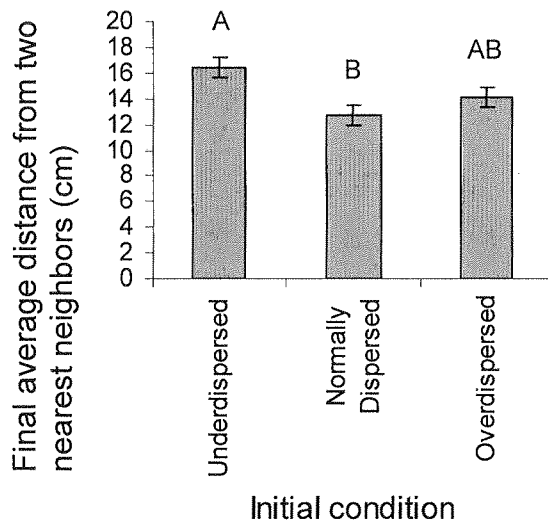
be greater than the benefits (e.g., of increase capture rate, predator swamping, etc.). However, most of our data still suggest that *Myrmeleon* seek out a specific optimal distance from their neighbors.

Our data on rates of encountering prey do not reveal clustered larvae to encounter more prey per capita than do solitary larvae. However, some technical difficulties may have interfered with our results, and it may be worth retesting this hypothesis after modifying the methods as follows. First, the ants tended to trace the edges of our enclosures. In some trials this resulted in an exceptionally low number of encounters. For other trials in which *Myrmeleon* constructed pits along the edge of the box, the encounter rates were especially high. Using larger enclosures (i.e., with a larger area-to-perimeter ratio) might limit the effect of this behavior.

It is important to note that, because our enclosures were so small, we used antlion number per enclosure as a proxy for antlion density. Therefore, our results may have been confounded by effects of number as well as effects of density. In larger enclosures, we could have kept the number of antlions constant while only changing the levels of dispersion as a more direct measure of the effect of distance between antlions on capture rates.

We also found that several parts of our experiments would have benefited from increased precision. For example, it sometimes took 10-15 seconds to replace a captured ant. Since ants were captured at a higher rate in the enclosures with

FIG. 2. *Myrmeleon* sp. at Palo Verde National Park, Costa Rica that were removed from their pits and placed in an underdispersed arrangement repositioned themselves to a greater distance from their nearest neighbors than did those placed in a normally dispersed arrangement. Bars are mean ± SE. Different letters above bars indicate statistical significant values

five pits, these enclosures contained only one ant for a disproportionate amount of time, thus biasing the results in favor of the one pit enclosures. Having more researchers to help us replace ants would have helped eliminate this bias.

Alternatively, it may be that clustering truly does not improve the rate of prey encounter per antlion. There are a number of alternative hypotheses that could explain the antlion aggregation behavior. For instance, aggregating may be a predator swamping strategy; larvae might have a better chance of surviving a predation event if they are one of many individuals in a patch. This hypothesis makes sense for small predators such as insects, but for bird predators, which could easily eat many larvae in a row, aggregating would actually decrease a larva's probability of survival, assuming predators seek out areas of high antlion density.

Another hypothesis is that *Myrmeleon* exhibit positive density dependence because they improve the substrate around them as they build their pits. Larvae might benefit from being close to one another because building, relocating, and expanding pits would be easier if their substrate had been improved by the action of their neighbors. This would be particularly relevant in high-disturbance landscapes where individuals would often need to rebuild or relocate their pits. A future study could investigate whether *Myrmeleon* larvae indeed improve their surrounding substrate by examining the size of soil grains before and after occu-

pation by larvae.

Finally, we did not investigate the exact mechanisms through which *Myrmeleon* larvae detect the presence and distance of nearby conspecifics; they may do this via vibrations, pheromones, or other signals. Examining these mechanisms would not only enhance our understanding of antlion natural history, but also offer a more precise definition of a distinct antlion cluster, which could be useful for subsequent population studies. Also, studying these mechanisms may serve as a stepping stone in understanding intraspecific communication in insects in general, and shed light on the relative importance of this communication in a species' regulation of density in order to maximize its fitness.

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INFLUENCE OF TEMPERATURE ON BUTTERFLY ABUNDANCE

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AND BRIANNA L. WILKINSON

Faculty Editor: Rebecca E. Irwin

Abstract: We investigated how temperature and wind speed influence butterfly abundance when habitat is kept constant. Because butterflies are poikilotherms, we hypothesized that temperature would be a primary factor driving changes in butterfly abundance. Our predictions were threefold: butterfly abundance would (1) increase with higher temperature, (2) decrease with greater wind speed, and (3) not be affected by the time of day. We tested these predictions by identifying and counting all of the butterflies that entered our quadrats and measuring the temperature and wind speed at each site. We found that butterfly abundance significantly increased with temperature, wind, and time. All three factors were significantly positively correlated with each other. We held wind constant and found that abundance still increased with both time and temperature, whereas when we held temperature constant, we found that wind and time had no effect on abundance. We therefore concluded that temperature was the most important factor that we measured associated with changes in butterfly abundance.

Key words: wind, temperature, poikilotherms

INFLUENCIA DE LA TEMPERATURA EN LA ABUNDANCIA DE MARIPOSAS

Resumen: Investigamos como la temperatura y la velocidad del viento influencian la abundancia de mariposas en el mismo hábitat. Debido a que las mariposas son poiquilotermas, nuestra hipótesis es que la temperatura sería un factor primordial determinando cambios en la abundancia de mariposas. Nuestras tres predicciones son que la abundancia de mariposas (1) se incrementa a temperaturas más altas, (2) decrece a mayor velocidad del viento y (3) que la hora del día no tiene ningún efecto. Probamos estas predicciones identificando y cuantificando todas las mariposas que ingresaban en nuestros cuadrantes y tomando lecturas de la temperatura y velocidad del viento en cada sitio. Encontramos que la abundancia de mariposas se incrementó significativamente en relación a la temperatura, viento y hora del día. Los tres factores están significativamente correlacionados entre sí. Sin embargo, cuando el viento es constante, la abundancia se incrementa en relación a hora del día y temperatura, mientras que cuando la temperatura es constante, el viento y la hora del día no tienen ningún efecto en la abundancia, por lo que concluimos que la temperatura fue el factor más importante asociado con cambios en la abundancia de mariposas.

Palabras clave: viento, temperatura, poiquilothermos

INTRODUCTION

Like all insects, butterflies are poikilotherms, meaning that they absorb heat from their environment to thermo-regulate (Ohsaki 1986). Jackson and Shelby (1996) found that butterflies preferentially choose sunny patches, like forest edges, more often than shadier forest interiors. This behavior is explained by the fact that butterflies need to raise their thoracic temperatures to a certain level in

order to fly (Rawlins 1980). Butterflies' dependence on the temperature of their environment plays an important role in determining the ranges of individual butterfly species. Climate change, and more generally rising ambient temperatures, has caused expansions in species' ranges (Davies et al. 2006).

We hypothesized that temperature plays a powerful role in determining butterfly abundance. Another factor that could influence butterfly abundance is wind. High wind speeds make it difficult for butterflies to control their direction of flight (Brattström et al. 2008). We predicted that butterfly abundance would (1) increase with temperature, (2) decrease with wind speed, and (3) not be affected by time of day.

METHODS

Our study site was located in Palo Verde National Park in the Guanacaste region of Costa Rica, at the beginning of the six-month dry season. The semideciduous tropical dry forest of this region has the lowest butterfly species diversity of any habitat found at similar elevations in Costa Rica. Additionally, diversity and

TABLE 1. We observed 20 species of butterflies in three families and six subfamilies on 14 and 15 January 2009 at Palo Verde OTS Station, Costa Rica. Identifications were made using DeVries (1987).

Family	Subfamily	Genus	Species	Size Class	Proportional Abundance
Pieridae	Pierinae	*Appias*	*drusilla*	M	.4252
Pieridae	Coliadinae	*Phoebis*	*agarithe*	M	.1561
Nymphalidae	Nymphalinae	*Anartia*	*jatrophae*	S	.1442
Pieridae	Pierinae	*Ascia*	*josephina josepha*	L	.1442
Pieridae	Coliadinae	*Eurema*	*boisduvaliana*	S	.0215
unknown	unknown	unknown	unknown	S	.0181
Papilionidae	Papilioninae	*Papilio*	*victorinus vulneratus*	L	.0172
Pieridae	Coliadinae	unknown	unknown	L	.0151
Pieridae	Pierinae	*Itaballia*	*demophile centralis*	S	.0140
Nymphalidae	Danainae	*Danaus*	*gilippus thersippus*	L	.0075
Nymphalidae	Danainae	*Danaus*	*plexippus*	L	.0065
Nymphalidae	Nymphalinae	*Anartia*	*fatima*	S	.0054
Papilionidae	Papilioninae	*Papilio*	*cresphontes* or *thoas nealces*	L	.0032
Nymphalidae	Nymphalinae	*Siproeta*	*stelenes biplagiata*	L	.0022
Nymphalidae	Nymphalinae	*Adelpha*	unknown	S	.0022
Pieridae	Coliadinae	*Phoebis*	*sennae*	M	.0022
Pieridae	Coliadinae	*Anteos*	*clorinde*	L	.0022
Nymphalidae	Heliconiinae	*Agraulis*	*vanillae*	L	.0014
Nymphalidae	Heliconiinae	*Heliconius*	*charitonius*	L	.0011
Papilionidae	Papilioninae	*Papilio*	*anchisiades idaeus*	L	.0011

abundance drop substantially during the extended dry season (DeVries 1987). Our study was conducted a few hundred meters southwest of the Palo Verde Organization for Tropical Studies (OTS) Field Station on the mornings of 14 and 15 January 2009. We observed a total of 20 species of butterflies from three families and six subfamilies (Table 1).

Ten 3 m x 2 m quadrats were established at the edge of the forest. All of the sites we selected had very similar characteristics. They were south-facing, with little shade, and composed almost exclusively of *Justicia* to control for effects of habitat variance on butterfly abundance. We observed each plot for 5 minutes, identifying and recording all butterflies that entered the plot, as well as measuring temperature and maximum wind speed. Butterflies were counted every time they entered a plot, meaning that if a butterfly exited and reentered the same plot, it was counted again. Each plot was observed once per hour during the morning, when butterfly activity is at its peak at this field site (personal observation). Observations were made for three hours, between 0800 and 1100, on the first day of data collection and for five hours, between 0700 and 1200, on the second day. We sampled an additional two hours on the second day to include a wider range of weather conditions in the early morning and mid-afternoon. Also, we sampled plots in reverse order on the second day so that time and plot were not confounded.

Butterfly abundance was non-normally distributed and no transformation would improve normality; thus, we used non-parametric tests to analyze the data. We used a Wilcoxon signed-rank test to compare butterfly abundance between the two days, and a Kruskal-Wallis test to compare butterfly abundance among plots. Additionally, we used Spearman's rank to analyze correlations between abundance and three possible predictors: temperature, wind, and time. We also used Spearman's rank to analyze correlations between temperature, wind, and time.

We also ran tests on two partial data sets. These data were normally distributed. One was of only observations where the temperature was between 32.0°C and 32.8°C ("temperature constant"). The other was of only observations where the wind speed was between 5.0 m/s and 5.9 m/s ("wind constant"). We used regressions to analyze the effects of temperature, wind, and time on abundance for each of these partial data sets. All statistical analyses were conducted using JMP v. 7 (SAS Institute, Inc. 2007).

RESULTS

Day and plot did not affect butterfly abundance (day: $\chi^2_1 = 2.54$, $P = 0.11$; plot: $\chi^2_9 = 7.91$, $P = 0.54$). There was a positive relationship between abundance and the three predictor variables, temperature, wind, and time (temperature: $\varrho = 0.40$, $P < 0.01$; Fig. 1; wind: $\varrho = 0.43$, $P < 0.01$; time: $\varrho = 0.48$, $P < 0.01$). However, temperature and wind were both strongly
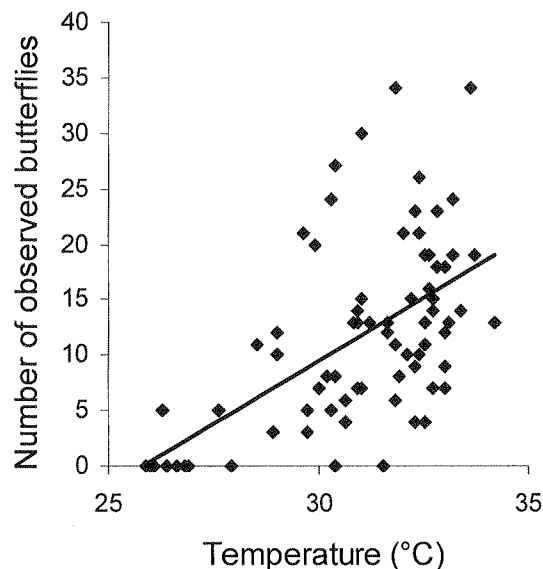
FIG. 1. The observed number of butterflies significantly increased with temperature (N = 76 plots) on 14 and 15 January 2009 at Palo Verde OTS Station, Costa Rica.

correlated with time (temperature: r = 0.81, n = 76, $P < 0.01$; wind: r = 0.76, n = 76, $P < 0.01$) and with each other (r = 0.82, n = 76, $P < 0.01$).

In order to differentiate between the effects of temperature, wind, and time on butterfly abundance, we analyzed sets of observations in which maximum wind speed was constant (within 1 m/s) and then ones in which temperature was constant (within 1 °C). Out of eighty total sets of observations, fourteen had wind speeds between 5.0 and 5.9 m/s. Among these, butterfly abundance was still strongly positively associated with both temperature and time (temperature: r^2 = 0.35, $F_{1, 11}$ = 5.90, P = 0.03; time: r^2 = 0.32, $F_{1, 11}$ = 5.29, P = 0.04). We then analyzed sets of observations with temperature held constant. Twenty of the eighty sets of observations had temperatures be-

tween 32.0°C and 32.8°C. With temperature held constant, there was no effect of wind or time on abundance (wind: r^2 = 0.03, $F_{1, 18}$ = 0.61, P = 0.44; Fig. 2; time: r^2 < 0.01, $F_{1, 18}$ = 0.00, $P > 0.99$; Fig. 3).

DISCUSSION

Our study found that butterfly abundance increases with temperature, and that temperature is more important in driving butterfly abundance than wind or time. Although the analyses at constant temperature were not as robust due to the relatively small number of points at the same temperature, they did allow us to differentiate between the effects of strongly correlated factors. From these analyses, we conclude that the strong positive association between temperature and abundance (Fig. 1) drove the significant association we observed between
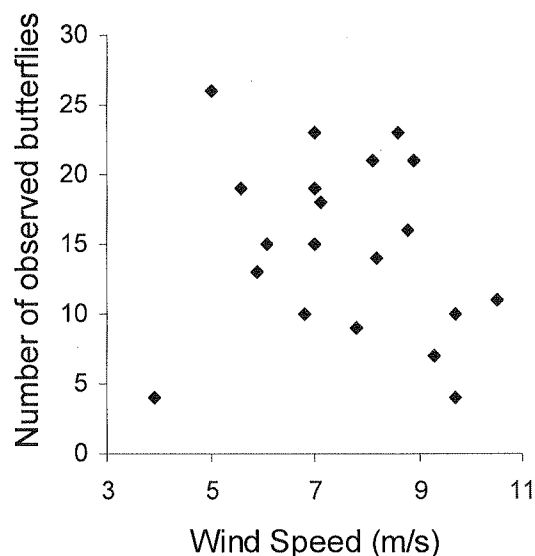
FIG. 2. The observed number of butterflies showed no relationship with wind speed in sets of observations when temperature was 32.0°C – 32.8°C (N = 20 plots) on 14 and 15 January 2009 at Palo Verde OTS Station, Costa Rica.
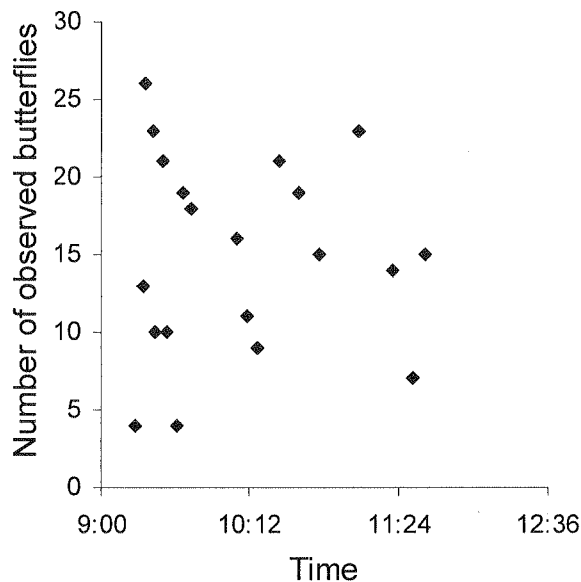
FIG. 3. The number of observed butterflies showed no relationship to time in sets of observations when temperature was 32.0°C – 32.8°C (N = 20 plots) on 14 and 15 January 2009 at Palo Verde OTS Station, Costa Rica.

abundance and wind and time. The importance of temperature in the morning is likely due to the fact that butterflies are poikilotherms who rely on external sources of warmth in order to fly (Rawlins 1980).

However, our study did not investigate the influence of temperature on butterfly abundance in the afternoon. All of our data were collected in the morning, due to preliminary observations that suggested butterflies were much less active in the afternoon. Yet temperatures tend to be higher later in the day in the dry forest area of Guanacaste. Presumably, different factors cause the lower butterfly abundance we observed in the afternoon. Possible explanations include stronger gusts of wind, predator avoidance, or nectar abundance. Our data only indicate

temperature as a factor that may enable butterfly foraging in the earlier part of the day. Investigations of butterfly abundance in the afternoons would provide a more complete picture of the factors influencing butterfly abundance, along with manipulations of temperature on butterfly physiology.

Sunshine is closely linked to temperature. Jackson and Shelby (1996) found that butterflies prefer warmer, sunnier forest edges over cooler, shadier forest interiors. However, their results were unclear as to whether this preference was due to the thermoregulation benefits or to improved foraging. This distinction was unclear because of the higher concentration of flowers found in sunnier areas. Our results indicate that the preference observed by Jackson and Shelby (1996) could be attributed to the butterflies' need for warmer temperatures to thermoregulate. Because we held habitat constant, we were able to eliminate the possibility that the butterflies were attracted to particular patches for better foraging. A further study could try to tease apart the specific effects of direct sunlight and increases in temperature on butterfly thermoregulation and abundance.

One consequence our study suggests is that, as butterflies are affected by increases in temperature, they will be strongly impacted by climate change. Already, studies have found changes in the ranges of certain species (Davies et al. 2006). Future studies could investigate whether butterflies increase in abun-

dance, as well as expand their ranges.

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Recent Elevation Shifts in Bird Distributions in Monteverde

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Abstract: To investigate possible upslope range expansion of lowland species, we compiled a preliminary list of bird species expected at 1500 masl and compared it to mist net captures. We mist netted at 1500 masl for a total of 135 mist net hours, catching 25 species. We found six species present near or outside the boundaries of their ranges: two above, three at the top, and only one at the bottom of their expected range, suggesting upslope range expansion. We suggest the probable cause is climate change, and that changes in high elevation bird communities could have profound effects on the cloud forest ecosystem.

Key words: global warming

Cambios de elevación recientes en la distribución de aves en Monteverde

Resumen: Para investigar un posible incremento en el límite superior del rango altitudinal de especies de tierras bajas, recopilamos una lista preliminar de las especies de aves esperadas a 1,500 msnm y la comparamos con datos de capturas con redes. Utilizamos redes a 1,500 msnm por un total de 135 horas-red y capturamos 25 especies. Encontramos seis especies no esperadas: dos arriba, tres el límite superior y una en el límite inferior de su rango esperado, sugiriendo una expansión del límite superior de su rango altitudinal. Sugerimos que una posible causa es el cambio climático y que los cambios altitudinales en las comunidades de aves podrían tener profundos efectos en el ecosistema de bosque nuboso.

Palabras clave: calentamiento global

Introduction

Changing climate in the Monteverde cloud forest may be affecting the elevational distribution of bird species. Distributional changes of several species in other taxa at Monteverde have been linked to the rising temperature, including the decline of several amphibians (Pounds et al. 2006). Since the 1970s, twenty-four previously lowland species of bats have colonized the cloud forest at Monteverde (LaVal 2004). Bat species moving upslope have had a significant effect on resident cloud forest species by competing for resources (LaVal 2004). There have also been documented shifts in the elevational ranges of some bird species at Monteverde (Michael and Patricia Fogden, unpublished).

Based on the studies cited above and the compelling evidence for global climate change, we predicted that we would find bird species above the normal ranges listed for each in Stiles and Skutch (1989).

Methods

We mist-netted birds at the Monte-

verde Biological Station, in the Monteverde Cloud Forest Reserve. Located in the Tilarán mountain range, between 1400 and 1800 masl, the reserve is characterized by semi-constant cloud cover and mist. With a canopy rich in epiphyte growth and biomass, the forest supports a diverse community of birds. We sampled along trails of the cloud forest, one site at 1500 masl and the other at 1700 masl. Four nets were placed at 1700 masl, a 25 minute walk up the Sendero Principal trail from the research station; these were almost always in the clouds during the period of sampling. We also set ten nets at 1500 masl along Sendero el Targuá, approximately a 5-minute walk downhill from the biological station.

We sampled on 21-23 January 2009, opening the nets from 0600 to 1030 daily and checking them every 40 min. At 1500

FIG. 1. Number of bird species caught over the cumulative number of mist net sampling hours at 1500 masl in Monteverde cloud forest on 21-23 Jan 2009.

masl we set 10 nets each for a total 13.5 hours over a three day period, for a total sampling effort of 135 mist-net hours. We set four additional nets at 1700 masl for a total of nine hours over a two day period, for a total sampling effort of 36 mist-net hours. We identified captured birds and, with the exception of hummingbirds, measured wing length, culmen length and total weight, and recorded sex and age when possible. We determined the expected elevational range for each species collected using Stiles and Skutch (1989).

Statistics

We chose to omit the data from the 1700 masl site because we caught only 6 birds, probably due to adverse weather. We included all species found at 1500 masl except for several individuals that escaped before identification. We plotted the cumulative rate of species collected per sampling hour to assess sampling saturation (Fig. 1).

RESULTS

We found 25 species total over the three days in the 1500 masl nets. Two species, the Stub-tailed Spadebill (*Platyrinchus cancrominus*; 2 individuals) and the Ochre-bellied Flycatcher (*Mionectes oleaginous*; 1 individual), were above their normal elevational ranges by 200m and 300m respectively. Three species, the Blue-crowned Motmot (*Momotus momota*; 1 individual), the Gray-throated Leaftosser (*Sclerurus albigularis*; 1 individual), and the Coppery-headed Emerald (*Elvira cupreiceps*; 6 individuals), were at

the upper limit (1500 masl) of their normal ranges. Only one species, the Prong-billed Barbet (*Semnonis frantzii*; 1 individual), was at the bottom of its normal range at 1500 masl. Overall, 5 of the 25 species were at or above their highest expected elevation and only one species was at the bottom of its range.

DISCUSSION

Our evidence strongly suggests that some birds are moving to higher elevations in the Monteverde Cloud Forest. Due to similar range shifts in other taxa, we suspect that climate change is the most likely explanation. An alternative hypothesis is that the birds are shifting their ranges due to loss of lower-elevation habitat. We believe that their presence in the cloud forest was unlikely to be a rare, chance event, since several species were involved.

The number of species we collected did not clearly reach saturation because of our small sample size. Since our sample was far from saturation, the number of species outside their normal range limits may be much larger than the number we found. The difficult weather conditions might make our conclusions more conservative, because lowland species may be less likely to move upslope during severe weather. Sampling at multiple elevations would give us more comprehensive information about current species ranges within the cloud forest. Even so, our sample at 1500 masl provides information on lowland species that are moving between the premontane and lower montane life zones, as defined by Holdridge (Haber 2000).

Interspecies niche competition may be one of the strongest consequences of upslope range extension; highland and lowland species share similar niches in their respective elevational ranges (Stiles 1983). If lowland species move upslope, many may find their niches occupied by a current cloud forest resident causing intense interspecies competition for resources. This could detrimentally affect either or both species, possibly causing local extinctions. There is also less highland than lowland habitat, so upward expansion of lowland species would increase highland densities considerably, possibly exacerbating competitive effects. Finally, highland species are limited in their upward range expansion by ridge-lines and mountaintops.

Birds also fill critical roles in the cloud forest as seed dispersal and pollination agents (Stiles 1983) with many plants relying on specialized mutualists. Alterations in the bird community structure will likely cause many cascading changes in the cloud forest community. The changing climate of Monteverde appears to be affecting the distribution of birds which in turn has broad implications for the entire cloud forest ecosystem.

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LONGER DRIP TIPS IN *PSYCHOTRIA* SPP.
DO NOT ENHANCE DRAINAGE OR INHIBIT EPIPHYLL GROWTH

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Abstract: We investigated the function of drip tips on *Psychotria* spp. leaves in the Monteverde cloud forest, and predicted that (1) leaves with longer drip tips would drain more water, and therefore (2) result in decreased epiphyll cover. We found no relationship between drip tip length and water drainage, or between drip tip length and epiphyll coverage. We were unable to control for many confounding factors that may affect epiphyll cover.

Key words: leaf morphology, water drainage, cloud forest

LAS PUNTAS DE GOTEO EN *PSYCHOTRIA* SPP.
NO MEJORAN EL DRENE DE AGUA O INHIBEN EL CRECIMIENTO DE EPIFILIA.

Resumen: Investigamos la función de las puntas de goteo en la hojas de *Psychotria* spp. en el bosque nuboso de Monteverde y predecimos que (1) las hojas con puntas de goteo de mayor longitud drenarían más agua y por consiguiente (2) resultarían en una cobertura menor de epifilia. No encontramos relación entre la longitud de las puntas de goteo y el drene de agua o entre la longitud de las puntas de goteo y la cobertura de epifilia. No pudimos aislar el efecto de muchos otros factores que confunden y que pueden afectar la cobertura de epifilia.

Palabras clave: morfología foliar, drenaje de agua, bosque nuboso

INTRODUCTION

We observed that several common understory trees of the genus *Psychotria* (Rubiaceae) have long acuminate tips, commonly known as drip tips. Burd (2007) found that drip tips increase water drainage. There are several proposed reasons why efficient water drainage may benefit a tree, including reducing water weight and light reflectance (Lücking and Lücking 2005).

Increased rainfall can lead to increased cover of certain epiphylls (Coley et al. 1993), which shade host leaves, blocking 30-70 percent of light (Lücking and Lücking 2005) and reducing photosynthesis of the leaf by 20-30 percent (Coley et al. 1993). Since epiphylls negatively affect leaves and require moisture, leaves should benefit from efficient water drainage.

Therefore, we hypothesized that *Psychotria* spp. drip tips act to rid leaves of water, because better drainage reduces epiphylls. We predicted that leaves with longer drip tips in relation to total length would drain more water. We also predicted that leaves with longer drip tips would have less epiphyll cover.

METHODS

We conducted this study on the trail east of Monteverde Cloud Forest Biological Station, Costa Rica, at approximately 1,500 meters asl. On 22 and 23 January 2009, we set four 15 m transects where many *Psychotria* spp. were evident at eye-level or below on the sides of the trail. At five intervals of 3 m, we sampled the nearest *Psychotria sp.* We counted up from the bottom of each tree a random number of branches, and from the base of each branch we counted outward a random number of leaves. By repeating this process, we chose five leaves within each tree. For each leaf, we measured the total length and drip tip length, defined as the distance between the point along the length of the leaf where the width was 1 cm and the distal tip of the leaf. Proportion drip tip length was calculated as drip tip length divided by total leaf length. Using a transparent grid overlay, we measured the total area as the number of 1 cm² grid squares filled within the

FIG. 1. Proportion drip tip length (relative to total length) in leaves of *Psychotria* spp. had no effect on the proportion of water shed by the leaf in montane cloud forest (n=10).

perimeter of the leaf. We counted the number of 6.25 mm² grid squares damaged by herbivory (within the perimeter of the leaf) and subtracted this value from our total area to give total leaf surface area. Finally, we counted the number of 6.25 mm² grid squares containing epiphylls. Proportion epiphyll cover was calculated as epiphyll cover divided by total leaf surface area.

We selected 10 additional *Psychotria* spp. leaves with varying drip tip lengths to measure water drainage. While holding a leaf at a 45° angle, we sprayed it five times in quick succession with a squirt bottle. We collected all water drained off the leaf between the first spray and 15 seconds after the final spray. No water was allowed to drain between the end of the 15 seconds and weighing the wet leaf. Proportion water drained was calculated as mass of water drained divided by the total mass of water sprayed onto the leaf surface.

RESULTS

Proportion drip tip length ranged from 0.02 to 0.22 among 109 leaves sampled. The proportion water drained ranged from 0.56 to 0.82. The proportion drip tip length had no effect on proportion water drained ($r^2 = 0.00$, $F_9 = 0.023$, $P = 0.88$, Fig. 1). Proportion epiphyll cover ranged from 0 to 0.28. We excluded a single outlier, due to inconsistent measurement technique of epiphyll cover. The proportion drip tip length had no effect on the proportion epiphyll cover after an arcsine-square root transformation ($r^2 = $

FIG. 2. Proportion drip tip length (relative to total length) of leaves in *Psychotria* spp. had no effect on the proportion of the leaf area covered by epiphyllic growth in montane cloud forest (n = 99). Proportion epiphyll cover was calculated as a proportion of total leaf area.

0.01, F_{98} = 0.964, P = 0.33, Fig. 2).

DISCUSSION

Our results contrast with the findings of past studies that drip tips do increase water drainage (Lücking and Lücking 2005, Burd 2007). While we focused on the length of the drip tip, those studies tested the effect of presence or absence of the drip tip. Therefore, we feel that variation in some other aspect of the geometry of the drip tip may be more important to water drainage than its length.

Although the studies cited above showed a relationship between drip tips and water drainage, they found, as we did, that this function did not translate into the prevention of epiphyll growth and establishment. Further studies could focus on other proposed functions of drip tips. The functional benefit may be mar-

ginal because there may be little evolutionary cost in investing in a drip tip. (Burd 2007). However, their prevalence on leaves of the montane cloud forest suggests that, through some mechanism, they do benefit trees.

Like many observational studies, we found it difficult to control for several confounding factors including, but not limited to, age of leaf, height of leaf, and canopy cover. Further studies could investigate the effect of each of these factors on epiphyll cover.

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Water-Shedding Strategies in Cloud Forest Leaves: Interactions Between Acuminate Tips and Leaf Surface Traits

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Abstract: Leaves in areas of high humidity often have acuminate leaf tips ("drip tips"). We tested the effectiveness of drip tips as compared to other water-shedding strategies, such as deep venation and waxy cuticles. We collected leaves from four species with differing leaf traits in the Monteverde cloud forest, sprayed them to simulate mist, and measured the proportion of water that drained off. *Conostegia xalapensis*, *Begonia involucrata*, and *Carpotroche platyptera* leaves shed more water with tips than without, but *Peperomia hernandiifolia* leaves did not. Among plastic leaf models, only *C. xalapensis* models shed more water with drip tips than without them. Both drip tips and leaf surface traits play an important role in water drainage.

Key words: drip tips, leaf venation, cuticles

Estrategias de Drene de Agua en Hojas del Bosque de Niebla: Interacciones entre Puntas Acuminadas y Características de la Superficie Foliar

Resumen: En regiones de alta humedad, las hojas frecuentemente tienen puntas acuminadas ("puntas de goteo"). Probamos la efectividad de las puntas de goteo mediante comparaciones con otras estrategias de drene de agua, como la profundidad de la venación o las cutículas cerosas. Colectamos hojas de cuatro especies con diferentes características foliares en el bosque nuboso de Monteverde, las rociamos para simular niebla y medimos la proporción de agua drenada. Las hojas de *Conostegia xalapensis*, *Begonia involucrata* y *Carpotroche platyptera* drenan más agua con puntas de goteo que sin ellas, aunque las hojas de *Peperomia hernandiifolia* no lo hacen. Entre los modelos de hojas de plástico, solo *C. xalapensis* eliminan más agua con puntas de goteo que sin ellas. Las puntas de goteo y características de la superficie juegan un papel importante en el drene de agua.

Palabras clave: puntas de goteo, venación foliar, cutículas

Introduction

Leaves in very moist areas tend to have acuminate tips ("drip tips"; Ellenberg 1985, Farji-Brener et al. 2002). Because diverse, distantly related taxa have drip tips, this morphology may be a convergent adaptation to shed water (Lightbody 1985; Burd 2007). Leaves with drip tips do shed water more effectively than those without (Dean and Smith 1978; Lightbody 1985; Ivey and DeSilva 2001; Farji-Brener et al. 2002). We investigated the roles of drip tips and other water-shedding traits.

Standing water on leaves presents five possible problems for a plant (Dean and Smith 1978; Lightbody 1985; Ivey

and DeSilva 2001). First, wetter leaves are more susceptible to epiphylls and fungi. Second, water on leaves might reduce temperature, decreasing both photosynthetic and transpiration rates (Givnish and Vermeij 1976). Third, a persistent layer of water can reflect sunlight and reduce photosynthesis. Fourth, standing water might leach nutrients from leaf tissue. Finally, more energy and structural support may be required to hold the weight of unshed water. Drip tips seem a small investment that might be favored by selection to reduce these problems (Burd 2007).

Our goals were to test the hypothesis that drip tips improve water drainage, and to distinguish between the efficacy of the drip tips vs. other potential water-shedding traits: deep venation that may serve as gutters and waxy, hydrophobic cuticles (Givnish and Vermeij 1976). We predicted that leaves with drip tips would shed more water than those with

tips removed (Dean and Smith 1978; Lightbody 1985; Ivey and DeSilva 2001; Farji-Brener et al. 2002). In addition, we used plastic leaf models to isolate the effect of drip tip morphology, keeping other water-shedding traits constant. We predicted that plastic leaf models would shed more water with tips than without, as for natural leaves. Finally, we predicted that the presence of other water-shedding traits would reduce the effect of drip tips in shedding water.

METHODS

We conducted our study in the Monteverde cloud forest on the S. Principal Trail near the Estación Biológica de Monteverde, Costa Rica on 22-23 January 2009. We collected a leaf that was not young or damaged from eleven plants for each of four species: *Begonia involucrata* (Begoniaceae), which has an asymmetric leaf with two drip tips; *Conostegia xalapensis* (Melastomataceae), which has
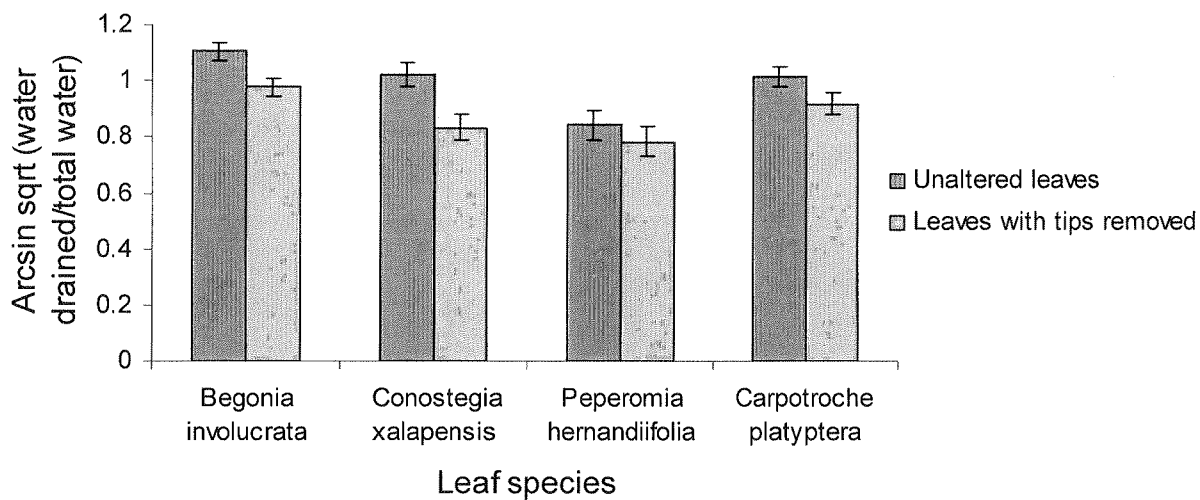
FIG. 1. In Monteverde, Costa Rica, significantly more water drained from leaves with drip tips than from tipless leaves in *Begonia involucrata*, *Conostegia xalapensis*, and *Carpotroche platyptera*, but not in *Peperomia hernandiifolia* (n = 11 leaves for each treatment for each species). Bars are means ± 1 SE.

pronounced lateral venation; *Peperomia hernandiifolia* (Piperaceae), which has a thick, waxy cuticle; and *Carpotroche platyptera* (Flacourtiaceae), which has a single long drip tip. To prevent wilting, leaves were kept in a bowl of water and tested within 1.5 hours of collection.

There were four treatments for each leaf. First, we used the unmodified leaf to quantify natural drainage. Second, we removed the drip tip, cutting at the inflection point of the acuminate tip and leaving a smooth, curved end, to test the effect of the tip on drainage. For the third and fourth treatments, we repeated these procedures on plastic leaf models. Water did not appear to flow off the plastic as it does off natural leaf surfaces so we attempted to enhance water flow by applying a thin layer of petroleum jelly. But drainage from the plastic surface still appeared different from natural leaf surfaces.

Before running each trial, the leaf was sprayed and dried to control for any persistent effects of wetting and drying. We suspended leaves at ca. 45° to the vertical, as in Lightbody (1985). To imitate conditions in a cloud forest, we used a spray bottle to apply mist from a distance of 1 m at an angle perpendicular to the leaf. We sprayed the leaf five times, for a total of ca. 2.5 ml of water. One bowl was held under the leaf for 5 seconds and a second bowl for another 55 seconds to compare initial drainage rates with drainage over a minute. We weighed both bowls and the leaf before and after spraying. We measured the amount of water applied, the amount drained after 5 seconds, the amount drained after 60 seconds, and the amount remaining on the leaf. We calculated the proportion of water shed by dividing the weight of water shed by the sum of water left on the leaf and water shed.

We normalized the data using the arcsine square-root transformation. All statistical analyses were conducted using JMP v. 7 (SAS Institute, Inc. 2007).

RESULTS

Across all species, leaves with tips shed more water than the leaves with tips removed (Fig. 1; paired-t_{43} = 5.37, $P <$ 0.01). This effect was strongest for *C. xalapensis* (paired-t_{10} = 4.15, $P <$ 0.01), where leaves with tips shed 23% more water than leaves without. *Begonia involucrata* leaves shed 13% more water with tips (paired-t_{10} = 4.22, $P <$ 0.01) and *C. platyptera* leaves shed 10% more water with tips (paired-t_{10} = 2.53, $P =$ 0.03), but there was no effect for *P. hernandiifolia* (paired-t_{10} = 1.08, $P =$ 0.31).

Across species, the amount of water shed by transparencies with tips was greater than without tips (paired-t_{43} = 2.20, $P =$ 0.03), a trend driven by the *C. xalapensis* transparencies (paired-t_{10} = 3.21, $P <$ 0.01), which shed 34% more water with tips than without. This trend did not hold for *B. involucrata* (paired-t_{10} = 1.30, $P =$ 0.22), *P. hernandiifolia* (paired-t_{10} = 1.09, $P =$ 0.30) or *C. platyptera* (paired-t_{10} = -0.14, $P =$ 0.89).

DISCUSSION

Drip tips do help leaves shed more

water in *B. involucrata*, *C. xalapensis*, and *C. platyptera*, but not in *P. hernandiifolia*. We suggest that this difference is due to an alternative water-draining trait: of the species we collected, *P. hernandiifolia*'s cuticle seemed thickest and waxiest. Alternatively, the cuticle may serve other functions, such as defense against herbivory, with improved drainage a side effect.

Conostegia xalapensis seems to rely heavily on drip tips, despite its deep surface venation. We propose that its venation may be a water-shedding strategy because the veins appear to lead water to the drip tip, which guides it off. The effects of veins and tips may be synergistic, so it may be advantageous to invest in both traits at once. In contrast, *P. hernandiifolia*'s waxy cuticle does not guide drops to the drip tip as venation appears to do. Thus drip tips may be less valuable to *P. hernandiifolia*.

Plastic leaf models produced mixed results. Future studies should use a different material as a proxy for leaf surfaces; our plastic showed hydrophilic tendencies and drained inconsistently. Furthermore, the effect of the drip tip alone may be very subtle and thus require more replicates to become apparent. More research must be done to tease apart the effects of the various water-shedding strategies.

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Bark Type and Vertical Resource Gradients Determine Bromeliad Distribution Within and Among Cloud Forest Trees

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Abstract: We quantified the distribution of bromeliad biomass within and among individual trees and offer ecological explanations for the observed trends. As hypothesized, structural complexity of bark was positively correlated with bromeliad mass. We developed a graphical model based on vertical gradients of nutrients, light, water, and habitat availability to predict the vertical distribution of bromeliads within trees. The model predicted that bromeliads should be most abundant at mid-canopy heights. Our field data showed that the middle two quarters of a tree (by height) contained 59% more bromeliad biomass, on average, than the upper and lower quarters. We suggest the modeling approach could be generalized to different habitat types and non-bromeliad epiphytes.

Key words: Monteverde, bark type, habitat availability

El tipo de corteza y gradientes verticales de recursos determinan la distribución de bromelias en individuos y especies de árboles del bosque nuboso

Resumen: Cuantificamos la distribución de la biomasa de bromelias de un árbol y entre diferentes árboles y ofrecemos explicaciones a los patrones encontrados. De acuerdo a nuestra hipótesis, la complejidad estructural de la corteza estuvo correlacionada positivamente con la masa de bromelias. Desarrollamos un modelo gráfico para predecir la distribución vertical de las bromelias en un árbol basado en gradientes verticales de nutrientes, luz, agua y disponibilidad de hábitat. El modelo arroja la predicción de que las bromelias deberían ser más abundantes a alturas medias del dosel. Nuestros datos de campo muestran que los dos cuartos intermedios de la altura del árbol contenían en promedio 59% más biomasa de bromelias que los cuartos superior e inferior. Sugerimos que el uso de modelos puede ser generalizado a diferentes tipos de hábitat y epífitas que no son bromelias.

Palabras clave: Monteverde, tipo de corteza disponibilidad de hábitat

INTRODUCTION

Many factors determine the distribution of bromeliads and other epiphytes within and among tropical forest trees. Although studies have focused on the distribution of bromeliads across different habitats, none has investigated the vertical distribution of bromeliads within a tree. An important factor in determining bromeliad colonization and germination success across trees may include tree bark type (Callaway et al. 2002), while access to nutrients, organic matter, and water may be more important factors within trees (Cascante et al. 2006). We focus on two species of tank bromeliads (*Vriesea* spp and *Guzmania* spp) growing on trees in a Costa Rican cloud forest.

We hypothesize that bark complexity is positively correlated with total tank
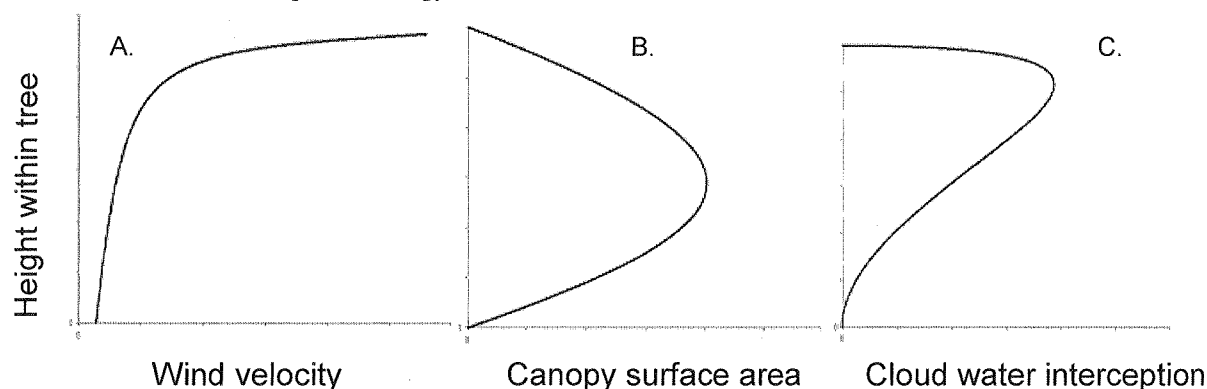
FIG. 1. (A) Graphical model of cloud water interception in cloud forest trees. Wind velocity increases with height within a tree. (B) Canopy surface area is greatest at mid-canopy height. (C) Combining wind velocity and canopy surface area we predict cloud water interception as a function of tree height (A x B = C) (Lovett 1982).

bromeliad biomass in a tree because bromeliads rely on bark substrate for colonization and germination (Barthlott et al. 2001). We also develop a graphical model of the vertical gradients of resource and habitat availability. The model serves as the foundation of our prediction of how bromeliads are vertically distributed within trees.

MODEL DEVELOPMENT

We develop a model of the vertical distribution of resources and habitat availability for bromeliads in cloud for-

ests. The model predicts a mid-canopy optimum for bromeliads. Based on micrometeorological studies of the forest canopy by Lovett et al. (1982), we adapted well-tested relationships between position in the canopy and water interception, to characterize water availability to bromeliads within cloud forest trees (Fig. 1). We also propose graphical models for organic matter deposition, exposure to sunlight, and habitat availability (branch surfaces) in relation to tree height (Fig. 2). As a result of cloud
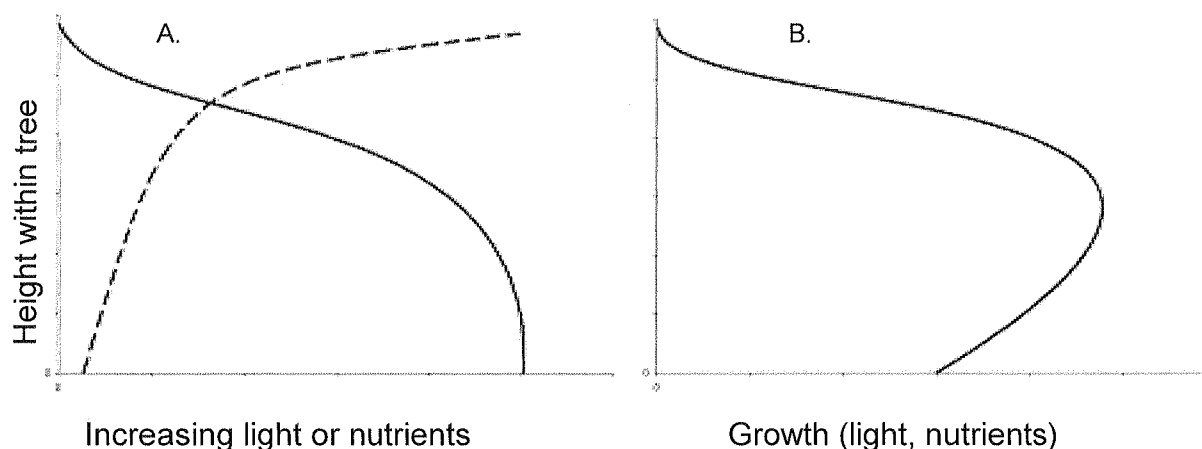
FIG. 2. Graphical model of growth potential to bromeliads in cloud forest trees. (A) Light availability (dashed line) increases with height within a tree, while nutrient availability (falling organic matter; solid line) decreases with height in a tree. (B) Combining light and nutrient availability we predict growth potential as a function of tree height (using a crude model, with growth proportional to nutrients x light).

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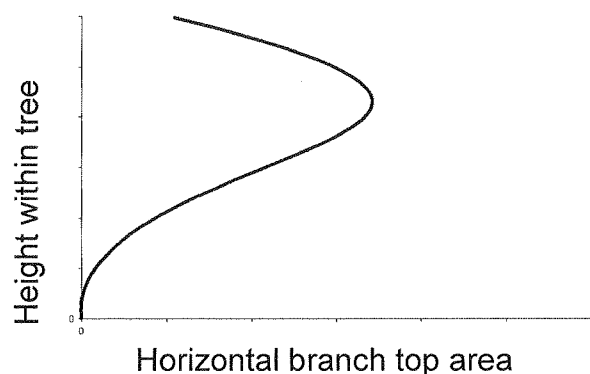
FIG. 3. Graphical model of habitat availability to bromeliads in cloud forest trees. We assume horizontal branch area is greatest at intermediate tree height in cloud forest trees. Horizontal branches are probably the most suitable substrates for colonization and growth of bromeliads.

water interception, Fig. 1C predicts that the vertical zone with maximum water availability is in the middle sections of the tree. Fig. 2B also indicates maximum growth potential at mid-canopy height as the result of the combination of light and nutrient availability. Finally, Fig. 3 proposes that the distribution of suitable habitat in the form of horizontal branch surface area within a tree also has a mid-height maximum due to the number of branches and branch diameters in this region. Thus, the combination of water interception, light and nutrient availability, and suitable habitat strongly suggest an optimal zone for bromeliads at mid-canopy height.

METHODS

We gathered 51 tank bromeliads from fallen trees along the Sendero Principal and Sendero Cariblancos northeast of the Monteverde Biological Station in Puntarenas Province, Costa Rica on 22 January 2009. To test our hypotheses about biomass distribution, we developed a model to predict the biomass of tank bromeliads based on their diameters. We first measured the diameter of each tank bromeliad directly above the root at its widest point. Then we determined the filled and empty mass using a 20-kg Camry spring scale for bromeliads over 300 g and a 500-g Pesola scale for those under 300 g. To determine filled mass we filled each tank to capacity with water and weighed it immediately. Each plant was dried before weighing again to obtain empty mass. We then plotted diame-
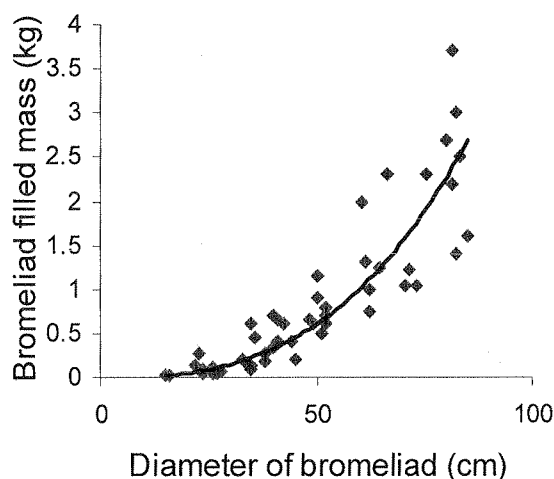
FIG. 4. Bromeliad filled mass as a function of diameter at widest point, in cloud forest at Monteverde, Costa Rica. Line shows best fit power function: $y = 1*10^{-5}$ (diameter)$^{2.8}$ (n = 51).

ter against maximum water-holding capacity; max holding capacity = $10^{-5} *$ (diameter)$^{2.8}$ ($R^2 = 0.86$, n = 51; Fig. 4).

We then sampled 10 trees along the Sendero Principal and two trees along the Sendero Cariblancos for a total of 12 replicates. All trees: 1) were separated by at least 50 m, 2) were at least 75% of canopy height and not overtopped by other
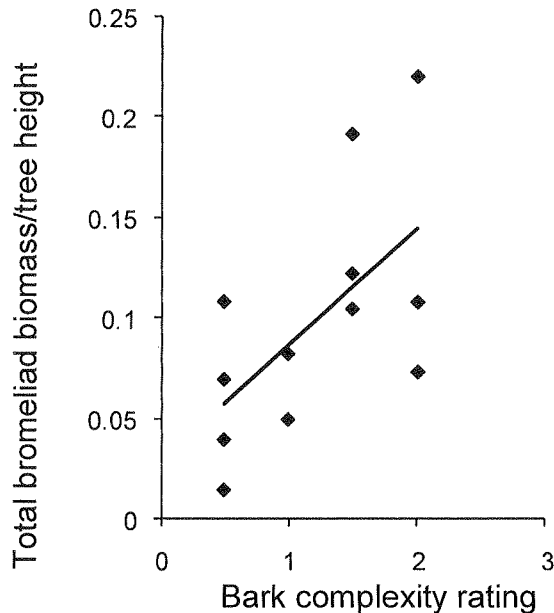
FIG. 5. Relation between bark complexity rating and total bromeliad biomass per unit tree height in cloud forest trees at Monteverde, Costa Rica (n = 12). Bark rating was scored on two scales: 0-3 for surface roughness and 0-3 for depth of grooves on trunk and branches. Overall bark complexity rating is the average of the two scores.

trees, 3) had epiphytic growth dominated by tank bromeliads, 4) had at least 75% of their tank bromeliads clearly visible, 5) were greater than 1 m in DBH, and 6) were located between 1,625 and 1,750 m above sea level. If several suitable trees existed in the same area we chose the focal tree randomly by flipping a coin. We estimated tree height by triangulating at a recorded radius using a clinometer. In each tree we counted total tank bromeliads, estimated the size of each, and noted its location in one of four vertical sections, with section one corresponding to the lowest quarter of the tree.

We quantified bark morphology on each tree by rating surface roughness from 0-3 and depth of grooves on the

trunk and branches from 0-3. We averaged these two indices to obtain an overall roughness score for a tree.

We grouped the bromeliads by size class and estimated mass for each size class from the regression of filled mass on basal diameter. We used a natural log transformation on the bromeliad number and mass to obtain normality of the data. We ran a linear contrast test with the *a priori* hypothesis that sections two and three would have greater bromeliad biomass and abundance than the first and fourth section. We used JMP version 4.02 for statistical tests (SAS Institute, Inc 1989-2000).

RESULTS

Bromeliad biomass per unit tree height increased with bark complexity rating ($r = 0.61$, Fig. 5). The bromeliad biomass and average number of bromeliads per section were significantly different ($F_{3,44} = 2.81$, $P = 0.05$ and $F_{3,44} = 3.58$, $P = 0.021$, respectively). As predicted, our linear contrasts showed sections two and three contained significantly more biomass and a higher average number of bromeliads per section than either the upper or lower sections ($F_{1,44} = 8.19$, $P = 0.006$ and $F_{1,44} = 3.97$, $P = 0.05$, respectively, Fig. 6). Using our regression model (filled biomass vs. maximum diameter) we estimated that maximum bromeliad biomass per tree of our 12 sampled trees ranged from 0.63 to 14.21 kg.

DISCUSSION

Our results support our hypothesis that bromeliad biomass would be posi-

tively correlated with bark complexity. We suggest that rougher and more grooved bark provides more secure colonization sites for airborne bromeliad seeds, retains more organic matter for germination, and provides anchoring sites for roots that can support more massive plants. Our conceptual model, suggesting an optimal zone for bromeliad growth at mid-canopy height, was supported by our empirical findings of greater bromeliad abundance and biomass in the mid-sections of trees.

As our modeling approach is quite general, it may be useful to predict the vertical distribution of bromeliads within trees in other habitats. However, the vertical distribution of resources would differ in some habitats, which may also be subject to different seasonal changes in resource availability. Thus, different resources may be limiting across different habitats. For instance, during the cloud forest dry season, cloud water interception severely limits bromeliad growth (Zotz and Thomas 1999). In contrast, in a tropical dry forest, bromeliad distribution would likely be limited by rainfall rather than cloud water interception. Seasonal differences are intense, many trees are deciduous, and cloud water interception is irrelevant. Clearly the shapes of the curves in Figs. 2 and 3 would need to be adjusted for application to different
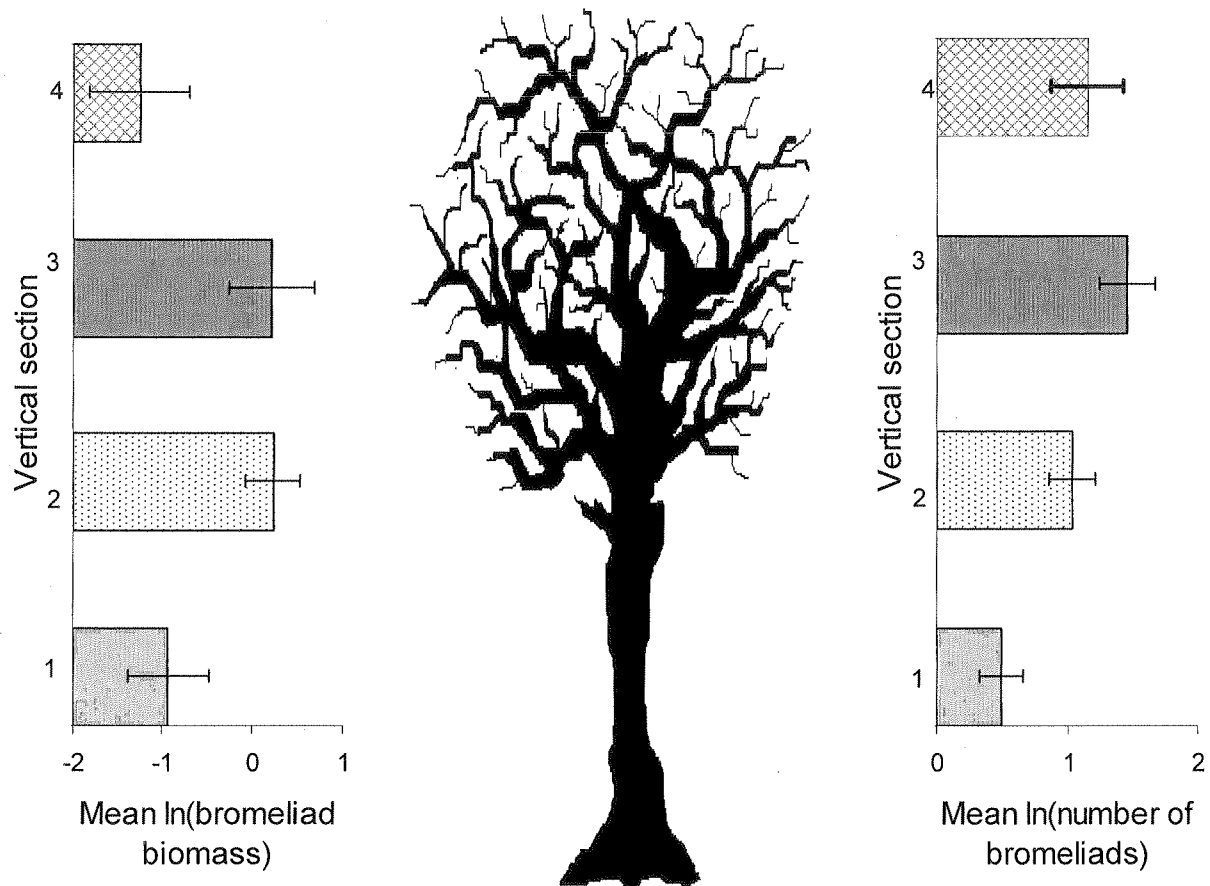
FIG. 6. Vertical distribution of tank forest at Monteverde, Costa Rica (n = 184). Bars show means ± 1 S.E. bromeliads within trees in cloud

habitat types.

Our model may also be applied to examine the distribution of other epiphytes which, like bromeliads, rely predominantly on falling organic matter and water through-fall. One limitation of our model is that it does not include stemflow, which may be an important source of water and nutrients for bromeliads and other epiphytes. Some epiphytes, e.g. mosses and lichens, rely primarily on nutrient inputs from stemflow. With the inclusion of stemflow our model could be adapted to study the distribution of epiphytes in other forest types and climatic conditions.

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Biotic Assessment of Continuing Pollution in Quebrada Guacimal, Monteverde

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Abstract: Previous surveys of Quebrada Guacimal, a Costa Rican stream historically polluted by inputs from gray water pipes and the Monteverde Cheese Factory (La Lechería), have shown that the freshwater invertebrate community structure varies along the stream based on each taxon's tolerance to water contamination. Our goals were to assess the current condition of the stream and to determine how stream health has changed since the most recent study. We sampled invertebrates from three sites (upstream of, at, and downstream from factory) based on earlier work in the stream, classified the organisms to family, and calculated estimates of water quality based on invertebrate diversity and composition. We predicted that the water quality and therefore the invertebrate communities in the stream would still be affected by contamination from surrounding development, but that the degradation would be less than in previous studies. As expected, we found that Family Biotic Index (FBI) increased from the upstream site to the downstream site. Consistent with this trend, percent Ephemeroptera, Plecoptera, Trichoptera (EPT) and family richness, evenness, and diversity decreased from the upstream site to the downstream site. We did not find clear evidence that stream conditions have improved in recent years.

Key words: organic pollution, Monteverde Cheese Factory, bioassessment

Traducción al español en la página 75.

INTRODUCTION

Aquatic bioassessment is an evaluation of fresh water conditions, often using organisms such as invertebrates and diatoms as indicators of water quality (Patrick 1949). The assemblage of these organisms varies based on the different tolerances of the taxonomic groups to environmental degradation caused by human activities. The Monteverde Cheese Factory (La Lechería) used Quebrada Guacimal as a dumping site for organic wastes from 1983 until 1993 (Gill 2000). Despite the alleged termination of waste deposition, studies from 1980-1990, 1995, and 2001 show a persistent difference in invertebrate community structure along the length of the stream spanning the old dumping site (Pouliot et al 1995, Gill 2000, Glastris et al 2001).

We evaluated the current conditions of the stream using indices based on the communities of invertebrates found at sites upstream and downstream of the factory. We then compared current invertebrate communities to those of previous years to assess evidence for change in the water quality of Quebrada Guacimal over time. We predicted that there would

be a gradual improvement in the water quality of Quebrada Guacimal due to the alleged cessation of organic dumping by the cheese factory.

METHODS

Study System

The Monteverde region of Costa Rica is often seen as a model for sustainable development based on ecotourism, but much remains unknown about the impacts of the large influx of tourists and rapid development (Gill 2000). We investigated the extent to which contamination from surrounding development is impacting Quebrada Guacimal on 21-23 January 2009. The physical characteristics of the sites we sampled have remained relatively constant, with a high percent canopy cover, cobble substrate and occasional boulders in riffles and runs, and sandy bottoms in pools. Studies in 1995 and 2001 found the greatest taxonomic richness in the upstream site, with a total of eight orders present (Pouliot et al 1995, Glastris et al 2001). Additionally, the 2001 study observed that there were numerous sources of gray water pollution entering the stream, in addition to the cheese factory's inputs (Glastris et al. 2001).

Field Methods

Following the methods of previous Dartmouth Foreign Study Programs studies, we used the bridge over Quebrada Guacimal as a reference point and sampled sites near those of the 2001 study to allow for closer comparisons across years. The first sampling site ("Downstream") was 47 m downstream of the bridge; the second site ("At Factory") was 60 m upstream of the bridge and was directly beneath a discharge pipe; the final site ("Upstream") was 180 m upstream of the bridge (see Glastris et al. 2001). We chose our sites within the range of the sites sampled by previous studies and attempted to minimize the influence of potentially confounding factors including canopy cover, substrate composition, and water flow. To control for these factors we chose sites with similar canopy cover, and then sampled the invertebrate communities from a range of substrate types and stream depths to obtain a composite representation of the habitats present.

At each of the three sites, we kicknet-sampled using a 30 cm diameter D-net, with 2 mm mesh size, for 60 seconds; we repeated this four times at each site, and combined these into one composite sample. We took width and depth measurements at each of the four sample locations and averaged those, for each site. We also measured dissolved oxygen (DO), pH, and temperature at the three sites using a Milwaukee SM600 Dissolved Oxygen Meter and SM102 pH Meter. We mixed each sample thoroughly and divided it into four equal sections, then randomly selected one section to count and classify the organisms to family level. We then searched the remaining three sections for any families that had not been counted in the first section, to assess the total number of families pre-

TABLE 1. Abundance of invertebrate families at each of the sampled sites (upstream of, at, and downstream from Monteverde Cheese Factory) on 21-23 January 2009. Family Biotic Index (FBI) weights the proportion of individuals in each family with a tolerance value for that family. Low tolerance values indicate greater sensitivity to pollution and higher values indicate a greater tolerance to pollution. "Present" indicates that a family was present in the entire sample from that site but not in the subsample used to determine abundance.

| Order | Family | FBI | Number of individuals | | |
			Upstream	At Factory	Downstream
Coleoptera	-------------	----	0	0	0
Diptera	Blood-red Chironomidae	8	1	39	27
Diptera	Chironomidae	6	2	177	91
Diptera	Empididae	5.5	0	Present	1
Diptera	Psychodidae	8.5	0	0	1
Diptera	Simulidae	6	0	88	306
Diptera	Stratiomyiidae	N/A	Present	0	0
Diptera	Syrphidae	10	0	1	0
Ephemeroptera	Baetidae	4.5	20	4	14
Ephemeroptera	Leptophlebiidae	2.5	3	0	0
Ephemeroptera	Trichorithidae	4	9	0	3
Hemiptera	Naucoridae	N/A	Present	0	0
Hemiptera	Veliidae	6	Present	Present	Present
Lepidoptera	Pyralidae	5	Present	0	0
Megaloptera	Corydalidae	0	Present	0	0
Odonata	Calopterygidae	5.5	1	2	0
Odonata	Coenagrionidae	8.5	1	1	0
Odonata	Libelluliidae	9	9	13	1
Plecoptera	---------------	--	0	0	0
Trichoptera	Hydropsychidae	3.5	2	Present	0
Trichoptera	Lepidostomatidae	1	4	0	0
Trichoptera	Rhyacophilidae	0.5	Present	Present	0
Acarina	Hydracarina	N/A	Present	4	0
Decapoda	Unidentified	N/A	2	0	0
Turbellaria	Planariidae	1	0	4	4

sent at each site.

Data Analysis and Interpretation

We calculated family richness, evenness, and diversity. To further assess stream health, we calculated the Family Biotic Index (FBI), percent composition of the dominant family, and percent EPT. Any one of these measures alone provides a limited basis for inference, but, when considered together, they offer a quite reliable and comprehensive bioassessment (Taylor 2007). FBI weights the proportion of individuals in each family with a tolerance value for that family (Hilsenhoff 1988) Families sensitive to contamination have lower weightings in the FBI. Thus, lower FBI values indicate a healthier stream.

A lower percentage of the dominant family indicates a more even distribution of individuals among species, which corresponds to greater stream health. Conversely, more polluted streams tend to have greater dominance by a single family (Taylor 2007). The percent EPT index is the combined proportion of three low-

TABLE 2. Tolerance values for dominant families at three sites (upstream of, at, and downstream from Monteverde Cheese Factory) on 21-23 January 2009. Greater tolerance values indicate higher tolerance of a family to environmental degradation caused by contamination. Water health decreases as one travels downstream.

Site	Dominant Family	% Composition	Tolerance Value
Upstream	Baetidae	37.04	4
At Discharge	Chironomidae	53.12	6
Downstream	Simulidae	68.30	6

tolerance invertebrate orders: Ephemeroptera, Plecoptera and Trichoptera. A higher percent EPT indicates a healthier stream (Taylor 2007). Formal statistics could not be calculated on changes in percent EPT over time because we did not have estimates of error in EPT values.

RESULTS

We found large differences in the invertebrate community composition between sites upstream and downstream from the cheese factory. The pollution-tolerant families Simulidae and Chironomidae, which were absent or uncommon upstream, dominated the community downstream (Table 1). In contrast, Baetidae, a low tolerance family, dominated upstream (Table 2). Species

richness and evenness were lower downstream (Table 3). Biotic ecosystem health indicators showed that health was reduced at downstream sites: percent EPT was 97% lower at downstream sites while FBI was 21% greater downstream (Table 3). In recent years percent EPT has increased upstream but decreased downstream (Fig. 1). Abiotic factors (DO, temperature, and pH) did not differ notably among sites (Table 4; $F_{2,6} = 4.47$, $P = 0.06$).

DISCUSSION

Our FBI at and downstream of the cheese factory indicate that the water quality at these sites is "fairly poor, with substantial pollution likely" (Hilsenhoff 1988), so pollution at these sites apparently has persisted, consistent with the

TABLE 3. Summary of diversity and ecosystem health indices at three sites at Monteverde Cheese Factory on 21-23 January 2009. Percent EPT refers to percent of sample made up of insects in the orders Ephemeroptera, Plecoptera, and Trichoptera. A higher percent EPT indicates a healthier stream. Refer to Table 1 for FBI. All indices indicate that ecosystem health decreases as one travels downstream.

	Upstream	At Factory	Downstream
Total individuals	54	333	448
FBI	4.99	6.29	6.03
Percent EPT	70.4	2.1	0.5
Family richness	10	9	8
Rarefied family richness	10	5.46	3.99
Total families present	18	14	10
Shannon-Weiner diversity index	1.87	0.98	0.84
Rarefied Shannon-Weiner diversity index	1.87	1.03	0.78
Evenness	0.81	0.45	0.40

low family diversity, richness, and evenness values we found there. The very low percent EPT and the high percent dominance by dipterans currently indicate that the invertebrate assemblages at these sites are heavily skewed towards pollution-tolerant families. In contrast, FBI at the upstream site indicates that the quality of water upstream of the cheese factory is "good, with some organic pollution probable" (see Hilsenhoff 1998). Relatively high family diversity, richness,
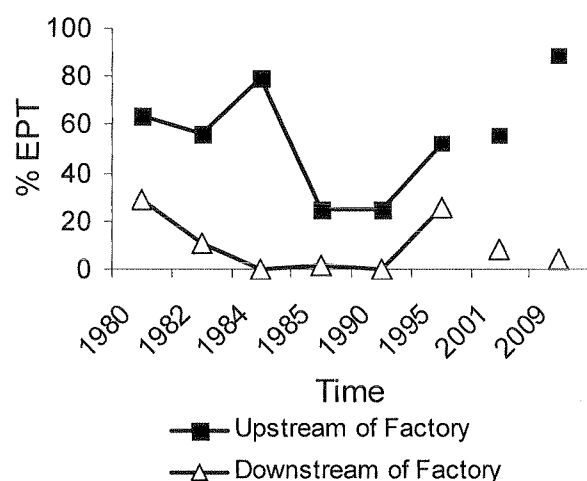
FIG. 1. Change in % EPT upstream and downstream of the Monteverede Cheese Factory over 29 years. See Table 3 for definition of % EPT.

and evenness, percent EPT and percent dominance by ephemeropterans all support this assessment. Our conclusion that pollution is more severe downstream than upstream is especially strong because we found higher family richness upstream of the cheese factory; unpolluted streams tend to increase gradually in family richness in the downstream direction (Bistoni and Heud 2002).

Our understanding is that there is relatively little development above our upstream sample, but even that comparatively clean site appears to be somewhat impacted according to its FBI, percent dominance, and family richness values. Past Dartmouth studies have found plecopterans and coleopterans both upstream and downstream of the cheese factory. However, we did not find either of these orders, although we believe our sampling methods were (at least) as thorough as in the earlier studies. The absence of these two pollution-intolerant groups suggests that water quality has decreased over the past 14 years, both upstream and downstream of the cheese factory.

The long-term trend in water quality upstream of the cheese factory remains unclear. Changes in percent EPT indicate an improvement of water quality upstream of the cheese factory since 1995, while trends in family presence indicate the opposite. This contradiction could potentially be resolved by examining trends in FBI, family richness, and family diversity data. However, as past OTS and Dartmouth studies (Pouliot et al. 1995, Gill 2000, Glastris et al. 2001) classified organisms only to order, we were unable to extract these higher resolution data.

It is clear from our data that the stream remains polluted, especially downstream of the cheese factory, but we cannot identify the exact sources. The cheese factory has obviously polluted the stream, but many other inputs may be contributing. Our bioassessment data are

supported by our personal observations: the two most downstream sites had foul odor, thick mats of unknown fibrous debris, murky water, and pipes discharging odorous material. Although the cheese factory allegedly stopped discharging waste into the stream in 1993, fibrous material directly beneath a large pipe

TABLE 4. Summary of abiotic factors at three sites at Monteverde Cheese Factory on 21-23 January 2009. Data are reported mean (1 S.E.). Repeated measures were only conducted for pH.

	Upstream	At Factory	Downstream
Dissolved Oxygen (DO)	9.0	8.6	8.7
pH	6.81 (0.010)	6.76 (0.003)	6.59 (0.093)
Temperature (°C)	15.0	15.1	15.0

from the factory warrants investigation. We observed a total of six active inputs, excluding the cheese factory, in just the stretch of stream we sampled— ranging from a pipe of rushing water to one slowly discharging orange slime and producing a surface sheen on the stream.

The lack of trends across sites in temperature and DO was not surprising since sites were chosen (see Methods) to have similar canopy cover (which influences water temperature) and flow rate (all had riffles that replenish DO). We noticed that all had periphyton, which also replenishes DO. Our pH values decreased from upstream to downstream, but not significantly. We did not have equipment to measure nutrient loading or inorganic and organic pollutants, but instead relied on standard bioassessment methods.

The implications of the stream degradation we observed are far-reaching. Quebrada Guacimal originates in the cloud forest, high on the continental divide, forming the headwaters of a large watershed upon which many people depend. The persistent pollution of Quebrada Guacimal is likely a symptom of rapid growth with insufficient infrastructure to reduce environmental impacts. This demonstrates the negative impacts large scale development can have on the Monteverde region (Gill 2000).

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Evaluación biótica de la contaminación continua en la Quebrada Guacimal, Monteverde

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Resumen: Observaciones previas de la quebrada Guacimal, un arroyo costarricense históricamente contaminado por aportes de aguas grises de tuberías de la Lechería Monteverde, han mostrado que la estructura de la comunidad de invertebrados dulceacuícolas varía a lo largo de la quebrada en base a la tolerancia de cada taxón a la contaminación. Nuestras metas fueron determinar la condición actual de la quebrada y determinar cómo la salud de la quebrada ha cambiado desde el estudio más reciente. Basados en trabajo anterior en la quebrada, muestreamos invertebrados en tres sitios (aguas arriba, en el sitio y aguas abajo de la lechería), clasificamos los organismos hasta familia y generamos estimaciones de calidad del agua basados en diversidad y composición. Nuestra predicción fue que la calidad del agua, y por consecuencia las comunidades de la quebrada, estarían aún afectadas por contaminación consecuencia de asentamientos de la periferia, pero que la degradación sería menor que la encontrada en estudios anteriores. Como lo esperábamos, encontramos que el Índice de Familias Bióticas se incremento desde un sitio aguas arriba hacia el sitio aguas abajo. Consistente con esta tendencia, el porcentaje de Ephemeroptera, Plecoptera, Trichoptera y la riqueza por familias, homogeneidad y diversidad disminuyó del sitio aguas arriba hacia el sitio aguas abajo. No encontramos evidencia clara de que las condiciones de la quebrada han mejorado en años recientes.

Palabras clave: contaminación orgánica, Lechería Monteverde, bioevaluación

Introducción

Una bioevaluación acuática es una examen de condiciones dulceacuícolas que frecuentemente usa organismos como invertebrados y diatomeas como indicadores de calidad del agua (Patrick 1949). El ensamble de esos organismos se basa en las diferentes tolerancias de los grupos taxonómicos a la degradación ambiental causada por actividades humanas. La lechería Monteverde utilizó la quebrada Guacimal como sitio de descargas de aguas residuales de 1983 a 1993 (Gill 2000). Aun con la supuesta termina-

ción de esas descargas, estudios de 1980-1990, 1995 y 2001 muestran una diferencia persistente en la estructura de la comunidad de invertebrados a lo largo de la quebrada abarcando el antiguo sitio de descargas (Pouliot et al. 1995, Gill 2000, Glastris et al. 2001).

Evaluamos la condición actual de la quebrada utilizando índices basados en la comunidad de invertebrados encontrados en sitios aguas arriba y aguas abajo de la lechería. A continuación comparamos las comunidades de invertebrados encontradas en el presente con las de

años previos para identificar evidencia de cambios en la calidad del agua en la quebrada Guacimal a través del tiempo. Nuestra predicción es que encontraríamos un incremento gradual en la calidad del agua de la quebrada Guacimal como consecuencia del supuesto cese de descargas orgánicas de la lechería.

MÉTODOS

Sistema de estudio

La región de Monteverde, Costa Rica, es frecuentemente vista como un modelo de desarrollo sustentable basada en ecoturismo, aunque en gran medida se desconocen los impactos del elevado flujo de turistas y el acelerado desarrollo de asentamientos humanos (Gill 2000). Investigamos la magnitud del impacto de este desarrollo en la periferia de la quebrada Guacimal del 21-23 enero 2009. Las características físicas de los sitios que muestreamos han permanecido relativamente constantes, con un alto porcentaje de cobertura del dosel, sustrato pedregoso y grandes rocas en remansos y fondos arenosos en sus pozas. Los estudios en 1995 y 2001 encontraron la mayor riqueza taxonómica en el sitio aguas arriba, con un total de ocho órdenes presentes (Pouliot et al. 1995, Glastris et al. 2001). Adicionalmente, el estudio de 2001 observó que había numerosas fuentes de aguas grises ingresando al sistema, en adición a los aportes de la lechería (Glastris et al. 2001).

Métodos de campo

Siguiendo los métodos de estudios previos de Dartmouth FSP, utilizamos el puente sobre la quebrada Guacimal como punto de referencia y muestreamos sitios cercanos a los del estudio de 2001 para permitir comparaciones más cercanas entre años. El primer sitio de muestreo ("Aguas Abajo") estaba 47 m aguas abajo del puente; el segundo sitio ("En la Fábrica") estaba 60 m aguas arriba del puente y estaba directamente debajo de un tubo de descarga; el sitio final ("Aguas Arriba") estaba 180 m aguas arriba del puente (ver a Gastris et al. 2001). Elegimos nuestros sitios dentro del rango de sitios muestreados por previos estudios y tratamos de minimizar la influencia de factores que podrían confundir como cobertura del dosel, composición del sustrato y flujo de agua. Para controlar el efecto de esos factores escogimos sitios con cobertura del dosel similar y a continuación muestreamos las comunidades de invertebrados de una variedad de tipos de sustrato y profundidades de agua para obtener representaciones compuestas de los hábitats presentes.

En cada uno de los tres sitios muestreamos con redes de golpeteo "D" de 30 cm de diámetro y malla de 2 mm por 60 seg y los repetimos en cuatro ocasiones en cada sitio y combinamos éstos en una muestra compuesta. Tomamos mediciones de ancho y profundidad en cada una de las cuatro localidades de muestreo y las promediamos para cada sitio. También medimos el oxígeno disuelto (OD), pH y temperatura en los tres sitios utilizando un medidor de oxígeno disuelto Milwaukee SM600 y un medidor de pH

TABLA 1. Abundancia de familias de invertebrados en cada uno de los sitios muestreados (aguas arriba, en el sitio, y aguas abajo de la lechería Monteverde) del 21-23 enero 2009. El Índice de Familias Bióticas (IFB) pondera la proporción de individuos de cada familia con un valor de tolerancia para cada familia. Los valores bajos de tolerancia indican una mayor sensibilidad a la contaminación y los valores más altos una mayor tolerancia a ésta. "Presente" indica que la familia estaba presente en la muestra completa para ese sitio, pero no en la sub-muestra utilizada para determinar la abundancia.

Orden	Familia	IFB	Número de individuos		
			Arriba	En sitio	Abajo
Coleoptera	--------------	----	0	0	0
Diptera	Blood-red Chironomidae	8	1	39	27
Diptera	Chironomidae	6	2	177	91
Diptera	Empididae	5.5	0	Presente	1
Diptera	Psychodidae	8.5	0	0	1
Diptera	Simulidae	6	0	88	306
Diptera	Stratiomyiidae	N/A	Presente	0	0
Diptera	Syrphidae	10	0	1	0
Ephemeroptera	Baetidae	4.5	20	4	14
Ephemeroptera	Leptophlebiidae	2.5	3	0	0
Ephemeroptera	Trichorithidae	4	9	0	3
Hemiptera	Naucoridae	N/A	Presente	0	0
Hemiptera	Veliidae	6	Presente	Presente	Presente
Lepidoptera	Pyralidae	5	Presente	0	0
Megaloptera	Corydalidae	0	Presente	0	0
Odonata	Calopterygidae	5.5	1	2	0
Odonata	Coenagrionidae	8.5	1	1	0
Odonata	Libelluliidae	9	9	13	1
Plecoptera	---------------	--	0	0	0
Trichoptera	Hydropsychidae	3.5	2	Presente	0
Trichoptera	Lepidostomatidae	1	4	0	0
Trichoptera	Rhyacophilidae	0.5	Presente	Presente	0
Acarina	Hydracarina	N/A	Presente	4	0
Decapoda	Unidentified	N/A	2	0	0
Turbellaria	Planariidae	1	0	4	4

SM102. Mezclamos cada muestra cuidadosamente y la dividimos en cuatro secciones iguales, posteriormente seleccionamos una sección para contabilizar y clasificar los organismos hasta familia.

Después examinamos las restantes tres secciones en busca de familias que no fueron encontradas en la primera sección para determinar el número total de familias presentes en cada sitio.

TABLA 2. Valores de tolerancia para familias dominantes en tres sitios (aguas arriba, en el sitio, y aguas abajo de la lechería Monteverde) del 21-23 enero 2009. Los valores de tolerancia mayores indican una mayor tolerancia de esa familia a la degradación ambiental causada por la contaminación. La calidad del agua decrece conforme se viaja aguas abajo.

Sitio	Familia dominante	Composición %	Valor de tolerancia
Aguas arriba	Baetidae	37.04	4
En el sitio	Chironomidae	53.12	6
Aguas abajo	Simulidae	68.30	6

Análisis y interpretación de datos

Utilizamos nuestros datos de 2009 para calcular riqueza de familias, homogeneidad y diversidad. Para determinar la salud de la quebrada, calculamos el Índice de Familias Bióticas (IFB), porcentaje de composición de la familia dominante, y porcentaje de EPT. Dado que ninguna de estas mediciones por separado provee una base robusta para hacer inferencias, éstas fueron consideradas en conjunto para obtener una bioevaluación confiable y extensiva (Taylor 2007). El IFB pondera la proporción de individuos en cada familia con un valor de tolerancia para ésta (Hilsenhoff 1988). Las familias sensibles a la contaminación tienen menor influencia en el IFB. Así, valores menores de FBI indican una quebrada con mejor salud.

Un porcentaje más bajo de la familia dominante indica una distribución más homogénea de individuos entre especies, que corresponde a una mayor salud de la quebrada. Por el contrario, las quebradas más contaminadas tienden a tener mayor dominancia de una sola familia (Taylor 2007). El porcentaje del índice EPT es la proporción combinada de los tres órdenes de menor tolerancia: Ephemeroptera, Plecoptera y Trichoptera. Un porcentaje mayor de EPT indica una quebrada más sana (Taylor 2007). No pudimos calcular análisis estadísticos formales en los cambios de porcentaje de EPT a través del tiempo porque no disponíamos de las estimaciones de error en valores de EPT.

RESULTADOS

Encontramos grandes diferencias en la composición de la comunidad de invertebrados entre sitios en diferentes posiciones respecto a la lechería. Las familias Simulidae y Chironomidae, que son tolerantes a la contaminación y estuvieron ausentes o son poco comunes aguas arriba, dominan la comunidad aguas abajo (Tabla 1). En contraste, la familia Baetidae es poco tolerante y domina aguas arriba (Tabla 2). La riqueza y homogeneidad fueron menores en la parte baja de la quebrada (Tabla 3). Los indicadores bióticos de salud del ecosistema muestran que ésta se reduce en sitios aguas abajo: el porcentaje de EPT fue 97% más bajo en sitios aguas abajo mientras que el IFB fue 21% mayor en la misma dirección (Tabla 3). En años recientes, el porcentaje de EPT se ha incrementado en la parte alta de la quebrada pero decrecido en la parte baja (Figura 1). Los factores abióticos (OD, temperatura y pH) no difieren de manera notoria entre sitios (Tabla 4; $F_{2,6} = 4.47$, $P = 0.06$).

DISCUSÓN

El IFB en el sitio y aguas debajo de la lechería indican que la calidad del agua en estos sitios es "moderadamente pobre, donde es posible contaminación sustancial" (Hilsenhoff 1988), lo que indica que la contaminación en estos sitios aparentemente ha persistido; esta es consistente con la baja diversidad de familias y los valores de riqueza y homogeneidad que encontramos aquí. El muy bajo porcentaje de EPT y el muy alto porcentaje de dominancia por dípteros indican que los ensambles de invertebrados en estos si-

tios están fuertemente sesgados hacia familias tolerantes a la contaminación. En contraste, el IFB en los sitios aguas arriba indican que la calidad del agua arriba de la lechería es "buena, con probable contaminación orgánica" (ver Hilsenhoff 1998). La relativamente alta diversidad de familias, riqueza y homogeneidad, porcentaje de EPT y porcentaje de dominancia por efemerópteros son argumentos de soporte para esta aseveración. Nuestra conclusión de que la contaminación es más severa aguas abajo que arriba es particularmente robusta porque encontramos una mayor diversidad de familias arriba de la lechería siendo que las quebradas tienden a incrementar gradualmente ésta en dirección aguas abajo (Bistoni & Heud 2002).

Nuestro entendimiento es que hay relativamente pocos asentamientos humanos arriba del sitio de nuestra muestra aguas arriba, pero aún el sitio comparativamente limpio parece tener algún impacto según señala su IFB, porcentaje de dominancia, y valores de riqueza de familias. Estudios anteriores de

Dartmouth han encontrado plecópteros y coleópteros arriba y debajo de la lechería. Sin embargo, no encontramos ninguno de estos órdenes, aunque consideramos que nuestros métodos de muestreo fueron al menos tan detallados como los de estudios anteriores. La ausencia de estos dos grupos intolerantes a la contaminación sugiere que la calidad del agua ha declinado en los pasados 14 años en sitios arriba y debajo de la lechería.

La tendencia de largo plazo en la calidad del agua arriba de la lechería no es clara. Los cambios en el porcentaje de EPT indican una mejora en la calidad del agua arriba de la lechería desde 1995, mientras la tendencia en la presencia de familias indica lo contrario. Esta contradicción podría potencialmente ser resuelta examinando los datos de las tendencias de IFB, riqueza y diversidad de familias. Sin embargo, dado que estudios anteriores de la OET y Dartmouth (Pouliot et al. 1995, Gill 2000, Glastris et al. 2001) clasifican a los organismos sólo hasta orden, no pudimos extraer estos datos de mayor resolución.

TABLA 3. Síntesis de diversidad e índices de salud de ecosistemas en tres sitios de la lechería Monteverde del 21-23 enero 2009. El porcentaje EPT se refiere al porcentaje de la muestra compuesto por insectos de los órdenes Ephemeroptera, Plecoptera y Trichoptera. Un porcentaje alto de EPT indica una quebrada sana. Refiérase a la Tabla 1 para IFB. Todos los índices indican que la salud del ecosistema decrece al desplazarse aguas abajo.

	Aguas arriba	En el sitio	Aguas abajo
Total de individuos	54	333	448
IFB	4.99	6.29	6.03
Porcentaje de EPT	70.4	2.1	0.5
Riqueza de familias	10	9	8
Riqueza de familias rarificada	10	5.46	3.99
Total familias presentes	18	14	10
Indice Shannon-Wiener de diversidad	1.87	0.98	0.84
Indice Shannon-Wiener de diversidad rarificado	1.87	1.03	0.78
Homogeneidad	0.81	0.45	0.40

Es claro según nuestros datos que la quebrada sigue contaminada, especialmente aguas abajo de la lechería, pero no pudimos identificar las fuentes exactas. La lechería obviamente ha contaminado la quebrada, pero muchas otras descargas también podrían contribuir. Los datos de nuestra bioevaluación tienen el soporte de otras observaciones: los dos sitios debajo tienen mal olor, natas de un desecho fibroso indeterminado, aguas turbias y tuberías descargando materiales apestosos. Aunque la lechería alega haber finalizado las descargas de desechos en 1993, el material fibroso directamente debajo de un gran tubo de la lechería requiere ser investigado. Excluyendo la lechería, observamos un total de seis descargas activas tan sólo en la sección de la quebrada que muestreamos, variando desde un tubo con agua corriente hasta una descarga lenta de una sustancia naranja que deja una superficie brillante en la superficie.

La ausencia de cambios de temperatura y OD no nos sorprendió, dado que los sitios que elegimos (ver Métodos) tienen una cobertura de dosel similar (que influencia la temperatura del agua) y tasa de flujo de agua (que tiene ondulaciones

FIG. 1. Cambio en el porcentaje de EPT arriba y debajo de la lechería Monteverde durante 29 años. Consulte la Tabla 3 para una definición del porcentaje de EPT.

que recargan el OD). Notamos que todos tenían perifiton (una mezcla compleja de algas, cianobacterias, microbios heterotróficos y detritus bénticos), que ayuda en la recarga de OD. Nuestros valores de pH decrecen de aguas arriba a aguas abajo, aunque no de manera significativa. No dispusimos de equipos para mediciones de carga de nutrientes o contaminantes orgánicos e inorgánicos; a cambio confiamos en el método estándar de bioevaluación.

Las implicaciones de la degradación de la quebrada que observamos son de grandes alcances. La quebrada Guacimal se origina en el bosque de niebla, en la parte alta de la división continental, en los inicios de una gran cuenca de la cual depende mucha gente. La contaminación persistente en la quebrada Guacimal en posiblemente un síntoma del rápido crecimiento humano con infraestructura in-

TABLA 4. Síntesis de factores abióticos en tres sitios de la lechería Monteverde del 21-23 enero 2009. Los datos reportados son promedio (1 D.E) Las mediciones repetidas sólo fueron hechas para el pH.

	Aguas arriba	En el sitio	Aguas abajo
Oxígeno disuelto (OD)	9.0	8.6	8.7
pH	6.81 (0.010)	6.76 (0.003)	6.59 (0.093)
Temperatura (°C)	15.0	15.1	15.0

suficiente para reducir los impactos al ambiente. Esto demuestra que el desarrollo a gran escala puede tener impactos negativos en la región de Monteverde (Gill 2000).

LITERATURA CITADA

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Substrate and Succession: Two possible factors affecting Inverte-brate diversity and abundance in *Chusquea longifolia* nodes

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Faculty Editor: David R. Peart

Abstract: We investigated the maturation of invertebrate communities in organic matter that collects in leaf whorls in bamboo (*Chusquea longifolia*) nodes. We hypothesized that older (higher) nodes would contain more fine particulate organic matter (FPOM), and thus (1) provide a more physically complex habitat that can support a higher invertebrate diversity and (2) be productive enough to support greater invertebrate abundances. In older nodes, we expected greater abundance and diversity due to population growth and colonization respectively. We found that the proportion of predators increased from 21% in younger nodes to 32% in older nodes, which suggests that older nodes may be more productive of prey biomass. The amount of FPOM was positively correlated with taxonomic richness but node age was not. We suggest that colonization may occur so quickly that low nodes have already accumulated most colonizing taxa. We suggest future experiments to estimate productivity and colonization rates.

Key words: leaf litter

Sustrato y sucesión: Dos posibles factores que afectan la diversidad de inverte-brados en nodos de *Chusquea longifolia*

Resumen: Investigamos la maduración de comunidades de invertebrados en la materia orgánica que se acumula en los nodos foliares del bambú (*Chusquea longifolia*). Nuestra hipótesis es que los nodos más viejos (más altos) contendrían más partículas finas de material orgánico (PFMO) y por ello (1) proveen un hábitat físicamente más complejo que puede auspiciar una diversidad de invertebrados mayor y (2) ser suficientemente productiva para mantener abundancias mayores de invertebrados. En los nodos más viejos, esperamos mayor abundancia y diversidad en respuesta a crecimiento y colonización respectivamente. Encontramos que la proporción de depredadores se incremento de 21% en los nodos más jóvenes a 32% en los nodos más viejos, lo que sugiere que los nodos más viejos son más productivos. La cantidad de PFMO esta positivamente correlacionada con la riqueza taxonómica, pero la edad del nodo no estaba relacionada con ésta. Sugerimos que la colonización puede ocurrir de manera tan rápida que los nodos bajos ya habrían adquirido la mayoría de los taxa colonizadores. También sugerimos experimentos futuros para estimar las tasas de productividad y colonización.

Palabras clave: hojarasca

Introduction

In classic succession, community composition changes over time. We investigated whether invertebrate communities in nodes of *Chusquea longifolia* undergo successional changes. *Chusquea longifolia* leaves form small baskets (leaf whorls) at each node that collect leaf litter. Invertebrate detritivores and herbivores colonize the node, process the litter, and establish a prey base upon which

predators may persist in that node. Growth in *C. longifolia*, like most Poaceae, occurs from the basal meristem upward; higher nodes are older than lower nodes.

We predicted greater taxonomic richness in the older (higher) nodes for two reasons. First, older nodes have had more time to be colonized than younger nodes. Second, older nodes may provide a more physically complex habitat that can support a more diverse community. Specifically, we predicted that older nodes have accumulated more fine particulate organic matter (FPOM) from decomposition, and that nodes with more FPOM can support more taxa.

We also expected the older nodes to support greater abundances of these taxa for similar reasons. First, in older nodes, populations have had more time to grow toward carrying capacity. Second, invertebrates may be more productive in nodes with more FPOM. FPOM is more decomposed than coarse litter, and has a larger surface area—qualities that may make it a better food resource, and potentially a better habitat or refuge for some species. Because we expected older nodes to contain more FPOM, we predicted larger invertebrate populations in old than in young nodes.

METHODS

Our study site was ca. 0.5 km along the upper entrance to the loop trail northeast of Cuericí Biological Station at Cerro de la Muerte, Costa Rica. On the mornings of 30-31 January 2009, we collected bamboo nodes containing approximately the same amount of litter from bamboo patches on both sides of the trail. We collected 18 nodes from 18 individual plants: nine "low" nodes, from the lower third portion of bamboo stems, and nine "high" nodes, from the upper third. We extracted all loose leaf litter from each node by shaking the contents of the node into a bucket and then examined the litter and the node for invertebrates. The invertebrates were classified into morphotypes and categorized by feeding guild (herbivore/detritivore, predator, scavenger, or generalist). We weighed the largest arthropods to estimate total invertebrate biomass. Leaf litter and organic matter were sifted with a 0.5 and 0.125 cm mesh and weighed to estimate the proportions of different sized litter particles.

We compared the proportional abundances of predators and herbivores/detritivores, the amount of FPOM, and morphotype richness, in high versus low nodes using paired t-tests. We used proportional abundances to standardize for differences in total arthropod abundance among nodes. We used morphotype richness, based upon recognizable arthropod orders and morphological differences within orders, because it allowed us to designate feeding guilds when we could not identify all arthropods to family or lower levels. We used a linear regression to test for the effect of FPOM on taxonomic richness. Data were analyzed using JMP 7.0 (SAS Institute, Inc. 2007).

We excluded one outlier for FPOM mass from our analysis. A saw was used

to cut that node from the stem and contaminated the organic matter of that node with large amounts of sawdust, skewing our proportional FPOM measurement for the node.

RESULTS

Predators comprised 21% of the community in low nodes compared to 32% in high nodes (paired-t_{16} = 3.31, P = 0.004; Fig. 1). Herbivores and detritivores composed 72% of the community in low *C. longifolia* nodes compared to 64% in high nodes (paired-t_{16} = 2.37, P = 0.031; Fig. 1). The mean FPOM mass in low nodes was 1.27 g, compared to 2.82 g in high nodes (paired-t_{15} = 2.92, P = 0.01). The mass of FPOM in a node was positively related to
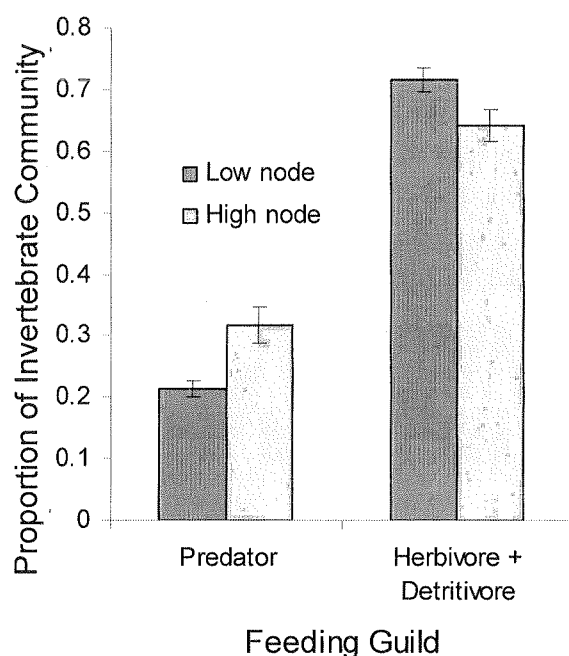
FIG. 1. Invertebrate community composition in organic matter collected by leaf whorls at high and low nodes in *Chusquea longifolia* in the understory of oak forest at Cuericí. Predator abundance was proportionally greater in high nodes while the proportion of herbivore and detritivore abundance was greater in low nodes (n = 18 sampled nodes).

taxonomic richness (r^2 = 0.40, $F_{1,15}$ = 10.2, P = 0.006; Fig. 2). Invertebrate biomass was not greater in high nodes than in low nodes (paired-t_{16} = 0.29, P = 0.78).

DISCUSSION

We found more FPOM in the higher, older nodes, which indicates that litter in these nodes has decomposed more over time. This supports the expectation that the physical habitat of nodes changes with node age. Further, FPOM mass was positively correlated with taxonomic richness, which matches our initial prediction that FPOM may provide a more complex habitat that can support a greater number of species. However, we did not detect a difference in taxonomic richness between older and nodes. This suggests that FPOM drives species richness, rather than age per se.

It is surprising that age is not related to taxonomic richness, even though they are both correlated with FPOM mass. We suggest two possible explanations. First, our taxonomic classification may not have been sensitive enough to detect a trend with age. Our morphotype classifications were relatively coarse and we included only organisms visible to the naked eye. But smaller organisms probably inhabit these nodes, particularly nodes with large amounts of FPOM; future investigators might consider using microscopy to enhance their classification. Alternatively, age might not influence taxonomic richness on the timescale we investigated. Nodes may be colonized by new species relatively quickly, soon after
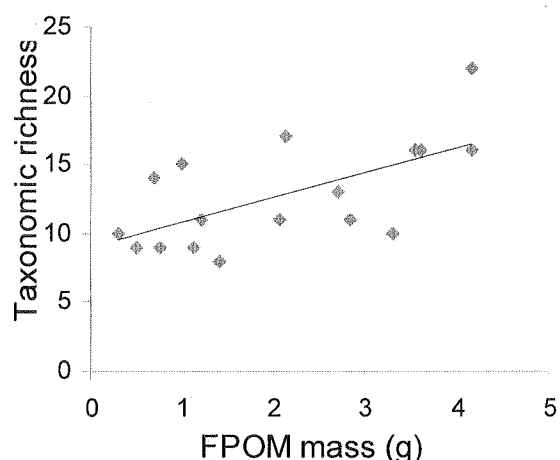
FIG. 2. Taxonomic richness (see text for details) increased with FPOM (fine particulate organic matter) mass collected by leaf whorls in *Chusquea longifolia* nodes in the understory of oak forest at Cuericí. This is described by the line $Y = 1.83X + 8.9$ where X is FPOM mass and Y is morphotype richness (n = 17 samples).

the node starts collecting litter. By the time a node is just a few years old (like our low nodes), most of the macro-invertebrate species may have already colonized the node, which would explain why there is little difference in richness between low and high nodes. Nodes with more FPOM may support more colonizers and FPOM may tend to increase with time, but neither of these relationships appears strong enough for age to have a significant effect on taxonomic diversity. This explanation is consistent with our finding that the proportional abundance of predators was higher in older nodes; even though colonization may occur quickly, the proportional abundances of predators and non-predators may change on a slower time scale.

Future investigators might try to determine how quickly colonization occurs by removing all contents of nodes in the field, restocking them with fresh litter, then observing the rates at which different taxa colonize those nodes. Setting up traps on the stem between nodes may help to determine migration rates between nodes.

It is intriguing that higher nodes do not have higher abundances of invertebrate taxa as predicted. High nodes do have a higher predator-to-prey ratio than low nodes, suggesting that older node communities are ecologically distinct from younger ones, even though they are neither more taxonomically abundant nor more taxonomically diverse. In order to support a higher proportion of predators, prey must be more abundant, more productive, or easier to catch in these older nodes. Because the prey were not more abundant in older nodes, future investigators might test for differences in prey productivity by excluding predators from low and high nodes and comparing productivity after release from predation. Experimenters could also test for differences in prey capture rates by standardizing the number of predators and prey in old and new nodes to see if the predators catch more in the old nodes.

In conclusion, we feel this is a promising and unexplored biological system that merits future investigation.

Control of Leaf Angle Reduces Environmental Stresses on Immature *Anthurium supervivencia* Leaves

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Abstract: We observed that young expanding leaves of *Anthurium supervivencia* were held at a more vertical angle than mature leaves. We hypothesized that this provides an advantage for young expanding leaves by reducing environmental stresses such as over-exposure to sunlight. We also predicted that immature leaves would desiccate faster than mature leaves, and that immature leaves held at vertical angles would gain less heat in direct sunlight than those held at horizontal angles. Our results supported all of our predictions and suggest that heat and water stress may be reduced by vertical leaf angle in immature leaves of *A. supervivencia*.

Key words: desiccation, heat, solar radiation, growth strategy, plant physiology

En Control del Ángulo de las Hojas Reduce el Estrés Ambiental en Hojas Inmaduras de Anthurium supervivencia

Resumen: Observamos que las hojas jóvenes en expansión de *Anthurium supervivencia* están dispuestas en un ángulo más vertical que las hojas maduras. Nuestra hipótesis es que esto provee ventajas a las hojas jóvenes en desarrollo reduciendo estreses ambientales como la sobreexposición a la luz del sol. Predecimos que las hojas inmaduras se desecarían más rápido que las hojas maduras y que las hojas inmaduras dispuestas en ángulos verticales ganarían menos calor bajo luz directa del sol que las que se encuentran a ángulos horizontales. Nuestros resultados dan soporte a todas nuestras predicciones y sugieren que el estés por calor y agua en *A. supervivencia* puede ser reducido por medio de un ángulo más vertical en sus hojas inmaduras.

Palabras clave: deshidratación, calor, radiación solar, estrategia de crecimiento, fisiología de plantas

INTRODUCTION

Plants use an array of physiological adaptations to cope with environmental stresses. In the tropics, new leaves often have delayed greening, hypothesized to reduce the cost of losing new leaves to herbivory (Coley and Kursar 1996). We reasoned that plants that exhibit delayed greening may develop additional strategies to reduce environmental stresses placed on their delicate new leaves.

We observed that in *Anthurium supervivencia* (Araceae) leaves with delayed greening were held at a more vertical angle than mature (green) leaves. A steeper leaf angle may minimize exposure of expanding leaves to sunlight, heat gain, water loss, and ultraviolet-induced DNA damage. We examined whether reduced leaf angle decreases leaf temperature and desiccation. We also tested whether expanding leaves orient away from the
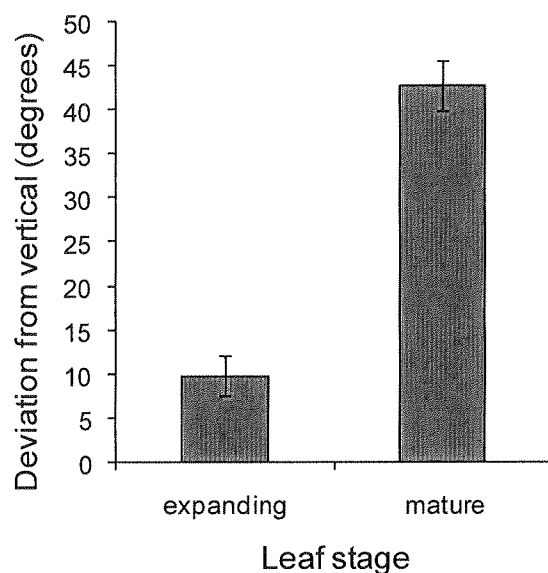
FIG. 1. Expanding leaves of *Anthurium supervivencia* at Cuericí, Costa Rica were held at a more vertical angle than were mature leaves, on plants in the field (n = 25). Bars are means ± 1 S.E.

compass direction of most intense sunlight as a further means of reducing excessive sun exposure.

METHODS

Beginning at the upper entrance of the main loop trail near the Cuericí Biological Reserve on 30 January 2009, we sampled the first 25 available *A. supervivencia*, a shade-tolerant understory plant, that fit the following criteria: 1) the newest leaf on the plant had signs of delayed greening, 2) there were at least two older leaves, 3) the plant was within 2m of the trail, 4) there was little or no sign of herbivore damage, 5) the plant only received light filtered by the canopy as opposed to direct sunlight. For the youngest three leaves, we measured the compass direction of the central vein of each leaf (leaf direction), leaf length

(petiole to leaf tip), and leaf angle from vertical (i.e. a completely vertical leaf has zero leaf angle). For each plant, we determined the direction of most intense sunlight by examining the path of the sun and estimating the direction of least canopy cover. For the first three plants examined (at 8:30 am), we marked the youngest three leaves and noted their direction to test whether leaf direction follows the angle of the sun (heliotropism). We returned at 4:00 pm on the same day and again measured the direction of these leaves.

To compare the rates of desiccation between expanding and more mature leaves, we collected ten leaf pairs (youngest, expanding leaf matched with the second-youngest leaf) from *A. supervivencia*, including ca. 20 cm of petiole on each leaf, and submerged the petioles in water directly after cutting to prevent wilting. After returning to the lab, we removed the petioles and surface water, and recorded initial leaf mass. We allowed the leaves to desiccate in the shaded lab for five hours and weighed them again to calculate the proportional loss of mass due to desiccation.

To test whether vertical leaf angle reduced heat gain from solar radiation, we collected seven pairs of expanding leaves from 14 plants within 3 m of the same trail. We standardized for size and color within each leaf pair. The seven leaf pairs were placed in direct sunlight and attached to a railing with one leaf held vertically and the other horizontally. We waited one hour and measured leaf tem-

perature by wrapping the leaf around a thermometer probe (Milwaukee SM102 Smart pH Meter).

All analyses were one-tailed simple t-tests performed in JMP 7.0 (SAS Institute, Inc. 2007).

RESULTS

We found no evidence of heliotropism in *A. supervivencia*. All tested leaves faced the same direction at 4 p.m. as when tested at 8:30 a.m. Expanding leaves were held at a more vertical angle than mature leaves (t_{48}= -9.05, $P < 0.001$; Fig 1). As predicted, expanding leaves deviated more from the estimated direction of most intense sun than did mature leaves (t_{48}= 1.82, $P = 0.037$; Fig 2). Expand-

FIG. 3. Over a period of 5 hrs in a shaded lab, detached expanding leaves of *A. supervivencia* at Cuericí, Costa Rica lost more water in proportion to the weight of the leaf than did mature leaves (n = 10). Bars are means ± 1 SE.

ing leaves desiccated significantly more than mature leaves over 5 hrs (t_{16} = -3.26, $P = 0.0025$; Fig 3). Expanding leaves held vertically absorbed less heat from solar radiation than did expanding leaves held horizontally (t_{12}= -4.31, $P = 0.0005$; Fig 4).

DISCUSSION

Our data support the prediction that expanding leaves are held at a more vertical angle than mature leaves. This verticality does not seem to result from a less sturdy leaf and petiole structure, or lack of turgor pressure, because the junction between leaf and petiole was composed of firm tissue, which held the leaves in this vertical orientation (personal observation).

Results from the desiccation and heat gain experiments support our hypothesis that holding expanding leaves vertically

FIG. 2. Expanding leaves of *Anthurium supervivencia* deviated from the direction of the sun more than did mature leaves on plants in the field at Cuericí, Costa Rica (n = 25). The direction of leaves was defined as the compass direction of the central vein of each leaf. Bars are means ± 1 SE.

is advantageous because it minimizes the exposure to intense sunlight. Expanding leaves are more susceptible to damage by intense sunlight than mature leaves because they desiccate faster and absorb more heat due to their darker hue. Furthermore, our finding that expanding leaves deviate more from the direction of most intense sunlight than do mature leaves also affirms that a reduction in sunlight exposure may be important to avoid damage in expanding leaves.

We sampled plants in shade to examine leaf orientation relative to the direction of most intense sunlight. However, we suspect that the benefits of a more vertical angle in expanding leaves may be even greater for plants in clearings, which would experience the strongest solar radiation from directly above at noon. Exposed plants in tropical alpine zones are especially prone to heat and water stress because of more rapid evaporation resulting from high winds and the intense radiation that penetrates thin atmospheres.

The regularity with which expanding leaves were held vertical in *A. supervivencia* suggests that it might be instructive to investigate similar patterns across species. This may provide insights into the adaptive history of the genus *Anthurium*, and perhaps the family Araceae. If vertical-leaf orientation in expanding leaves is not widespread, it suggests that only some species experience enough heat and/or desiccation stress in their expanding leaves to gain from the tradeoff of avoiding physical stress at the cost of re-

duced photosynthesis. In particular, if only species that exhibit delayed greening hold expanding leaves vertically, it would imply (1) that only species exhibiting delayed greening suffer enough heat and desiccation stress, or (2) that vertical angle occurs only when there is little or no cost of reduced photosynthesis, due to the lack of chlorophyll in expanding leaves of plants exhibiting delayed greening.

On the other hand, the vertical angle of expanding leaves may be nearly universal in the genus (or the family), irrespective of whether a species has delayed greening. Such a consistent pattern would imply that strong shade tolerance in the genus (or family) has been associated in evolutionary time with severe costs of heat and desiccation stress in expanding leaves, so that the potential gain
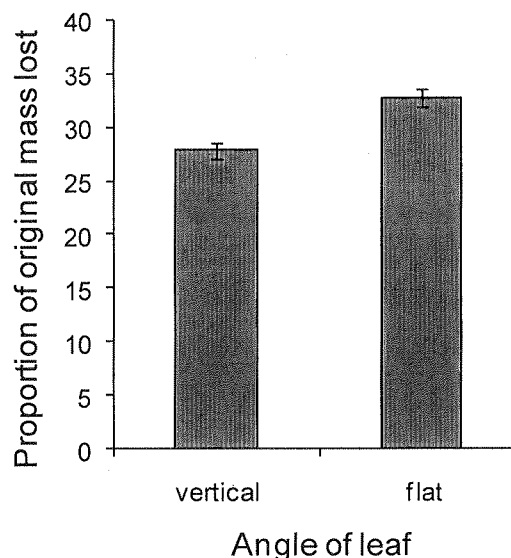
FIG. 4: Detached expanding leaves of *Anthurium. supervivencia* held at a horizontal angle were hotter than those held at a vertical angle after 1 hr of exposure to direct sunlight (n = 7) on the lab porch, at Cuericí, Costa Rica. Bars are means ± 1 SE.

in photosynthesis by holding the leaf more horizontally, even in green expanding leaves, has been insufficient to balance those costs.

Based on these arguments, we recommend a survey of *Anthurium* (or a wider survey of the Araceae), to quantify the frequency of vertically-held expanding leaves, and the association of this trait with delayed greening.

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Caterpillar Preference for Newly Expanded *Begonia* sp. Leaves

Charles W. Knape, Emily L. Pizzichemi, and Brianna L. Wilkinson

Faculty Editor: David R. Peart

Abstract: To test the effect of leaf age on an unidentified species of Lepidoptera's foraging preference, we performed a cafeteria-style experiment with *Begonia* sp. Our results agreed with our prediction that the caterpillars would choose to eat a larger portion of young recently expanded leaves than mature leaves, due to the probable lower structural defenses and higher nutrient content of young leaves.

Key words: Cuericí, plant defense, plant growth, trade-off

Preferencia de Orugas por Hojas de *Begonia* sp. Recientemente Desarrolladas

Resumen: Para investigar el efecto de la edad de las hojas en las preferencias de forrajeo en orugas de lepidópteros, desarrollamos un experimento de elección de alimento en *Begonia* sp. Nuestros resultados confirman nuestra predicción de que las orugas elegirían comer una proporción mayor de hojas jóvenes recientemente desarrolladas en vez de hojas maduras, debido probablemente a menores defensas estructurales y mayor contenido nutritivo en las hojas jóvenes.

Palabras clave: Cuericí, defensas de plantas, crecimiento de plantas, compensación

Introduction

Most of the herbivory on a tropical leaf occurs during the short period of expansion (Coley and Barone 1996). Herbivores prefer these young leaves due in part to the higher nitrogen, water, and protein concentrations and less structural defense than in older leaves (Coley and Barone 1996). We predicted that caterpillars (Lepidoptera) would preferentially eat more of recently expanded *Begonia* sp. leaves than mature leaves in a cafeteria-style experiment.

Methods

At 1000 on 29 January 2009, we found a dense aggregation of an unidentified species of Lepidoptera caterpillars on a partly eaten *Begonia* sp. leaf in the primary forest east of Cuericí Biological Station in central Costa Rica, at an elevation of 2600 m. In the lab, we placed these 25 caterpillars with *Begonia* sp. leaves, allowed them to forage overnight, and noted the area each had eaten by morning. This confirmed that *Begonia* sp. was a food source for these caterpillars, and provided an estimate for the area each caterpillar would consume in one night. We assumed all *Begonia* leaves used for the experiment were the same species, based on leaf shape.

On the following evening, 30 January, we ran a cafeteria-style experiment, offering the caterpillars a choice between a young, recently expanded leaf and a mature leaf. For this experiment, we col-

lected 50 leaves of the same *Begonia* sp. from wild plants, choosing 25 recently expanded leaves and 25 mature leaves based on relative position on the plant, color, and toughness. We cut a 4-cm² square from an area of each leaf that had no prior herbivore damage. At 1700, we placed each caterpillar under one of 25 separate plastic bowls containing a square of recently expanded leaf and a square of mature leaf, making sure the leaf squares did not touch each other. We placed the caterpillar in a random orientation equidistant from each leaf. We left the bowls undisturbed until 0800 on 31 January (i.e. for a total of 15 hrs), and then counted the area eaten from each leaf square using a transparent grid of 6.25 mm² squares.

RESULTS

We calculated the difference between recently expanded leaf area eaten and mature leaf area eaten for each caterpillar. The distribution of this difference, which had a mean of 0.34 cm², was shifted significantly in a positive direction (away from the expected mean of 0 cm², which would have indicated equal consumption of each leaf type). This shift indicated that caterpillars ate more of the recently expanded leaves than the mature leaves ($t_{23} = 3.03$, $P = 0.003$; Fig. 1). For this analysis, we excluded one caterpillar, which did not eat either leaf square. Analyses were done in JMP v. 7.0 (SAS Institute, Inc. 2007).

DISCUSSION

The caterpillars preferred recently ex-

panded leaves to mature leaves when foraging in the lab setting, supporting our hypothesis and the synthesis of Coley and Barone (1996). We observed that in their natural habitat caterpillars considerably reduced the area on leaves where they aggregated. In the field, the caterpillars' herbivory patterns may depend on the proportions of recently expanded and mature leaves that they encounter. To see if lab results predict field patterns, a future study could investigate whether a caterpillar confined to two leaves on a wild plant in the field would prefer a recently expanded leaf to a mature one.

Juveniles of many Lepidoptera species aggregate during time of inactivity and while feeding, which increases their metabolic rate and growth, and may al-
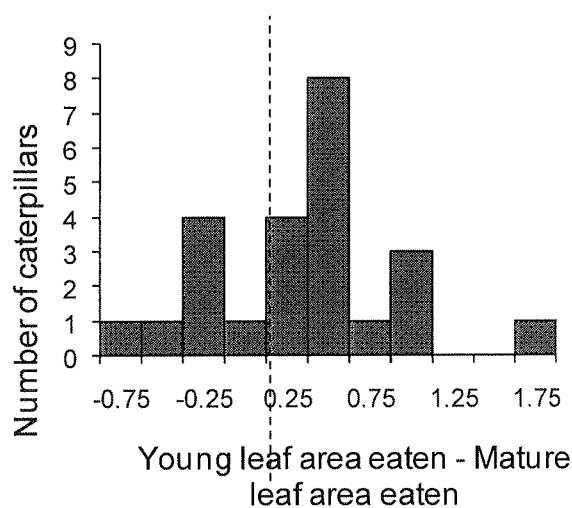
FIG. 1. Larvae of an unidentified lepidopteran ate significantly more recently expanded leaf area than mature leaf area in a cafeteria-style experiment run overnight in Cuericí (n = 24). Each larva had access to two 4-cm² *Begonia* sp. leaf squares, one newly expanded and one mature. The vertical line in this figure represents the expected mean of 0 cm², indicating equal consumption of each leaf type.

low increased leaf consumption (Stamp and Bowers 1990). When we first found them in the Cuericí forest, the caterpillars were tightly aggregated on a leaf. In the lab, when the caterpillars were not confined to their bowls, they attempted to aggregate. Preventing aggregation may have decreased the caterpillars' metabolic rates and leaf consumption, negatively impacting our results. In the field, the aggregation by caterpillars might result in damaging fewer leaves more, instead of distributing damage over many leaves. Another cafeteria-style experiment could determine whether aggregations of caterpillars show the same preferences for newly expanded leaves as individual caterpillars.

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Responsible resource use: Impact of a biological station and trout hatchery on stream macroinvertebrates

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Abstract: The Cuericí Biological Station is an ecological educational center that also works to practice sustainable land use and conservation in the Costa Rican highlands. We investigated the separate and combined impacts of Cuericí's septic and gray water systems, trout hatchery, and agricultural land use on aquatic organisms in the stream flowing through the station. We sampled three stream sites spanning the length of the station and its associated facilities. Macroinvertebrate abundance at the lower site was significantly higher than that of the upper and middle sites, suggesting that Cuericí is impacting the stream, mostly due to the input of nutrients from the trout aquaculture system. However, our results do not clearly indicate deterioration in stream health from upstream to downstream sites. Assessing the impact on the stream water beyond Cuericí would require additional sampling further downstream.

Key words: bioassessment, organic pollution, stream health, sustainable water use

Traducción al español en la página 101.

Introduction

Bioassessment uses aquatic macroinvertebrate communities to evaluate fresh water conditions, based on the different tolerances of invertebrate taxonomic groups to degradation of stream water quality (Patrick 1949). We investigated the effects of the Cuericí Biological Station on Quebrada Leones, a stream running through the property, using bioassessment and basic water quality measurements, at sites above, adjacent to, and below Cuericí's possible inputs (see Fig. 1). The owners and managers of Cuericí seek to provide resources for human consumption at the station while practicing sustainable land use and environmental stewardship (Post et al. 2007). Cuericí is located high in the watershed of the Cordillera de Talamanca and includes primary oak forest, a trout hatchery, and other agricultural land.

Cuericí's founder, Carlos Solano, recognizes the significance of the station's location at the stream's headwaters, and considers it an important responsibility to use water resources wisely and protect the health of aquatic ecosystems (C. Solano, personal communication.). One of Cuericí's founding missions is to demonstrate how human habitation does not have to come with environmental degradation.

Our objective was to investigate the water systems surrounding Cuericí, measure the impact of Cuericí on the stream, and determine which stream inputs from Cuericí systems are most re-

sponsible for these effects. Hereafter we refer to the station and associated pro- duction systems as "Cuericí". Based on information in Alexander et al. (2002), we
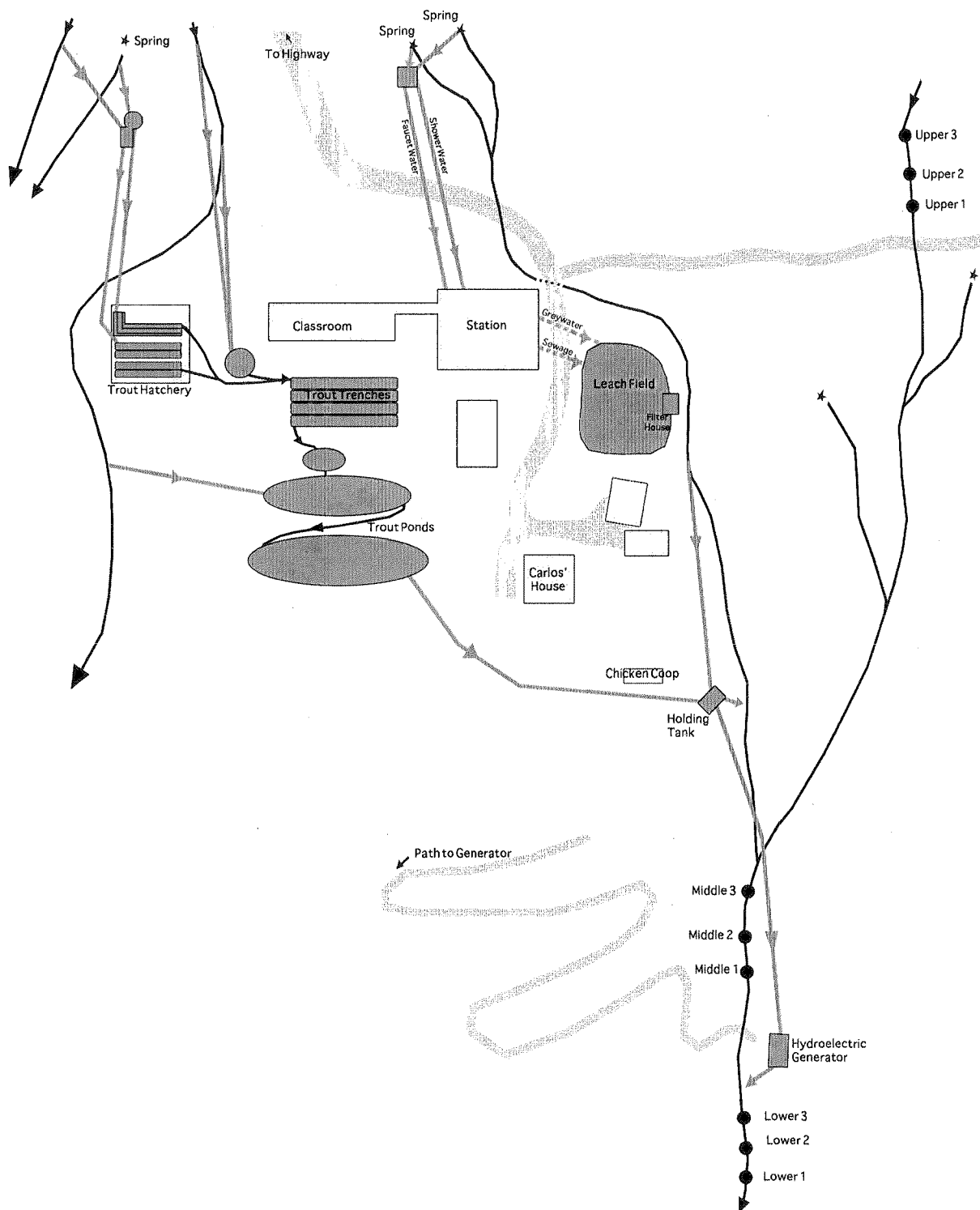
FIG. 1. Map of the Cuericí Biological Station showing streams in black, buildings in white, trout ponds in dark gray and roads and paths in pale gray. Sampling sites for invertebrates are labeled as points (Lower 1, etc.) on the major stream, the Quebrada Leones.

predicted that macroinvertebrate abundance and diversity would increase progressively from the site above Cuericí, downstream to the site below Cuericí. We expected this increase in macroinvertebrate abundance and diversity because nutrient inputs from Cuericí's land use and aquaculture should increase cumulatively in the downstream direction, supporting more autochthonous (within the stream) production in the stream and resulting in more food for the invertebrate community.

METHODS

Study System

The Cuericí Biological Station is at 2,600 masl near Cerro de la Muerte, in the San Jose province of Costa Rica. Several streams and springs that flow through Cuericí are used to supply water to the aquaculture system and for direct human use. One large stream (Quebrada

Leones) flows along the eastern length of the station and is susceptible to various inputs (Fig. 1). Septic and gray water from the station is filtered through a leachfield. Water from the trout system is combined with spring water in a settling tank that is piped to a hydroelectric generator and then returned to the stream. When water is abundant and the tank is above capacity, excess water also drains into the stream (Fig. 1). We designed our study to determine which sources of inputs (if any) from Cuericí significantly affect the stream macroinvertebrate community.

Field Methods

We chose three sites along the Quebrada Leones (Fig. 1). The upper site was just above the grassy, gravel access road that runs uphill northeast from the station, and is therefore not affected by inputs from Cuericí. The middle site was just below the confluence of the main

TABLE 1. Diversity and impact measures for invertebrate communities at three sites along Quebrada Leones spanning the Cuericí Biological Station (n = 3 samples per site). The tolerance values are used in calculations of the Family Biotic Index (FBI). Higher values of tolerance indicate greater tolerance to pollution (Hilsenhoff 1988). Parentheses indicate averaged values across samples before rarefaction. Statistical analyses were run after rarefaction.

	Upper Site	Middle Site	Lower Site
Total Abundance	51	44	180**
Rarefied Richness	9.76 (10.33)	6.43* (6.67)	8.83 (10.33)
Rarefied Diversity	1.71 (1.73)	1.44* (1.46)	1.86 (1.95)
Rarefied Evenness	0.75 (0.74)	0.79 (0.79)	0.86 (0.84)
Family Biotic Index (FBI)	3.17	3.54	4.11†
Proportion EPT	0.65	0.67	0.65
Dominant Family	Lepidostomatidae	Lepidostomatidae	Baetidae
% Dominance	45.6	35.7	26.5
Tolerance Value	1.00	1.00	4.64

spring with the stream, where any possible pollutants from Cuericí, other than the main inflow of trout water (Fig. 1), were likely to be present. Pollutants entering above the middle site may include (1) filtrate from the leachfield which includes separated pathways to process gray water and sewage waste from the station, (2) the waste of grazing animals that are all on open pasture, and (3) a small inflow of water from the trout ponds. The lower site was just downstream of the output from the hydroelectric generator; this site receives (in addition to the above inputs) the main outflow from the trout ponds and some water taken directly from the main spring above (Fig. 1). Thus, this site experiences the cumulative effects of all pollutants from Cuericí that may flow into the stream.

At each site along the stream, we chose three separate sampling pools at least 4 m apart. We measured pH, dissolved oxygen, and temperature in each pool using a Milwaukee SM102 pH meter and a SM600 Dissolved Oxygen meter. We kick-net sampled aquatic macroinvertebrates once in each pool for 60 seconds, using a 30 cm edged D-net with 2 mm mesh. Our kick-net sampling included stirring up benthic material and passing our hands over the surfaces of rocks to remove attached organisms. Pools were sampled moving upstream, to avoid any disturbance-related bias in downstream sample sites.

Each sample was haphazardly poured onto a grid divided into eight equal sections. We randomly selected one section at a time and removed invertebrates for counting and identification to family. We randomly selected more sections as needed, until we reached 50 individuals. To estimate the total number of macroinvertebrate abundance in each sample, we multiplied the number of macroinvertebrates counted by 8/ (number of sample sections counted).

Data Analysis

To assess the effect of Cuericí on stream health we calculated the abundance, family richness, evenness, and Shannon-Wiener diversity index for each site. We also calculated the FBI (Family Biotic Index), percent EPT index (Ephemeroptera, Plecoptera and Trichoptera), and the percent of total individuals in the most common (dominant) family. Together these indices gave us a more comprehensive picture of stream health than any one alone. FBI assigns a pollution tolerance value to each invertebrate family and is weighted by the proportion of total individuals in that family. The family tolerance values have been determined in the literature (Hilsenhoff 1988). Higher tolerance values are pre-assigned to families less sensitive to pollution, while low values are assigned to sensitive families. Thus, lower FBI values indicate a healthier stream. Percent EPT is the combined relative abundance of three invertebrate orders that are intolerant to pollution: Ephemeroptera, Plecoptera and Trichoptera. A higher EPT value indicates a healthier stream (Taylor 2007).

Percent of total individuals in the
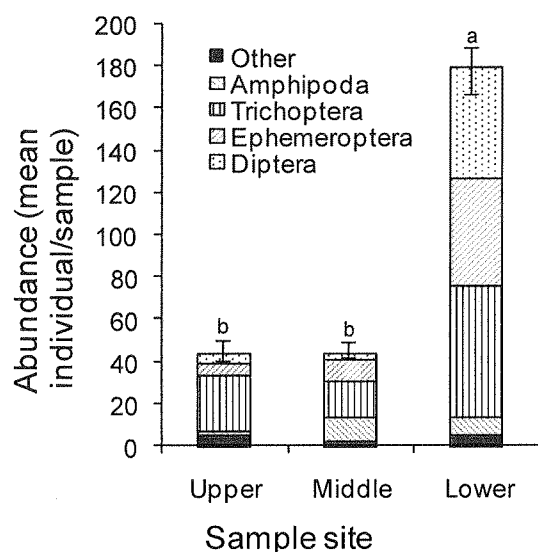
FIG. 2. Mean macroinvertebrate abundance for dominant taxa across sites along Quebrada Leones spanning the Cuericí Biological Station (n=3 samples per site). Different letters above bars signify that means are significantly different (p = .05). Bars are mean ± 1 S.E.

dominant family provides an index of evenness; a lower value indicates a more even distribution of individuals among species, which corresponds to greater stream health (Taylor 2007).

We also classified each family into one of four functional feeding groups: 1) Collector/Shredder/Scavenger, 2) Scraper, 3) Filter-feeder, 4) Predator (Pennak 1953; Dudgeon 2008). We compared the relative abundances of these groups among the sites. Differences in the relative abundances of these foraging guilds can indicate differences in resource availability in the stream. Higher relative abundance of Collectors, Shredders, and Scavengers indicates that more resources are derived from allochthonous inputs (i.e. from outside the stream). Greater relative abundance of Scrapers and Filter-feeders indicates a greater im-

portance of autochthonous (within stream) primary production.

We used an ANOVA F-test and Tukey's HSD to determine whether the means of abundance and diversity indices were different among sites. Because some samples contained fewer than 50 macroinvertebrates, we rarefied our data to the lowest number of macroinvertebrates found in any sample, before calculating diversity, richness, and evenness indices. We used Ecosim v. 7.72 (Acquired Intelligence Inc. 2005) for rarefaction and JMP 7 (SAS Institute, Inc. 2007) for statistical tests.

RESULTS

The mean total abundance of macroinvertebrates in the lower site was four to five times greater than in the middle or upper sites ($F_{2,6}$ = 21.54, P = 0.0018, Fig. 2). The lower site had significantly greater (rarefied) richness and diversity than the middle site ($F_{2,6}$ = 7.09, P = 0.0263, and $F_{2,6}$ = 5.49, P = 0.0441 respectively, Table 1). Although differences among sites for the FBI, evenness, and percent EPT indices were not significant (FBI: $F_{2,6}$ = 3.82, P = 0.085; evenness: $F_{2,6}$ = 1.32, P = 0.335; EPT: $F_{2,6}$ = 0.05, P = 0.951), sample means of FBI and evenness increased from the upper to lower site, while there was no trend in percent EPT.

In terms of community structure, the proportional abundance of Collectors/Shredders/Scavengers was at least twice as great in upper and middle sites compared to the lower site (Fig. 3). The lower site contained seven to twenty times

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more filterers, and two to three times more predators than the middle and upper sites respectively (i.e. by numbers of organisms, not morphotypes; Fig. 3).

DISCUSSION

The difference in macroinvertebrate abundance between the lower and upper sites shows that the Cuericí Biological Station is having an effect on the stream. The similarity in abundance between the middle and upper sites suggests that the leachfield, livestock around the station, and the small amount of trout water overflow have minimal effects. Based on these findings, the leachfield system appears to be effective at keeping the station's sewage and gray water pollutants from entering the stream.

The higher proportional abundance of predators in the lower site suggests that it is more productive overall. The higher proportional abundance of collectors, shredders, and scavengers in both the middle and upper sites suggests that these communities are more dependent on autochthonous (internally produced) primary production than at the lower site. The marked increase in proportional abundance of filterers in the lower site further indicates that there is more autochthonous production below the station and its associated production systems.

However, the effect of Cuericí on macroinvertebrate diversity and evenness is less clear. These values are lowest in the middle site, suggesting an effect from either the leachfield or the incoming spring water. However, since diversity and evenness does not significantly differ between the upper and lower sites, it appears any such effect on the middle site is
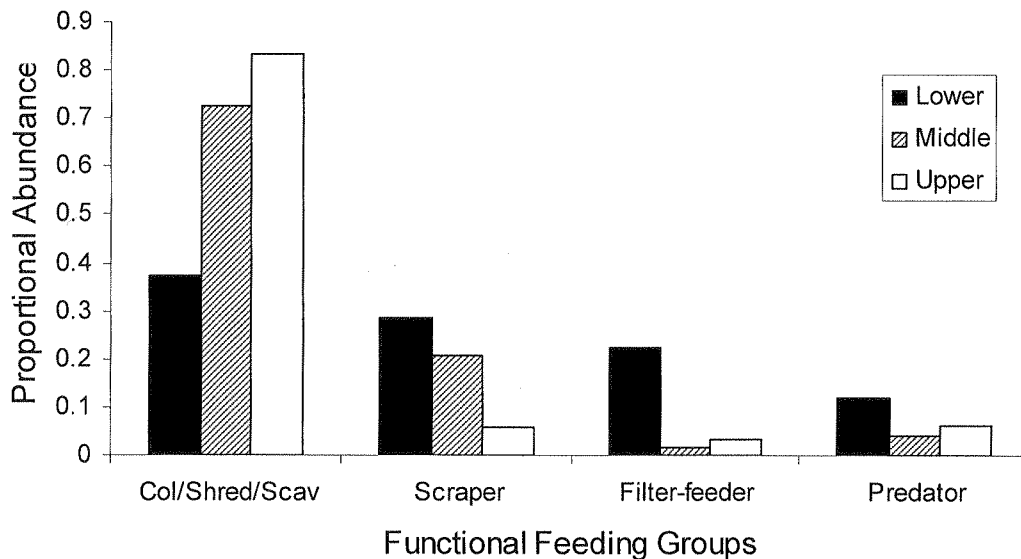
FIG. 3. Proportional abundances (by numbers of individuals) of four macroinvertebrate functional feeding groups at three sites along Quebrada Leones spanning the Cuericí Biological Station (n = 3 samples per site). The lower site had the smallest proportion of Collectors/Shredders/Scavengers and the greatest proportions of Scrapers, Filter-feeders, and Predators.

transient. Overall, our findings suggest that the large inflow of water from the trout hatchery system (via the hydroelectric generator) is having the greatest effect on the stream.

These inputs from the trout hatchery to the stream are probably in the form of nutrients from trout food and excretion. At 2,600 masl, stream headwaters are probably nutrient poor, so adding nutrients is likely to increase the abundance and diversity of aquatic life (Dudgeon 2008). Further study would be needed to measure Cuericí's organic and inorganic inputs to the stream.

Conclusion

Cuericí's goal is to balance human needs with conservation through the sustainable use of natural resources, recognizing that humans cannot exist in isolation from the environment. We found that Cuericí's activities do influence the invertebrate communities in the stream, most likely through the inflow of nutrients from the trout aquaculture system. Macroinvertebrate abundance strongly increases after the inflow of trout water; however, we found no clear evidence of detrimental effects on the stream's overall health. The increase in evenness downstream suggests an improvement of stream health, while the increase in FBI index downstream from 3.1 to 4.1 suggests a slight decrease in the stream's health from an unimpacted to a slightly impacted stream (Hilsenhoff 1988). Perhaps the most important follow-up to this study would be to determine whether the changes we found at the

lower site persist downstream of the station and the trout aquaculture system. If they do, Cuericí would be contributing to any cumulative effects that human activities along the stream may have on aquatic life and people downstream. However, if the effects we documented dissipate rapidly, Cuericí may have no negative impact on water quality downstream.

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TABLE 2. Numbers of macroinvertebrates by family sampled at three sites along Quebrada Leones spanning the Cuericí Biological Station (n = 3 samples per site). "Tolerance" refers to the tolerance values of pollution used for calculation of the Family Biotic Index (FBI) (Hilsenhoff 1988).

Order	Family	Tolerance	Upper Site	Middle Site	Lower Site
Amphipoda	Gammaridae	5.75	24	32	25
Coleoptera	Elmidae	3.81	1	0	4
Coleoptera	Psephenidae	4.25	1	0	0
Coleoptera	Unidentified	4.00	2	1	0
Diptera	Chironomidae	5.86	3	0	45
Diptera	Culicidae	6.50	5	0	0
Diptera	Simuliidae	6.25	0	2	109
Diptera	Tabanidae	5.00	1	0	4
Diptera	Tipulidae	4.40	7	6	0
Ephemeroptera	Baetidae	4.64	8	26	140
Ephemeroptera	Ephemeridae	4.00	1	0	4
Ephemeroptera	Leptophlebiidae	3.40	6	6	8
Isopoda	Asellidae	7.50	5	2	4
Plecoptera	Perlidae	1.46	6	4	7
Rhynchobdellida	Glossiphoniidae	6.50	1	0	0
Trichoptera	Helicopsychidae	3.00	0	1	9
Trichoptera	Hydropsychidae	4.17	0	0	11
Trichoptera	Lepidostomatidae	1.00	71	48	95
Trichoptera	Eptoceridae	4.29	9	1	19
Trichoptera	Rhyacophilidae	1.40	1	1	55

Uso responsable de recursos: El impacto de una estación biológica y criadero de truchas en macroinvertebrados acuáticos

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Resumen: Las Estación Biológica Cuericí es un centro educativo que trabaja en la práctica del uso sustentable y conservación de recursos en las tierras altas de Costa Rica. Investigamos los impactos de los sistemas sépticos y de aguas grises, criadero de truchas y uso agrícola de la tierra (check the use of the word "gray" in English version) en la quebrada que cruza la estación, muestreando tres sitios a lo largo ésta y en instalaciones adyacentes. La abundancia de macroinvertebrados en el sitio aguas abajo fue significativamente más alto que el de los sitios arriba e intermedio. Nuestros resultados sugieren que Cuericí impacta la quebrada, principalmente por el aporte de nutrientes del sistema de acuacultura de truchas. Sin embargo, nuestros resultados no indican claramente el deterioro en la salud de la quebrada de sitios aguas arriba a sitios aguas abajo. Determinar el impacto en la quebrada más allá de Cuericí requeriría muestras adicionales que se extiendan aguas abajo.

Palabras clave: bioevaluación, contaminación orgánica, salud de la quebrada, uso sostenible del agua

Introduccion

Las bioevaluaciones usan comunidades de macroinvertebrados para evaluar las condiciones de cuerpos de agua dulce, basados en la tolerancia diferencial de grupos taxonómicos a la degradación de la calidad del agua de las quebradas (Patrick 1949). Investigamos los efectos de la Estación Biológica Cuericí en la quebrada Leones, un arroyo cercano, utilizando una bioevaluación y mediciones básicas de la calidad del agua en sitios arriba, adyacentes y debajo de posibles aportes de Cuericí (Fig. 1). El dueño y el gerente de Cuericí buscan proporcionar recursos para el consumo humano en la estación mediante la práctica del uso sustentable de la tierra y el cuidado ambiental (Post et al. 2007). Cuericí se ubica a lo alto de una cuenca en la Cordillera de Talamanca e incluye bosque de roble primario, un criadero de truchas y tierras agrícolas.

Carlos Solano, el fundador de Cuericí, reconoce el significado de la localización de la estación en las parte alta de la cuenca regional y considera como responsabilidades vitales el uso inteligente del recurso hídrico y la protección de los ecosistemas acuáticos (C. Solano, com. pers.) Una de las misiones fundamentales de Cuericí es demostrar cómo la habitación humana no tiene que tener el costo de la degradación ambiental.

Nuestro objetivo fue investigar los

sistemas acuáticos que rodean a Cuericí, medir el impacto de Cuericí en la quebra- da y determinar qué aportes de los siste- mas de Cuericí son mayormente respon-
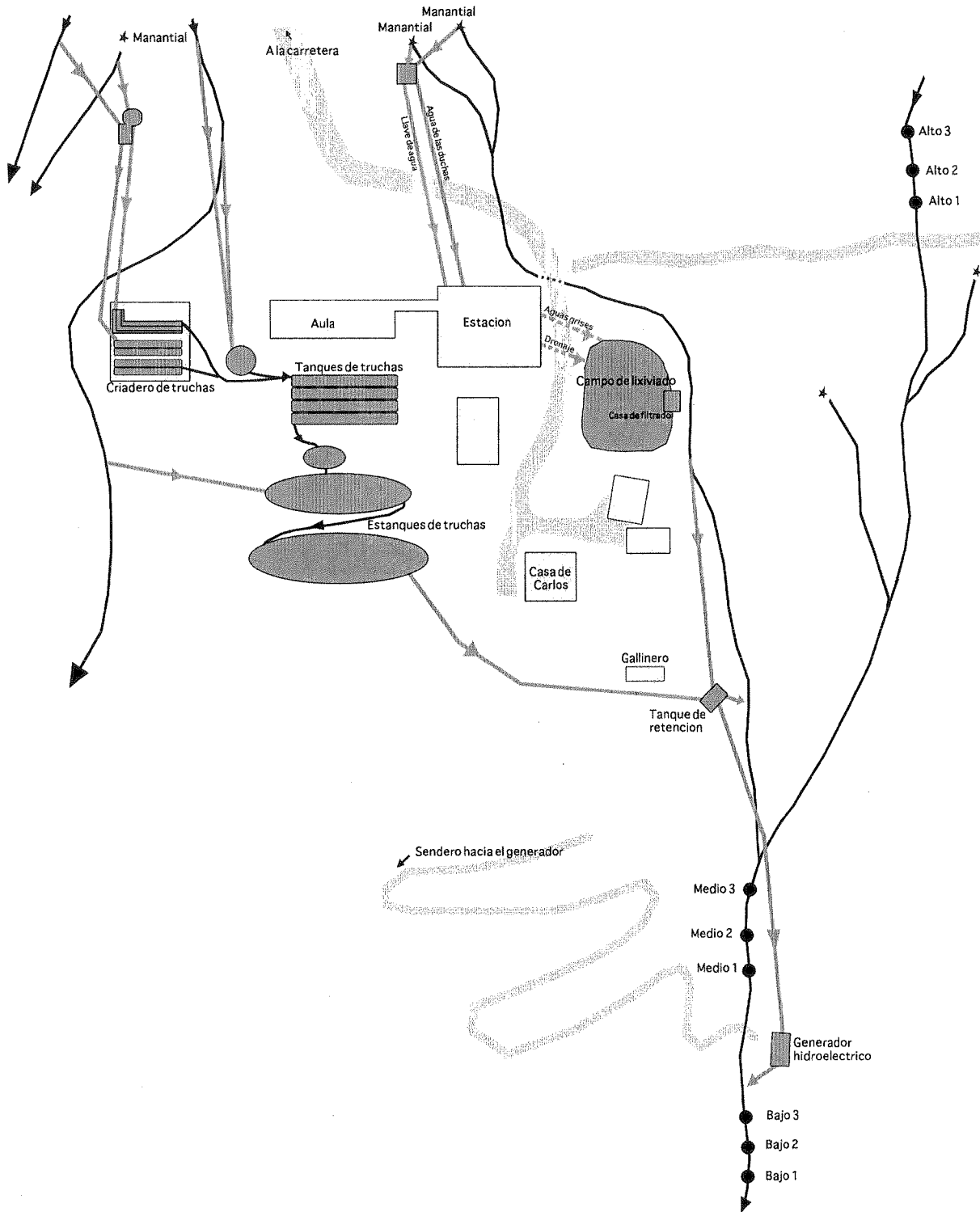
FIG. 1. Mapa de la Estación Biológica Cuericí mostrando las quebradas en negro, edificios en blanco, estanques de truchas en gris oscuro (check "gray" in original) y caminos y senderos en gris pálido. Los sitios de muestreo de invertebrados están marcados como puntos (Bajo 1, etc.) en la quebrada.

TABLA 1. Diversidad y medidas de impacto en comunidades de invertebrados en tres sitios a lo largo de la quebrada Leones, Estación Biológica Cuericí (n=3 muestras por sitio). Los valores de tolerancia son usados en los cálculos del Índice de Familias Bióticas (IFB). Los valores de tolerancia más altos indican mayor tolerancia a la contaminación (Hilsenhoff 1988). Los paréntesis indican los valores promedio de las muestras antes de rarificar. Los análisis estadísticos fueron hechos después de la rarefacción.

	Sitio Superior	Sitio Medio	Sitio Inferior
Abundancia Total	51	44	180**
Riqueza Rarificada	9.76 (10.33)	6.43* (6.67)	8.83 (10.33)
Diversidad Rarificada	1.71 (1.73)	1.44* (1.46)	1.86 (1.95)
Homogeneidad Rarificada	0.75 (0.74)	0.79 (0.79)	0.86 (0.84)
Índice de Familias Bióticas (IFB)	3.17	3.54	4.11†
Proporción EPT	0.65	0.67	0.65
Familia Dominante	Lepidostomatidae	Lepidostomatidae	Baetidae
% Dominancia	45.6	35.7	26.5
Valor de Tolerancia	1.00	1.00	4.64

sables de estos efectos. En adelante, nos referimos a la estación y los sistemas de producción asociados como "Cuericí". Basados en la información de Alexander et al. (2002), nuestra predicción fue que la abundancia y diversidad de macroinvertebrados se incrementaría progresivamente desde el sitio aguas arriba hasta el sitio aguas abajo de Cuericí. Esperamos este incremento en la abundancia y diversidad de macroinvertebrados porque los aportes de nutrientes del uso del suelo en Cuericí y acuacultura se deberían incrementar cumulativamente en la misma dirección que el flujo de aguas, proveyendo una mayor producción autóctona (productividad primaria independiente de aportes externos) en la quebrada y resultando en más alimento para la comunidad de invertebrados.

MÉTODOS

Sistema de estudio

La Estación Biológica Cuericí se ubica a 2,600 msnm cerca de Cerro de la Muerte, en la provincia de San José, Costa Rica. Varias quebradas y manantiales que fluyen a través de Cuericí son utilizados para proveer de agua al sistema de acuacultura y para uso humano directo. Una quebrada grande fluye a lo largo del límite oriental de la estación y es susceptible a varios aportes. Las aguas grises y sépticas son filtradas a través de un campo de lixiviado cercano. El agua del sistema de truchas es combinada con agua de manantial en un tanque de sedimentación que es entubada hacia un generador hidroeléctrico y regresada a la quebrada. Cuando el agua es abundante y el tanque está arriba de su capacidad, el exceso se drena a un manantial que finalmente fluye a la quebrada (Fig. 1). Diseñamos nuestro estudio para determinar cuáles aportes de Cuericí (si los hubiere), afectarían significativamente la comunidad de macroinvertebrados.

Métodos de campo

Elegimos tres sitios a lo largo de la quebrada al este de Cuericí (Fig. 1). El sitio superior esta justo arriba del camino de acceso con pasto que corre cuesta arriba al noreste de la estación y por tanto no es afectado por aportes de Cuericí. El sitio intermedio está justo después de la unión del manantial principal con la quebrada, donde cualquier contaminante posible de Cuericí, diferente al aporte principal de agua de las truchas, está presente con mayor probabilidad. Los contaminantes que ingresan arriba del sitio intermedio pueden incluir (1) aportes del campo de lixiviado que usa sistemas separados para procesar aguas grises y desechos de drenaje de la estación, (2) el desecho de animales que pastorean a campo abierto y (3) un pequeño aporte de agua de los estanques de truchas. El sitio inferior esta justo debajo de la salida del generador hidroeléctrico; este sitio recibe (adicionalmente a los aportes anteriores) agua de los estanques de truchas y agua tomada directamente del manantial principal arriba (Fig.1). Este sitio experimenta el efecto cumulativo de todos los contaminantes de Cuericí que pudieran llegar a la quebrada.

En cada sitio a lo largo de la quebrada, escogimos tres remansos separados por al menos 4 m de distancia. Medimos el pH, oxígeno disuelto y temperatura en cada remanso utilizando un medidor de oxígeno disuelto Milwaukee SM600 y un medidor de pH SM102. Muestreamos macroinvertebrados acuáticos a través de redes de golpeteo en cada remanso, usando una red "D" de 30 cm con malla de 2 mm por 60 seg para obtener una muestra en cada sitio. Nuestro muestreo de golpeteo incluye agitar material béntico y tallar la superficie de las piedras. Los remansos fueron muestreados de abajo hacia arriba para evitar afectar los sitios de muestreo aguas abajo.

Cada muestra fue mezclada y vaciada en un cuadrante dividido en ocho secciones iguales. Cada sección fue elegida aleatoriamente por turno y los invertebrados fueron sustraídos para cuantificarlos e identificarlos hasta familia. Más secciones fueron seleccionadas aleatoriamente, una por turno, hasta que alcanzamos 50 individuos.

Análisis de datos

Para estimar la abundancia de macroinvertebrados en cada remanso, multiplicamos el número de individuos cuantificados por ocho (número de secciones de la muestra que fueron cuantificados). Para determinar el efecto de Cuericí en la salud de la quebrada, calculamos la abundancia, riqueza por familia, uniformidad y el índice de diversidad de Shannon-Wiener para cada sitio. También calculamos el IFB (Índice de Familias Bióticas), porcentaje EPT (Ephemeroptera, Plecoptera y Trichoptera) y el porcentaje total de individuos en la familia dominante. Estos índices nos dieron una imagen más completa de la salud de la quebrada que cualquiera de ellos por separado. El IFB determina un valor de tolerancia a cada familia de invertebrados y es este es ponderado en base a la proporción del total de indivi-
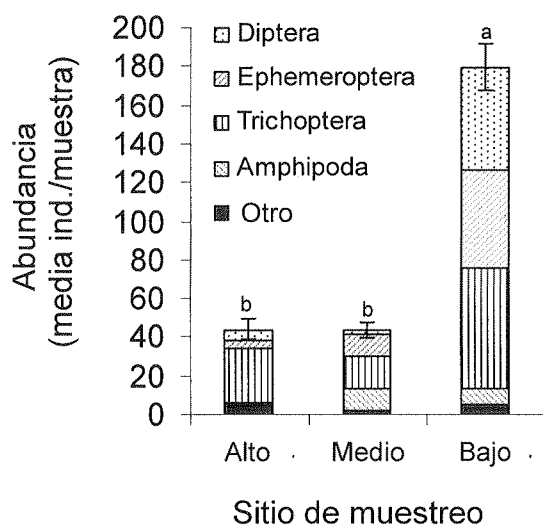
FIG. 2. Abundancia media de macroinvertebrados de los taxa dominantes a lo largo de la Quebrada Leones en la Estación Biológica Cuericí (n = 3 muestras por sitio). Las diferentes letras sobre cada una de las barras significan que las medias son significativamente diferentes (α =0.05). Las barras de error representan una desviación estándar.

duos en dicha familia (Hilsenhoff 1988). Los valores de tolerancia más altos están pre-asignados a familias menos sensibles a la contaminación, mientras que los valores bajos están asignados a familias sensibles. Así, los valores más bajos de IFB indican una quebrada más sana. El porcentaje de EPT es la abundancia relativa de los tres órdenes de invertebrados que son intolerantes a la contaminación: Ephemeroptera, Plecoptera y Trichoptera. Un valor más alto de EPT indica una quebrada más sana (Taylor 2007).

También clasificamos cada familia en uno de cuatro grupos funcionales de forrajeo: 1) Recolector/Desmenuzador/ Carroñero, 2) Raspador, 3) Filtrador, y 4) Depredador (Dudgeon 2008 y Pennak 1953). Comparamos la abundancia relativa de esos grupos entre sitios. La diferencia en abundancias relativas entre estos gremios de forrajeo puede indicar diferencias en la disponibilidad de recursos en la quebrada. Una mayor abundancia relativa de Recolectores, Desmenuzadores y Carroñeros indica que más recursos se originan de aportes alóctonos (e.g. vienen de fuera de la quebrada). Una mayor abundancia relativa de Raspadores y Filtradores indica una mayor importancia de producción primaria autóctona (del interior de la quebrada).

Hicimos pruebas F del Análisis de Varianza (ANOVA) y de "Diferencias Honestamente Significativas" (DHS) de Tukey para determinar si las medias de abundancia y los índices de diversidad fueron diferentes entre sitios. Debido a que algunas muestras contenían menos de 50 macroinvertebrados, rarificamos nuestros datos al límite inferior del número de macroinvertebrados encontrados en cualquier muestra, antes de calcular diversidad, riqueza y homogeneidad. Utilizamos Ecosim v. 7.72 (Acquired Intelligence Inc. 2005) para rarificar y JMP 7 (SAS Institute, Inc. 2007) para análisis estadísticos.

RESULTADOS

La media de abundancia total de macroinvertebrados en el sitio inferior fue cuatro a cinco veces mayor que en los sitios medio y superior. ($F_{2,6}$= 21.54, P = 0.0018, Fig. 2). Adicionalmente, el sitio inferior tuvo una riqueza y diversidad (rarificada) mayor que el sitio medio ($F_{2,6}$ = 7.09, P = 0.0263, y $F_{2,6}$= 5.49, P = 0.0441,

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respectivamente, Tabla 1). Aunque las diferencias entre sitios para los índices IFB, homogeneidad y porcentaje de EPT no fueron significativas, la media de IFB y homogeneidad se incrementaron del sitio superior al inferior, mientras el porcentaje de EPT no mostro una tendencia consistente.

En términos de estructura de comunidades, la proporción de Recolectores/ Desmenuzadores/Carroñeros fue al menos el doble en el sitio superior y medio comparado con el sitio inferior (Fig. 3). El sitio inferior tuvo 7-20 veces más Filtradores, y tres y dos veces más Depredadores que los sitios medio y superior respectivamente (Fig. 3).

DISCUSIÓN

La diferencia en la abundancia de macroinvertebrados entre los sitios inferior y superior muestra que la Estación Biológica Cuericí tiene un efecto en la quebrada. La similitud en abundancia entre los sitios medio y superior sugiere que el campo de lixiviado, el ganado en la periferia de la estación y la pequeña cantidad de agua que se derrama de las truchas tienen efectos mínimos. En base a estos hallazgos, el sistema del campo de lixiviado parece ser efectivo en evitar que el drenaje y los contaminantes de aguas grises lleguen a la quebrada.

La mayor abundancia proporcional de Depredadores en el sitio inferior sugiere que éste es el más productivo de todos. La mayor abundancia proporcional de Recolectores, Desmenuzadores y Carroñeros en los sitios medio y superior sugiere que estas comunidades son más dependientes de productividad primaria autóctona (producida al interior) que en
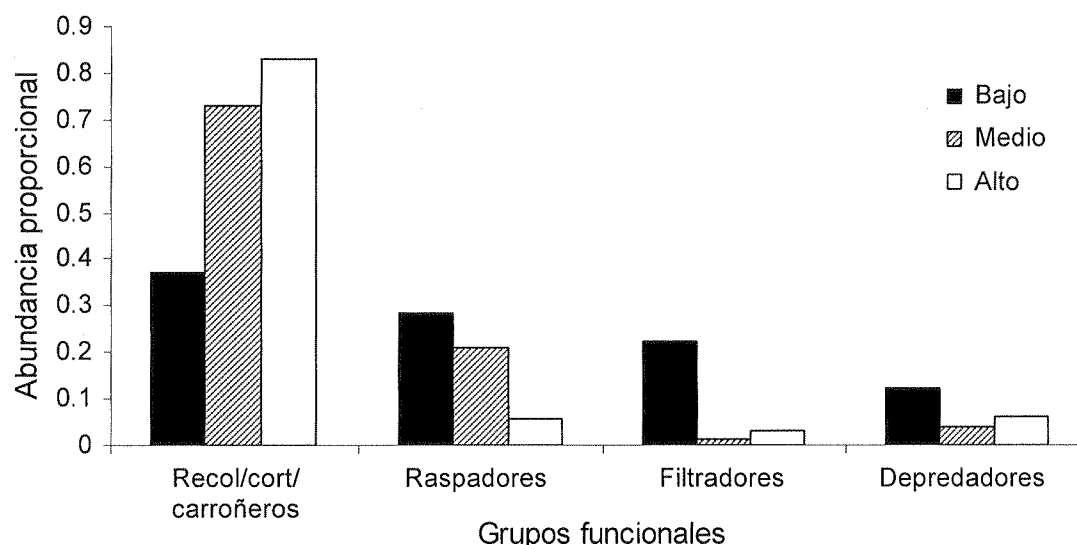
FIG. 3. Abundancias proporcionales de cuatro grupos funcionales de forrajeo en tres sitios en la Quebrada Leones a lo largo de la Estación Biológica Cuericí (n = 3 muestras por sitio). El sitio inferior tuvo la menor proporción de Recolectores/Desmenuzadores/Carroñeros y las más grandes proporciones de Raspadores, Filtradores y Depredadores.

el sitio inferior. El marcado incremento en la abundancia proporcional de filtradores en el sitio inferior es indicador de una mayor producción autóctona debajo de la estación y los sistemas de producción asociados.

Sin embargo, el efecto de Cuericí en la diversidad y homogeneidad de macroinvertebrados es menos clara. Estos valores, más bajos en el sitio intermedio, sugieren que el campo de lixiviado los afecta. Otra alternativa es que los aportes de agua de manantial puedan ser los responsables. Aun así, debido a que la diversidad y homogeneidad se recuperan en el sitio inferior, pareciera que este efecto es pasajero. En conjunto, nuestros hallazgos sugieren que los grandes flujos de agua del sistema de cría de truchas (vía generador hidroeléctrico) tienen el mayor efecto en la quebrada.

Los aportes del criadero de truchas a la quebrada son probablemente nutrientes del alimento de las truchas y sus excretas. Ubicado a 2,600 msnm, el sitio de origen de la quebrada es probablemente

TABLA 2. Número de invertebrados por familia muestreados en tres sitios a lo largo de la quebrada Leones, Estación Biológica Cuericí (n = 3 muestras por sitio). "Tolerancia" se refiere a los valores de tolerancia a la contaminación usados en el cálculo de Índice de Familias Bióticas (IFB) (Hilsenhoff 1988).

Orden	Familia	Tolerancia	Sitio Superior	Sitio Medio	Sitio Inferior
Amphipoda	Gammaridae	5.75	24	32	25
Coleoptera	Elmidae	3.81	1	0	4
Coleoptera	Psephenidae	4.25	1	0	0
Coleoptera	Unidentified	4.00	2	1	0
Diptera	Chironomidae	5.86	3	0	45
Diptera	Culicidae	6.50	5	0	0
Diptera	Simuliidae	6.25	0	2	109
Diptera	Tabanidae	5.00	1	0	4
Diptera	Tipulidae	4.40	7	6	0
Ephemeroptera	Baetidae	4.64	8	26	140
Ephemeroptera	Ephemeridae	4.00	1	0	4
Ephemeroptera	Leptophlebiidae	3.40	6	6	8
Isopoda	Asellidae	7.50	5	2	4
Plecoptera	Perlidae	1.46	6	4	7
Rhynchobdellida	Glossiphoniidae	6.50	1	0	0
Trichoptera	Helicopsychidae	3.00	0	1	9
Trichoptera	Hydropsychidae	4.17	0	0	11
Trichoptera	Lepidostomatidae	1.00	71	48	95
Trichoptera	Eptoceridae	4.29	9	1	19
Trichoptera	Rhyacophilidae	1.40	1	1	55

pobre en nutrientes y la adición de nutrientes puede incrementar la abundancia y diversidad de vida acuática (Dudgeon 2008: 232). Se requieren más estudios para medir los aportes orgánicos e inorgánicos de Cuericí a la quebrada.

Conclusión

La meta de Cuericí es balancear las necesidades humanas con la conservación a través del uso sustentable de recursos naturales, reconociendo que los humanos no pueden existir aislados de su ambiente. Encontramos que las actividades de Cuericí influencian la composición de invertebrados en la quebrada, muy posiblemente a través del flujo de nutrientes del sistema de acuacultura de truchas. La abundancia de macroinvertebrados se incrementa fuertemente después del flujo de agua de las truchas, sin embargo, no encontramos evidencia clara de efectos negativos en la salud total de la quebrada. El incremento de homogeneidad aguas abajo sugiere mejoras en la salud de la quebrada, mientras que el incremento del índice IFB aguas abajo, de 3.1 a 4.1, sugiere un ligero decremento en la salud de la quebrada de "no impactada" a "ligeramente impactada" (Hilsenhoff 1988). Quizá la más importante secuela a este estudio será determinar si los cambios encontrados en el sitio inferior persisten aguas abajo del sistema de acuacultura de truchas. De ser así, Cuericí podría estar contribuyendo a los efectos cumulativos de otras actividades humanas en la vida acuática de la quebrada. Sin embargo, si los efectos que documentamos se disipan rápidamente, Cuericí podría no tener impactos negativos en la calidad del agua en la parte baja de la quebrada.

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TROUT HATCHERY WATER QUALITY MONITORING: A BASELINE STUDY

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Faculty Editor: David R. Peart

Abstract: There is potential for Dartmouth FSP students to conduct an ongoing monitoring program of water quality at the Cuericí Biological Station. Information about changes in water quality over time, in both the nearby streams and the trout aquaculture system, will be useful for management. In this preliminary study we measured dissolved oxygen, pH, and water temperature in all of the sources, tanks and ponds of the trout aquaculture system to assess the water quality throughout. Because there is evidence that trout outflows have greater impact on stream water than any other activities at the station, monitoring water quality over time within the trout aquaculture system will be important to evaluate and control human impact on stream water in the future.

Key words: hatchery, sustainability, nutrient cycling

Traducción al español en la página 116.

STUDY SYSTEM

The Cuericí Biological Station is 2,600 masl in the San Jose province of Costa Rica, near Cerro de la Muerte. Cuericí provides services for visiting scientists and students to stay and study on the property, and also includes a working farm and trout hatchery. The trout hatchery produces fish for local use and consumption, year round. Susman et al. (2009) includes a full description of human activities at Cuericí that may influence water quality, and the locations of potential inflows to the springs and creeks around the station (see Fig. 1 in Susman et al. 2009).

Water entering the trout aquaculture system comes from the springs and creeks near Cuericí (Fig. 1, 1-3). The water flows through a series of trout tanks (Fig. 1, 4-9), trenches (Fig. 1, 10-13), and ponds (Fig. 1, 14-16) and then into a settling tank (Fig. 1, 17). We observed that when water flow is high the settling tank overflows, trickling into the nearby stream. Outflow from the trout ponds that does not overflow combines with stream water and is piped through the hydroelectric generator and finally into the stream.

SAMPLING METHODS

We took dissolved oxygen (DO), pH, and temperature measurements at each stage of the flow of water through the trout aquaculture system. At each of the water sources, we took measurements at only one point. For each of the tanks, trenches and ponds, we measured at two points: the inflow and outflow (Fig. 1). We took two sets of measurements, one on the evening of 29 January 2009 and
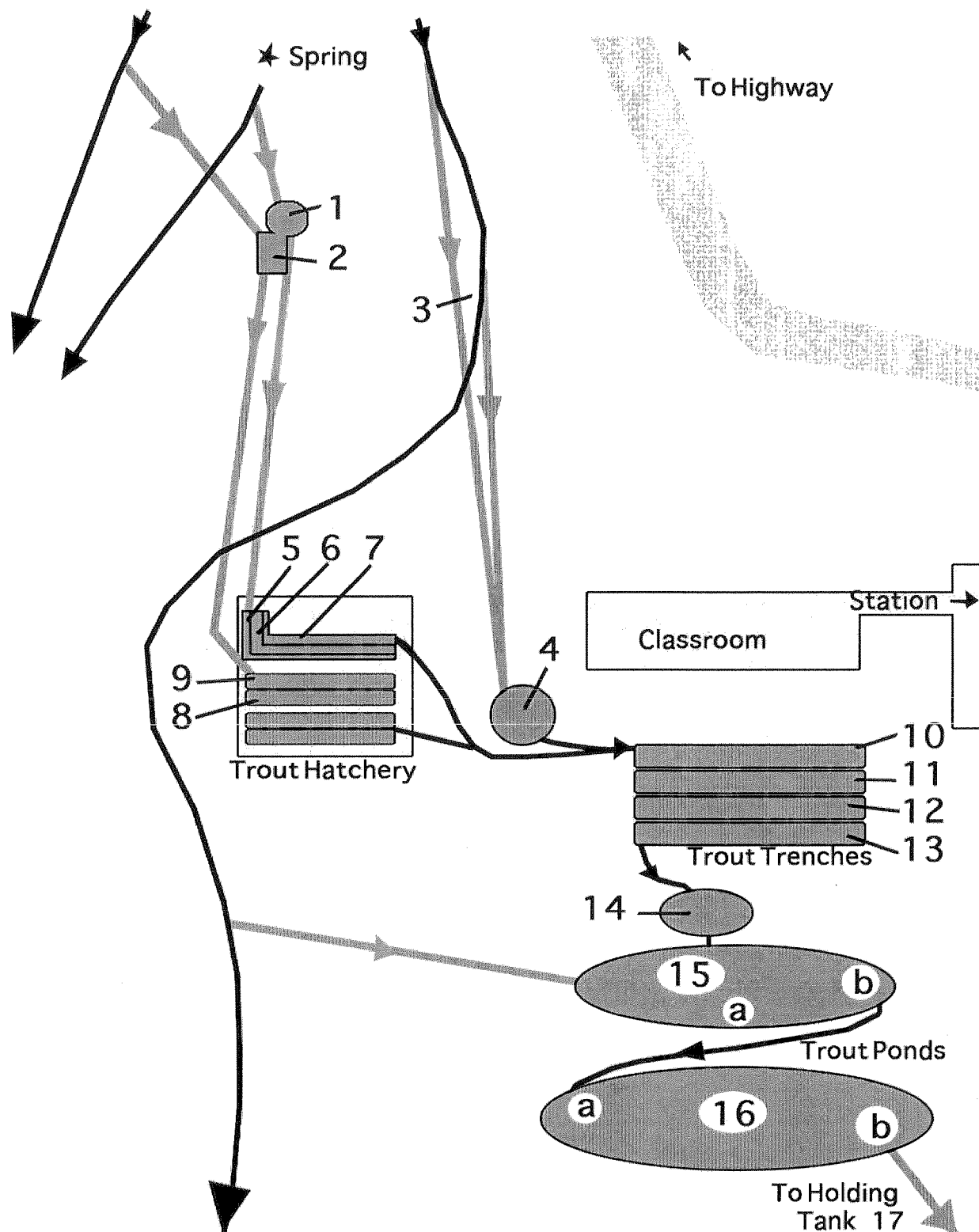
FIG. 1. Map of the Cuericí Biological Station showing streams in black, buildings in white, trout ponds in dark gray and roads and paths in pale gray. Sampling sites are numbered sequentially in the downstream direction as water flows into and through the trout aquaculture system; "a" indicates inflow measurement location and "b" outflow (see Table 1). All sampling sites labeled with points on the stream. (Note: we took all measurements on the downhill side; 15a was taken directly across from the primary inflow.)

TABLE 1. Results from the sampling of the sources and ponds in the trout aquaculture system at the Cuericí Biological Station. The AM sampling time was at 7:45am on 30 Jan, and the PM sampling time was 4:30pm on 29 Jan. Site numbers correspond to the labeled locations in Fig. 1. In/out refers to inflow and outflow locations at those sites.

| Site # | Fish Size | In/out | 0730 | | | 1630 | | |
			DO	pH	Temp (°C)	DO	pH	Temp (°C)
1	-	-	9.5	5.79	11.3	7.7	6.02	12.1
2	-	-	8.9	5.77	11.1	7.9	6.01	12.1
3	-	-	8.9	5.78	11.1	8.2	5.8	11.9
4	small	in	8.8	5.65	11.1	6.9	5.61	12.8
		out	8.7	5.68	11.1	7	5.59	12.7
5	smallest	in	8.3	5.52	11.6	7.6	5.42	11.8
		out	8	5.55	11.5	7.6	5.41	11.8
6	smallest	in	8	5.57	11.5	7.6	5.41	12
		out	7.8	5.55	11.6	7	5.38	12
7	smallest	in	7.7	5.55	11.6	6.3	5.39	12.1
		out	7.3	5.55	11.6	5.9	5.39	12.1
8	small	in	8.5	5.59	11.3	6.9	5.38	11.7
		out	8.4	5.59	11.3	6.8	5.38	11.8
9	small	in	8.6	5.63	11.2	7	5.39	11.8
		out	8.2	5.64	11.3	6.6	5.38	11.8
10	big	in	8.5	5.71	11.3	7	5.35	10.7
		out	8.4	5.74	11.4	6.9	5.44	12
11	medium	in	8.2	5.69	10.4	6.8	5.48	12.1
		out	8.1	5.68	11.6	6.6	5.46	11.8
12	medium	in	8.2	5.75	10.5	6.8	5.51	12.4
		out	7.9	5.77	11.1	6.6	5.53	12.7
13	medium	in	7.8	5.7	11.4	6.6	5.57	13.2
		out	7.6	5.64	11.4	6.4	5.54	13.6
14	big	in	8.3	5.74	11.4	6.3	5.45	13.8
		out	8	5.54	11.4	6.2	5.38	13.9
15	medium	in	8	5.54	12.7	6.9	5.45	13.7
		out	8	5.52	12	7	5.5	14.2
16	big	in	8.5	5.32	11.5	6.7	5.6	14.2
	medium	out	7.4	5.3	13	6.5	5.47	13.6
17	-	-	-	-	-	8.1	5.48	11.8

the other on the morning of 30 January   2009. We used a Milwaukee SM600 Dis-

solved Oxygen Meter and SM102 pH Meter. We calibrated the pH meter before taking measurements on 29 January and recalibrated the DO meter at the start of each sampling session.

STATISTICAL ANALYSES

We first averaged the morning and afternoon values of DO, pH, and temperature for each location to remove the effect of time of day, yielding 30 time-averaged values (Table 1); with these we evaluated changes in DO, pH, and temperature as water moves through the system. We then compared DO, pH, and temperature values between morning and afternoon, using all sample points and a paired t-test, to see if the time of day affected the measurements.

RESULTS

Across the entire trout aquaculture system, DO decreased steadily as the water flowed through the ponds (when averaged across morning and evening times for each pond), as expected due to the cumulative downstream effects of fish respiration with minimal turbulence. Although springs are usually low in oxygen, the spring inputs appeared to have become well aerated prior to reaching the sampling site. The pH values were highest at the three sources before the aquaculture system but stayed relatively constant within the system. Temperature increased as the water flowed through the ponds, as would be expected due to solar radiation and respiration.

Time of day also had an effect: both DO and pH were significantly higher in the morning (DO: t_{56} = 9.90, P < 0.0001; pH: t_{56} = 2.96, P = 0.0045) while temperature was significantly higher in the evening (t_{56} = -5.59, P < 0.0001). We found no significant difference between the inflow and outflow points of ponds for DO, pH, or temperature using paired t-tests (DO: t_{50} = -1.05, P = 0.299; pH: t_{50} = -0.41, P = 0.68; temperature: t_{50} = 0.66, P = 0.51).

LITERATURE CITED

Susman, D. L., Marguerite N. Dashevsky, Robin M. Meyers, Jonathan M. Wachter, and Sarah E. Wengert. 2009. Responsible resource use: Impact of a biological station and trout hatchery on stream macroinvertebrates. Dartmouth Studies in Tropical Ecology 2009, pp. 95-101.

Monitoreo de la calidad del agua en el criadero de truchas: Un estudio base

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Profesor Editor: David R. Peart

Traducción de Ernesto Ruelas Inzunza.

Resumen: Los estudiantes del curso FSP de Dartmouth tienen el potencial de conducir un programa de monitoreo de calidad del agua a largo plazo en la Estación Biológica Cuericí. La información sobre cambios de la calidad del agua en las quebradas cercanas y el sistema de acuacultura de truchas será de utilidad para su manejo. En este estudio preliminar, medimos el oxígeno disuelto, pH y temperatura del agua de todas las fuentes, tanques y estanques de acuacultura de truchas para determinar su calidad en todo el sistema. Debido a que hay evidencia de que los flujos salientes tienen mayor impacto en el agua de las quebradas que cualquier otra actividad de la estación, el monitoreo de su calidad a través del tiempo en todo el sistema será una importante forma de evaluar y controlar el futuro impacto humano en las quebradas.

Palabras clave: criadero, sustentabilidad, ciclo de nutrientes

Sistema de Estudio

La Estación Biológica Cuericí en la provincia de San José, Costa Rica, está a 2,600 msnm, cerca de Cerro de la Muerte. Cuericí provee a científicos visitantes y estudiantes servicios de hospedaje y para el desarrollo de estudios en sus terrenos e instalaciones que incluyen una granja en funcionamiento y un criadero de truchas. El criadero produce pescado para consumo local durante todo el año. Susman et al. (2009) incluyen una descripción completa de las actividades humanas que podrían influenciar la calidad del agua y los sitios de aporte de flujos en manantiales y quebradas alrededor de la estación (ver Fig. 1 en Susman et al. 2009).

El agua que ingresa en el sistema de acuacultura de truchas viene de manantiales y quebradas cerca de Cuericí (Fig. 1, 1-3). Esta fluye a través de una serie de tanques de truchas (Fig. 1, 4-9), canales (Fig. 1, 17) y estanques (Fig. 1, 14-16) y finalmente a un tanque de sedimentación (Fig. 1, 17). Los flujos salientes de los estanques de truchas que no se derraman se combinan con agua de la quebrada y ésta es entubada a través del generador hidroeléctrico y finalmente regresa a la quebrada.

Métodos de muestreo

Colectamos registros de oxígeno disuelto (OD), pH y temperatura en cada etapa del flujo de agua a lo largo de todo el sistema de acuacultura. En cada una de las fuentes de agua, tomamos registros
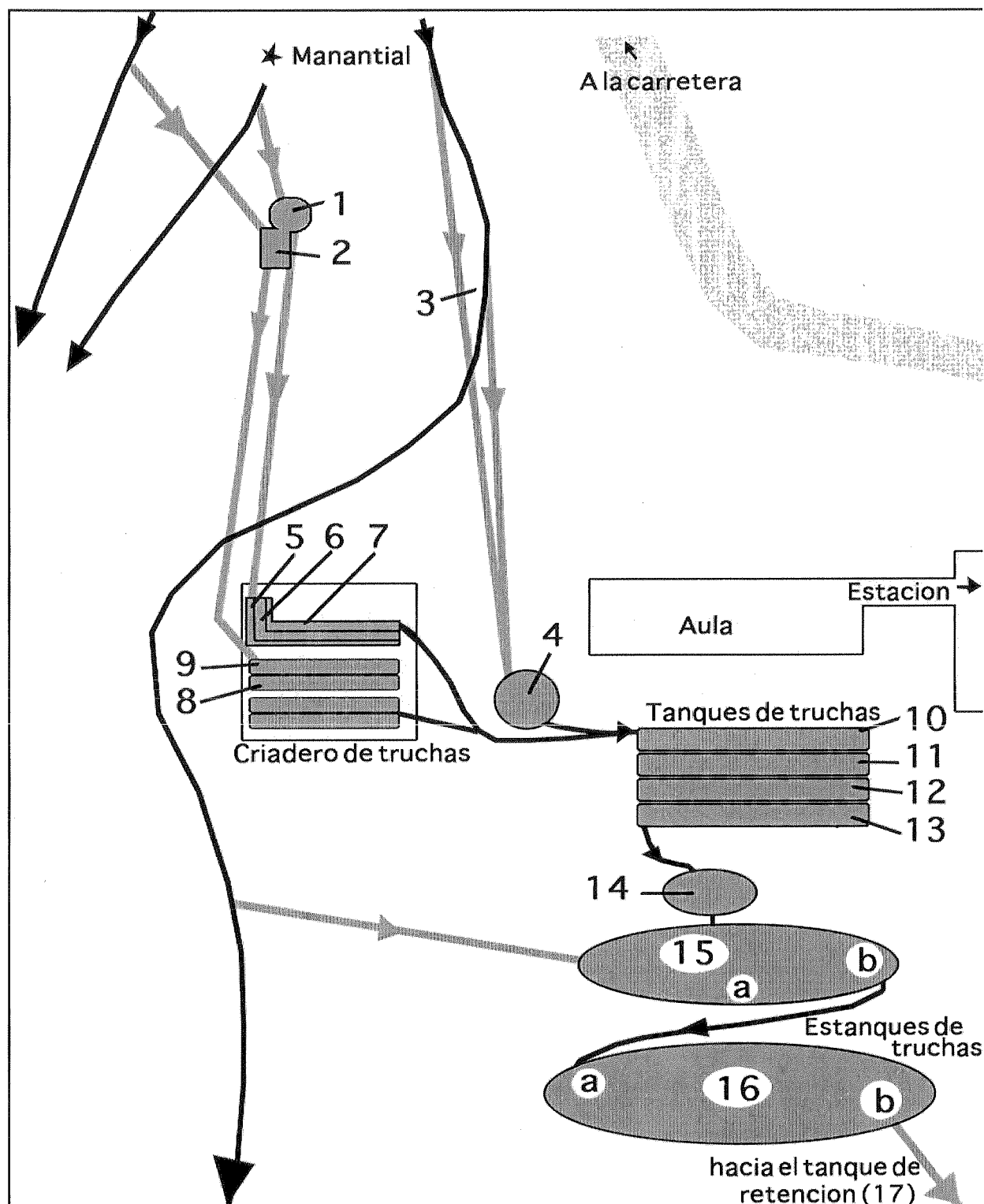
FIGURA 1. Mapa de la Estación Biológica Cuericí que muestra las quebradas en negro, los edificios en blanco, los estanques de truchas en gris oscuro y los caminos y senderos en gris claro. Los sitios de muestreo están numerados progresivamente en relación al flujo de agua y a través del sistema de acuacultura de truchas; "a" indica localidad de medición de aportes entrantes y "b" flujos de salida (ver la Tabla 1). Todos los sitios de muestreo están marcados con puntos en la quebrada (nota: tomamos todas las medidas en sitios cuesta abajo; 15a fue tomado directamente cruzando el aporte primario).

TABLA 1: Resultados de los muestreos de fuentes y estanques en el sistema de acuacultura de truchas en la Estación Biológica Cuericí. La hora de muestreo matutino fue a las 7:45 am el 30 de enero y el vespertino fue a las 4:30 pm del 29 de enero 2009. Los números de sitio corresponden a las localidades marcadas en la Fig. A1. Ingreso/salida se refiera a las localidades de flujos entrante y saliente en esos sitios.

Sitio #	Tamaño de los peces	Ingreso/ salida	0730			1630		
			OD	pH	Temp (°C)	OD	pH	Temp (°C)
1	-	-	9.5	5.79	11.3	7.7	6.02	12.1
2	-	-	8.9	5.77	11.1	7.9	6.01	12.1
3	-	-	8.9	5.78	11.1	8.2	5.8	11.9
4	pequeño	ingreso	8.8	5.65	11.1	6.9	5.61	12.8
		salidaa	8.7	5.68	11.1	7	5.59	12.7
5	mas pequeño	ingreso	8.3	5.52	11.6	7.6	5.42	11.8
		salidaa	8	5.55	11.5	7.6	5.41	11.8
6	mas pequeño	ingreso	8	5.57	11.5	7.6	5.41	12
		salidaa	7.8	5.55	11.6	7	5.38	12
7	mas pequeño	ingreso	7.7	5.55	11.6	6.3	5.39	12.1
		salidaa	7.3	5.55	11.6	5.9	5.39	12.1
8	pequeño	ingreso	8.5	5.59	11.3	6.9	5.38	11.7
		salidaa	8.4	5.59	11.3	6.8	5.38	11.8
9	pequeño	ingreso	8.6	5.63	11.2	7	5.39	11.8
		salidaa	8.2	5.64	11.3	6.6	5.38	11.8
10	grande	ingreso	8.5	5.71	11.3	7	5.35	10.7
		salidaa	8.4	5.74	11.4	6.9	5.44	12
11	mediano	ingreso	8.2	5.69	10.4	6.8	5.48	12.1
		salidaa	8.1	5.68	11.6	6.6	5.46	11.8
12	mediano	ingreso	8.2	5.75	10.5	6.8	5.51	12.4
		salidaa	7.9	5.77	11.1	6.6	5.53	12.7
13	mediano	ingreso	7.8	5.7	11.4	6.6	5.57	13.2
		salidaa	7.6	5.64	11.4	6.4	5.54	13.6
14	grande	ingreso	8.3	5.74	11.4	6.3	5.45	13.8
		salidaa	8	5.54	11.4	6.2	5.38	13.9
15	mediano	ingreso	8	5.54	12.7	6.9	5.45	13.7
		salidaa	8	5.52	12	7	5.5	14.2
16	grande	ingreso	8.5	5.32	11.5	6.7	5.6	14.2
	mediano	salida	7.4	5.3	13	6.5	5.47	13.6
17	-	-	-	-	-	8.1	5.48	11.8

en un solo punto. Para cada uno de los   tanques, canales y estanques, tomamos

mediciones en los puntos de flujo entrante y el saliente (Fig. 1). Tomamos dos series de mediciones, una en la tarde del 29 de enero y la otra en la mañana del 30 de enero de 2009. Utilizamos un medidor de oxígeno disuelto Milwaukee SM600 y un medidor de pH SM102. Calibramos el medidor de pH antes de tomar mediciones el 29 enero y recalibramos el medidor de OD al inicio de cada sesión de muestreo.

ANÁLISIS ESTADÍSTICOS

Obtuvimos el promedio de los valores de mañana y tarde de OD, pH y temperatura de cada localidad para eliminar el efecto de la hora del día, generando 30 valores promediados a todo el periodo de muestreo (Tabla 1). Con estos evaluamos cambios en OD, pH y temperatura cuando el agua circula a través del sistema. Para determinar si la hora del día afectaba las medidas, comparamos los valores del OD, pH y temperatura entre mañana y tarde utilizando todos los puntos de muestreo por medio de la prueba t pareada.

RESULTADOS

A lo largo de todo el sistema de acuacultura, el OD decreció constantemente mientras el agua fluyó a través de los estanques como lo esperábamos (cuando se promediaban entre los periodos de mañana y tarde para cada estanque), debido a efectos cumulativos de la respiración de los peces y una mínima turbulencia. Aunque los manantiales usualmente son bajos en oxígeno, los aportes a los manantiales parecen estar bien aireados an-

tes de llegar al sitio de muestreo. Los datos de pH tuvieron los valores más altos en las tres fuentes antes de ingresar al sistema de acuacultura, pero permanecen relativamente constantes al interior del sistema. Como era de esperarse, la temperatura se incrementó conforme al agua fluyó a través de los estanques, a consecuencia de la radiación solar y respiración.

La hora del día también tuvo un efecto: ambos, el OD y el pH, fueron significativamente más altos en la mañana ($t = 9.90$, gl = 56, $P < 0.0001$; $t = 2.96$, gl = 56, $P = 0.045$), mientras que la temperatura fue significativamente más alta en la tarde ($t = -5.59$, gl = 56, $P < 0.0001$). No encontramos diferencias significativas entre los puntos de flujo entrante y saliente de los estanques en OD, pH o temperatura según los resultados de las pruebas t pareadas ($t = -1.05$, gl = 50, $P = 0.299$; $t = -0.41$, gl = 50, $P = 0.68$; y $t = 0.66$, gl = 50, $P = 0.51$, respectivamente).

LITERATURA CITADA

Susman, D. L., Marguerite N. Dashevsky, Robin M. Meyers, Jonathan M. Wachter, y Sarah E. Wengert. 2009. Responsible resource use: impact of a biological station and trout hatchery on stream macroinvertebrates. Dartmouth Studies in Tropical Ecology, pp. 95-101.

Nectar-robbing birds forage optimally

Rebecca Davidson Wolf

Faculty Editor: David R. Peart

Abstract: I investigated whether two nectar-robbing bird species, *Diglossa plumbea* and *Panterpe insignis*, rob certain patches of flowers more than others by observing the number of slits pierced in flowers' corollas. Plants ("patches") with more total flowers had more slits per flower. This suggests that the nectar-robbers, like pollinators, forage optimally for nectar.

Key words: Slaty Flowerpiercer, Fiery-throated Hummingbird, optimal foraging theory

Aves ladronas de néctar forrajean óptimamente

Resumen: Investigué si dos especies de ladrones de néctar, *Diglossa plumbea* y *Penterpe insignis* roban ciertos parches de flores más que otros, mediante observaciones del número de perforaciones en la corola de las flores. Las plantas ("parches") con un número total mayor de flores tenían un número mayor de perforaciones por flor. Esto sugiere que los ladrones de néctar forrajean óptimamente, como los legítimos polinizadores.

Palabras clave: pinchaflor, colibrí, teoría de forrajeo óptimo

Introduction

Hummingbird-pollinated flowers provide nectar to reward pollinators. However, some birds take advantage of nectar without pollinating. At the Cuerici Biological Station in Costa Rica there are two nectar-robbing birds: *Diglossa plumbea*, the Slaty Flowerpiercer (Stiles and Skutch 1989), and *Panterpe insignis*, the Fiery-throated Hummingbird, which steals nectar from flowers too long for its beak (Colwell 1973). Slits on a flower show that nectar-robbers have extracted nectar.

Hummingbird pollinators forage optimally, visiting denser flower patches more often than less dense patches (Biedron et al. 2003). Reasoning that the same trend should be true for nectar-

robbers, I predicted plants with more flowers would have more nectar-robber slits per flower. Nectarivores cannot detect nectar (Önen et al. 2006), so they should not prefer flowers that have not been robbed. Thus, I predicted that slits would be distributed randomly among all flowers, across all plants.

Certain patches may be unavailable to the Fiery-throated Hummingbird, which hovers while feeding and cannot access flowers in dense vegetation (Colwell 1973). Inaccessible flowers should be robbed less, so I predicted that flowers in denser vegetation would have fewer slits per corolla.

Methods

I conducted this study along the

lower section of the main loop trail that heads east from the main building of Cuericí Biological Station, Cerro de la Muerte, Costa Rica. After the gate near
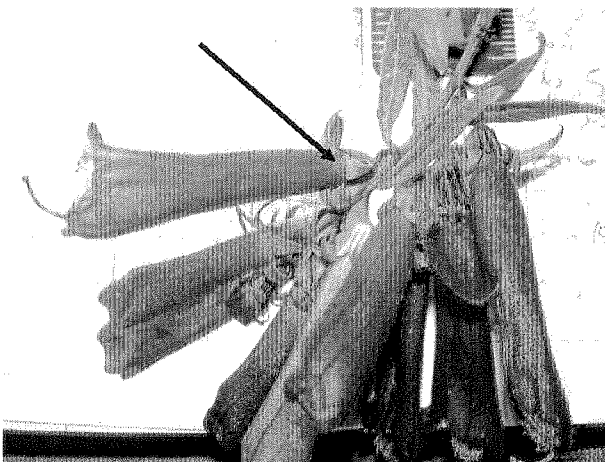
FIG. 1. Photograph of *Columnea glabra*. The arrow indicates a nectar-robber's slit in the side of one of the flowers, which appears yellow-green. Some slits were more brown in color.

the farmhouse, where the trail bends north and passes the blackberry farm, *Columnea glabra* (Gesneriaceae; Fig. 1) is abundant. The species has red, tubular flowers, suggesting that it is hummingbird-pollinated. I sampled all open flowers on each plant visible from the trail from where the trail bends north until to where it enters the forest, except when too high to reach (> 2 m) or damaged. For each flower, I measured the corolla length, number of slits, and slit length and width. Slits ranged from 0.5 mm to 6 mm long, averaging 1.58 mm; all were 1 mm wide or less. I also assessed accessibility to hummingbirds, based on whether it appeared there was enough open air space to hover in front of the flower. For plants where I could not sample all flowers, I estimated total number

of flowers by counting the number of clusters and multiplying by the average number of sampled flowers per cluster for that plant.

I used a chi-squared test, assuming a Poisson distribution, to test whether slits were randomly distributed in flowers, across all plants. Statistical analyses were done in JMP v. 7 (SAS Institute, Inc. 2007).

RESULTS

I examined 190 flowers on 16 plants and found 121 slits (Table 1). All flowers sampled had corollas at least 5 mm longer than the Fiery-throated Hummingbird's beak length of 20 mm (Stiles 1983).

Plants with more flowers had a greater average number of slits per flower (Spearman's r = 0.37, $P < 0.0001$; Fig. 2). Although it appeared visually that this pattern might be driven by a single plant (the top right point in Fig. 2), an analysis excluding that plant still found more slits per flower in plants with more flowers (Spearman's r = 0.19, $P = 0.02$). Some flowers were pierced up to four times, but having one slit did not affect a

TABLE 1. On average, there were 0.63 nectar-robbing slits per *Columena glabra* flower at Cuericí Biological Station, with most flowers having no slits and only few having more than two (n = 190 flowers sampled).

Slits per flower	Number of flowers
0	104
1	61
2	17
3	6
4	2

flower's likelihood of being pierced again ($\chi^2_4 = 0.38$, $P = 0.98$; Table 1).

There was no difference in average number of slits between accessible and inaccessible flowers ($\chi^2_1 = 0.23$, $P = 0.63$).

DISCUSSION

Plants with more flowers are more attractive to both pollinators (Biedron et al. 2003) and nectar-robbers (Fig. 1). Nectarivores forage optimally, spending more time on larger patches of flowers to maximize energy intake per unit effort (Begon et al. 1990). This may be especially important for small birds, which have relatively high energy needs (Stiles and Skutch 1989). Higher visitation may deplete nectar in high density patches, reducing rewards there. This would increase the relative rewards of foraging in low-density plots, probably maintaining some level of pollinator visitation there.

Although I found no difference in
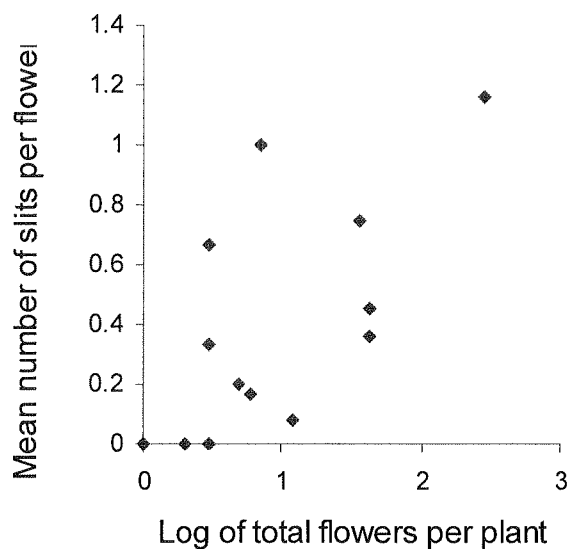
FIG. 2. Average number of slits per *Columnea glabra* flower at Cuericí Biological Station increased significantly with number of flowers on the plant (n = 190 flowers sampled).

nectar-robbing of flowers based on their accessibility, this may be because my assessment of accessibility was subjective. Alternatively, it might be because Slaty Flowerpiercers, which can access flowers surrounded by vegetation, were more abundant than Fiery-throated Hummingbirds (Table 2), which need more space to forage (Colwell 1973).

TABLE 2. Three Slaty Flowerpiercers but no Fiery-Throated Hummingbirds were captured in mist-nets at Cuericí Biological Station (unpublished data, Meyers et al.).

Bird species	Number of individuals captured in mist-nets
Slaty flowerpiercer	3
Fiery-throated hummingbird	0

Plants face a trade-off: flower features attractive to pollinators, such as red coloration (Stiles and Skutch 1989) and high patch density (Biedron et al. 2003), may also attract nectar-robbers. Nectar robbing may influence the plant's fitness and result in natural selection for traits that reduce robbing. For example, tougher corollas could impair nectar-robbers' ability to create slits without reducing pollinator visits. However, this plant appears not to have an effective defense. I suggest that nectar-robbing might have minimal effects on fitness. Pollinators frequently remove flowers' nectar, which can be replenished (Schoen et al. 2002). Furthermore, pollinators cannot judge nectar availability before probing a flower (Önen et al. 2006), so removal of nectar may not reduce a flower's likelihood of being pollinated, providing

nearby flowers provide sufficient re-
wards that birds return to the patch.

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What do ants know and how do they know it?
Leaf-cutter ant (Atta sp.) communication on pheromone trails

Eben E. B. Bein and Keng-Lou Hung

Faculty Editor: David R. Peart

Abstract: The success of an ant colony relies on organized information transfer among ants. We examined three potential sources of information that an *Atta* sp. worker may use on pheromone trails outside the nest: the object it picks up, the pheromone trail itself, and contact with nest-mates on the trail. Ants were able to recognize objects that normally occur on a given trail type (leaves cut by ants or ant-constructed refuse bundles); they treated them appropriately, and differently from objects that were not normally found on that trail type. However, ants did not appear to recognize objects precisely, i.e. in the context of how the colony processes resources. We found no evidence that ants detect the direction of the nest from trail cues; they appeared to gain directional information from contact with nest-mates on the trail. However, ants behaved independently from nearby nest-mates when holding an object not normally found on that trail.

Key words: pheromone trails, intraspecific communication, eusociality

¿Qué saben las hormigas y cómo lo saben?
La comunicación en hormigas arrieras (Atta sp.) en senderos de feromonas

Resumen: El éxito de una colonia de hormigas depende de la transferencia de información entre individuos. Examinamos tres potenciales fuentes de información que una obrera de *Atta* sp. podría utilizar en senderos de feromonas fuera del nido: los objetos que recoge, el sendero en sí mismo y el contacto con compañeros de nido en el sendero. Las hormigas fueron capaces de reconocer objetos que normalmente se encuentran en un tipo de sendero dado (hojas cortadas por hormigas o pilas de desecho construidas por hormigas), y los trataron apropiadamente y de manera diferente a los objetos que normalmente no se encuentran en ese tipo de sendero. Las hormigas no parecen reconocer objetos con precisión, e.g., en el contexto de cómo la colonia procesa recursos. No encontramos evidencia de que las hormigas detectan la dirección del nido por indicaciones del sendero, parecen obtener información direccional del contacto con compañeros de nido en el sendero. Sin embargo, las hormigas se comportaron de manera independiente de los compañeros de nido cercanos cuando portaban objetos que normalmente no se encuentran en el sendero.

Palabras clave: senderos de feromonas, comunicación intraespecífica, eusocialidad

INTRODUCTION

To be ecologically successful, ant colonies rely on a coherent, highly organized division of labor in which each ant carries out a specific task at a specific time and place. Somehow, each worker needs to obtain the information that directs its behavior. Much of this information is transmitted among individuals via

chemical signals (Holldobler 1995).

We examined three potential sources of information that influence the behavior of *Atta* sp. workers on pheromone trails outside the nest. First, leafcutter ants may receive cues directly from the chemical and tactile properties of objects they pick up on the trail. Second, ants may receive cues from the trail itself. Two trails from the same colony can have distinct pheromonal composition, as can two sections on a single trail (Jackson et al. 2007). Third, ants may receive cues directly from their nest-mates on the trail, either via physical contact or pheromones. Pheromones allow individuals to recognize nest-mates (Martin et al. 2008).

We observed how ants responded to objects placed on their pheromone trails and how they responded to being moved onto different pheromone trails to distinguish how ants use these three potential sources of information.

METHODS

We performed our experiments from 6-7 February 2009 on leafcutter ants of a nest located ca. 75 m south of the Corcovado research station, in the forest on the eastern border of the airstrip. This colony had one exposed refuse trail, as well as many leaf trails leading to the nest.

In the first experiment, we quantified how the ants reacted to objects placed on their trails: a leaf fragment taken from a worker of the same colony, a ball of freshly dumped leafcutter ant refuse from the same colony, or a leaf fragment rubbed in the colony's freshly dumped refuse. We tested each type of object 10 times on both a leaf trail and the refuse trail (referred to, for example, as the "leaf on refuse trail" experiment).

In the second experiment, we moved a leaf-carrying ant to the refuse trail to examine how the new trail affected the ant's behavior compared to two control treatments: a leaf-carrying ant moved from its leaf trail to a different leaf trail and a refuse-carrying ant taken from and placed back on the refuse trail. We replicated each treatment (experiment and controls) with 10 different ants.

We designed a third experiment to distinguish the effects of the trail from those of nest-mates on the trail. For each of three "exclusion" replicates, we set up blockades and removed all ants from a 2-m section on each of three different leaf trails. We placed a leaf-carrying ant from a different trail at the midpoint of each of the exclusion sections. We compared this ant's behavior to that of a leaf-carrying ant moved to a different leaf trail (in the presence of its nest-mates) as a control. We used 6 ants per replicate for a total of 18 ants.

In all experiments, we measured the time the target ant took to move the object 50 cm from its starting point on the trail ("processing time") and noted the number of times it changed directions during this processing time, while holding the object. We also noted the direction in which it carried the object past the 50 cm point (toward or away from nest or refuse heap), as an indicator of the ant's choice of direction.
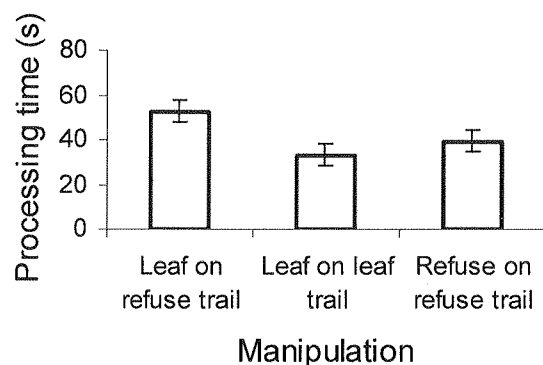
FIG. 1. In Corcovado National Park, Costa Rica, leaf-cutter ants that picked up leaves on a refuse trail took longer to move 50 cm from the starting point than did ants that picked up leaves on a leaf trail. Bars are means ± 1 S.E.

Statistical analyses were conducted using JMP 5.0 and Microsoft Excel.

RESULTS

Ants that picked up a leaf on the refuse trail took longer to move it 50 cm than did ants that picked up a leaf on the leaf trail, but not those that picked up refuse on the refuse trail ($F_{2,27}$= 4.01, P = 0.03; Student's t = 2.05; Fig 1). Ants that picked up a leaf on the refuse trail also travelled against the flow of load-
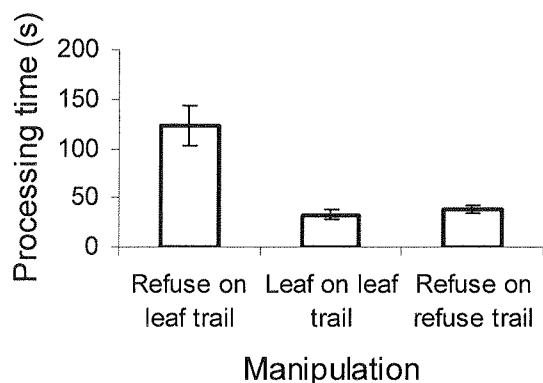
FIG. 2. In Corcovado National Park, Costa Rica, leaf-cutter ants that picked up refuse on the leaf trail took longer to move 50 cm from the starting point than did ants that picked up leaves on the leaf trail, or ants that picked up refuse on the refuse trail. Bars are means ± 1 S.E.

carrying nest-mates more often than did those that picked up a leaf on the leaf trail (χ^2_1 = 7.2, P = 0.007) and those that picked up refuse on the refuse trail (χ^2_1 = 5.6, P = 0.018).

Ants that picked up refuse on the leaf trail took longer to move it 50 cm than did both ants that picked up a leaf on the leaf trail and ants that picked up refuse on the refuse trail ($F_{2,16.02}$= 9.54, P = 0.0019; Student's t = 2.05; Fig 2). However, ants that picked up refuse on the leaf trail did not travel against the flow of load-carrying nest-mates more often than did those that picked up a leaf on the leaf trail (χ^2_1 = 1.8, P = 0.18) nor those that picked up refuse on the refuse trail (χ^2_1 = 0.9, P = 0.346).

Ants on the leaf trail that picked up a leaf rubbed in freshly dumped refuse took longer to move it 50 cm than did ants that picked up an untreated leaf on the leaf trail, but not longer than those that picked up refuse on the leaf trail ($F_{2,13.25}$= 17.82, P = 0.0002; Student's t = 2.05; Fig 3). Ants that picked up a leaf rubbed in freshly dumped refuse on the leaf trail did not travel against the flow of load-carrying nest-mates more often than did ants that picked up an untreated leaf on the leaf trail (χ^2_1 = 1.8, P = 0.18) nor those that picked up refuse on the leaf trail (χ^2_1 = 0, P = 1.0).

Ants that picked up a leaf rubbed in freshly dumped refuse on the refuse trail did not take longer to move it 50 cm than did ants that picked an untreated leaf on the refuse trail nor those that picked up refuse on the refuse trail ($F_{2,27}$ = 1.64, P =

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0.21; Fig 4). Ants that picked up a leaf rubbed in freshly dumped refuse on the
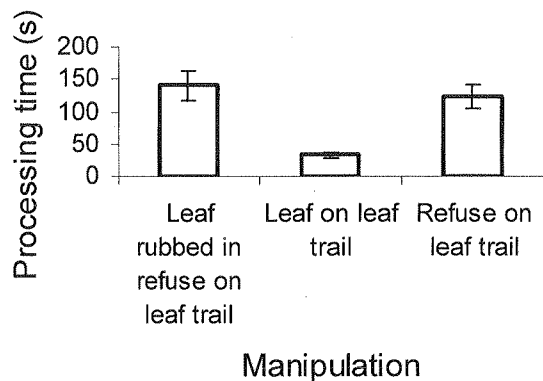
FIG. 3. In Corcovado National Park, Costa Rica, leaf-cutter ants that picked up leaves that were rubbed in freshly dumped refuse on the leaf trail took longer to move 50 cm from the starting point than did ants that picked up untreated leaves on the leaf trail. Bars are means ± 1 S.E.

refuse trail travelled against the flow of load-carrying nest-mates more often than did ants that picked up an untreated leaf on the refuse trail ($\chi^2_1 = 18$, $P < 0.001$), but not those that picked up refuse on the refuse trail ($\chi^2_1 = 0.2$, $P = 0.637$).

Leaf-carrying ants moved from their leaf trail to the refuse trail took longer to move 50 cm from the starting point than did both leaf-carrying ants moved from their leaf trail to a different leaf trail, and refuse-carrying ants removed from and then placed back onto the refuse trail ($F_{2,15.43} = 13.05$, $P = 0.0004$; $T = 2.05$; Fig 5). Leaf-carrying ants moved from their leaf trail to the refuse trail travelled against the flow of load-carrying nest-mates more often than did both leaf-carrying ants moved from their leaf trail to a different leaf trail ($\chi^2_1 = 6.25$, $P = 0.012$) and refuse-carrying ants removed from and then placed back onto the refuse trail (χ^2_1

$= 9.8$, $P = 0.002$).

Leaf-carrying ants moved from their leaf trail to the exclusion trail took longer to move 50 cm from the starting point than did leaf-carrying ants moved from their leaf trail to a different leaf trail ($F_{1,9.57} = 20.55$, $P = 0.0002$; $T = 4.53$; Fig 6). Leaf-carrying ants moved from their leaf trail to the exclusion trail did not travel against the direction of load-carrying nest-mates more often than did leaf-carrying ants moved from their leaf trail to a different leaf trail ($\chi^2_1 = 0.67$, $P = 0.41$), nor was their choice of direction different from random ($\chi^2_1 = 1.67$, $P = 0.2$).

DISCUSSION

Ants responded behaviorally to three primary cues: the object they picked up, the physical trail they were on, and contacts with nest-mates on the trail.

The object

Ants on a particular path recognized
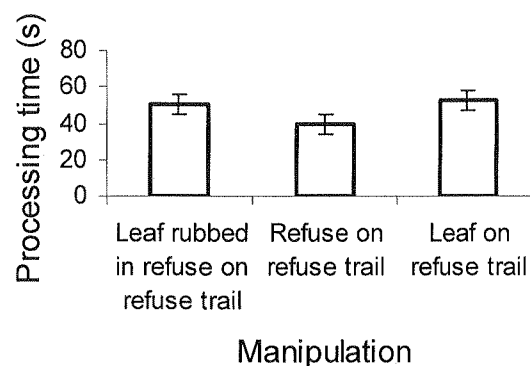
FIG. 4. In Corcovado National Park, Costa Rica, the time it took for leaf-cutter ants to move 50 cm from the starting point did not differ among ants that picked up leaves that were rubbed in freshly dumped refuse on the refuse trail, ants that picked up refuse on the refuse trail, and ants that picked up untreated leaves on the refuse trail. Bars are means ± 1 S.E.

objects normally found on that path and carried them in the appropriate direction. When a leaf was dropped on the leaf trail, an ant approaching from either direction consistently picked it up and carried it toward the nest. Similarly, when refuse was dropped in the refuse trail, an ant approaching from either direction consistently picked it up and carried it toward the refuse heap.

Ants treated objects not normally found on the path as different from those normally found there. For example, they did not treat a leaf in the refuse trail like refuse in the refuse trail; they abandoned the leaves 6 out of 10 times, while they carried refuse toward the refuse heap 9 out of 10 times. Ants also did not treat refuse in the leaf trail like a leaf in the leaf trail; on the leaf trail, it took ants more than a minute longer to choose a direction upon picking up refuse than upon picking up leaves. Further, ants that picked up refuse in the leaf trail changed direction an average of 4.9 times before committing to a final direction, vs. 0.2 directional changes in the "leaf on leaf trail" experiment. Because ants treated "normal" objects differently from "not normal" objects, it seems ants can differentiate between these two object classes.

However, ants did not seem to recognize the "full significance" of the object they picked up (i.e. in terms of the way the colony processes resources). Though they treated refuse in the leaf trail differently from a leaf on the leaf trail, they did not seem to recognize the refuse as something to be discarded. Instead, they changed directions several times and eventually carried it toward the nest in 7 out of 10 trials. Similarly, ants did not recognize a leaf in the refuse trail as a resource to be taken into the nest, and often discarded the leaf. Lastly, their behavior seemed strongly influenced by extraneous chemical signals on an object in addition to the chemical properties of the object itself. Thus, when a leaf was rubbed in refuse, it was treated more like refuse than like a leaf. Ants may be using chemical signals left on the objects by ants that had previously handled it, rather than (or in addition to) the intrinsic chemical properties of the objects themselves.

The trail

Even after our experimental treatments, it remains unclear what information ants get from the trail. We still do not know if the trail conveys directional
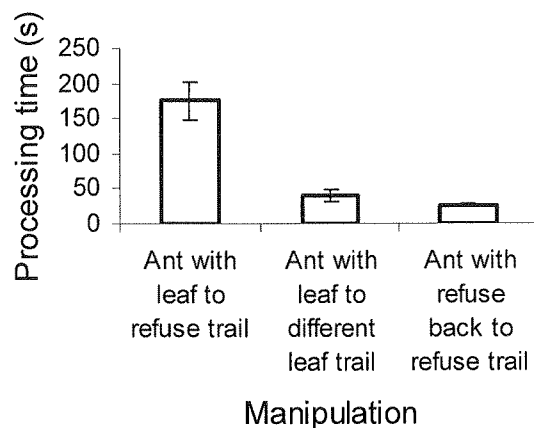
FIG. 5. In Corcovado National Park, Costa Rica, leaf-carrying leafcutter ants taken from a leaf trail and placed on a refuse trail took longer to move 50 cm from the starting point than did leaf-carrying ants transplanted among unmanipulated leaf trails, or refuse-carrying ants taken from and placed back on a refuse trail. Bars are means ± 1 S.E.

information. The directional choices of ants in the "exclusion" experiment were not significantly different from those of ants in either the "ant with leaf placed on a different leaf trail" experiment, or those predicted by the null hypothesis, in which ants randomly select their direction along trails.

But chemical cues on trails may inform ants of the type of task to be completed there. In our "ant with leaf in refuse trail" experiment, ants consistently wandered off trail, apparently in search of some signal they were not finding on the trail. If leaf and refuse trails are chemically distinguishable to ants, and if ants retain behavioral programming from one trail when moved to another, leaf-carrying ants may have recognized the refuse trail as the "wrong" trail and searched for the "correct" chemical signal that was consistent with prior programming. Alternatively, the nest-mates may inform an ant of the type of task being conducted on a particular trail. To determine what task information ants get from chemical signals on the trail, future investigators might compare how ants carrying a particular object act when placed on either a leaf trail or a refuse trail with nest-mates excluded.

Contact with nest-mates

Though it is unclear whether directional cues can be gleaned from the trail, ants seem to gain a strong sense of direction from contact with nest-mates. Leaf-carrying ants placed on a different leaf trail took their leaf towards the nest 8 out of 10 times when in contact with nest-
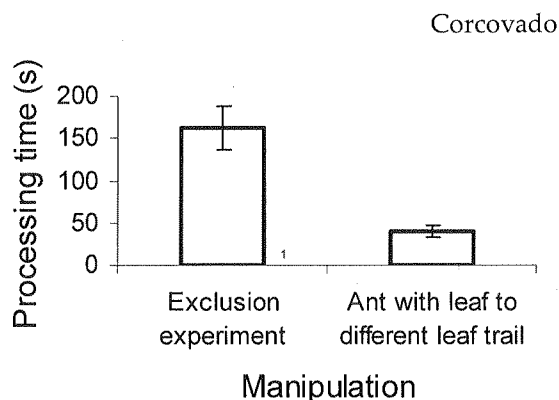
FIG. 6. In Corcovado National Park, Costa Rica, leaf-carrying leafcutter ants taken from an unmanipulated leaf trail and placed on a section of leaf trail where nest-mates were excluded took longer to move 50 cm from the starting point than did leaf-carrying ants transplanted among unmanipulated leaf trails. Bars are means ± 1 S.E.

mates compared to only 10 out of 15 times on trails where nest-mates were excluded. In the presence of nest-mates, ants that started moving the "wrong" way often came into physical contact with other leaf-carriers, and reversed direction and moved with the flow of returning leaf-carriers. Ants may be relaying directional information through this physical contact either directly, or via pheromonal exchanges; future investigators might simulate physical contact alone by tapping repeatedly on the front of the leaf an ant is carrying to see if that induces the ant to change direction.

However, contact with nest-mates does not by itself determine behavior. By comparing the "refuse on leaf trail" experiment to the "leaf on leaf trail" experiment, we can infer that ant behavior on leaf trails is influenced by encountering and picking up refuse: they changed directions more and took longer to choose their final direction than ants encounter-

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ing a leaf in leaf trails. Similarly, by comparing the "ant with leaf in refuse trail" and "ant with refuse in refuse trail" experiments, it is clear that a leaf-carrying ant maintained some prior programming and did not immediately become a refuse-carrier when it was placed in contact with refuse-carrying nest-mates. Instead, it maintained distinct behavior from nest-mates (apparently recognizing a leaf as distinct from refuse), and usually abandoned that leaf and wandered off trail, perhaps in search of a missing cue.

As future studies continue to investigate communication via contact with nest-mates, it is important to note that some crucial communication may be occurring at sites other than the trail. Investigators might devise ways to infer whether behavioral programming occurred in the nest, or perhaps at a leaf harvesting site, to further elucidate how nest-mates influence one another's behavior.

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Scared Shirtless and Swimming with Crocodiles: A Population Survey of *Basiliscus basiliscus* in Corcovado National Park

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Faculty Editor: David R. Peart

Abstract: As a continuation of earlier Dartmouth studies, we surveyed the *Basiliscus basiliscus* population in the Río Claro and two streams near Sirena Station in Corcovado National Park, Costa Rica. Based on negative trends observed between 1998-2001, we expected the population size to be low. As predicted, these lizards were less abundant around the Río Claro than in the most recent survey in 2001. We examined several factors that may influence local basilisk distribution, and found that smaller lizards were more frequently using open riverbank habitats than larger lizards. We suggest that further investigation of habitat availability may be needed to clarify the cause of the observed population decline at Corcovado.

Key words: chisbala, Jesus Christ lizard, population demographics

Un censo de *Basiliscus basiliscus* en el Parque Nacional Corcovado

Resumen: Para continuar estudios anteriores de estudiantes del Colegio Dartmouth, censamos la población del garrobo o chisbala *Basiliscus basiliscus* en el Río Claro y en dos quebradas cerca de la Estación Sirena en el Parque Nacional Corcovado, Costa Rica. En base a las tendencias observadas de 1998-2001, esperamos un tamaño poblacional menor. Como esperábamos, estas lagartijas fueron menos abundantes en la cercanía del Río Claro que en el más reciente censo efectuado en 2001. Investigamos varios factores que pueden influenciar la distribución local del garrobo. Las lagartijas más pequeñas se encontraban con mayor frecuencia en hábitats a la ribera del río que los individuos más grandes. Sugerimos que es necesario continuar la investigación de disponibilidad de hábitat para esclarecer la causa de los declines poblacionales observados en Corcovado.

Palabras clave: garrobo, chisbala, demografía de poblaciones

Introduction

The study of demographic variation and long-term population trends requires repeated samples over many years. To follow up on previous Dartmouth studies, we surveyed the population of *Basiliscus basiliscus* along the Río Claro and two smaller streams near the Sirena Station in Corcovado National Park, Costa Rica (Berg et al 1998). We evaluated the current status of the population and compared the stage class distribution and abundance to those of previous surveys. From 1998 through 2001, an annual survey of the basilisk population on the Río Claro showed an initial abrupt decline in abundance followed by several years of stable or slightly declining abundance (Braden et al. 2001). Based on this trend, and aware of the large gap between studies, we expected to find a reduced popu-

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lation of basilisks possibly comparable to the one last surveyed in 2001.

Due to the eight year gap in sampling at Corcovado, we decided not to estimate trend probabilities from 2001-2009, but instead combined stage class data from 2009 with demographic data from populations in the Guanacaste region of Costa Rica (Van Devender 1986) to project the growth of the basilisk population. We recognize that the Guanacaste data may not apply to Corcovado populations; thus, our projections are just a modeling exercise rather than an attempt to represent actual Corcovado population dynamics. Our main contribution is to provide updated estimates of population size and structure, which will be useful in later studies to project the Corcovado populations more realistically. We also propose mechanisms for the observed decline in the basilisk population on the Río Claro that merit further investigation.

Finally, we examined basilisk habitat preferences. Habitat preference may have evolved to reduce predation risk, and predation may influence survivorship and population dynamics. As in previous studies (Braden et al. 2001), we tested for effects of river width and amount of uncovered habitat on lizard abundance, as well as habitat preference at the individual level. We expected to find smaller, younger lizards in more open habitats and larger, reproductive-age lizards in more sheltered habitats, due to differential predation pressures and predator avoidance via habitat choice. We chal-

lenge the assertion that larger lizards push smaller ones into marginal, exposed habitat (Braden et al. 2001) and offer a plausible alternative explanation for this distribution pattern, based on life history observations from Van Devender (1986).

METHODS

On 6-7 February 2008, we continued the basilisk population survey begun by Berg et al. (1998) using identical sampling methods. We sampled 1,200 m of riparian habitat along the Rio Claro and 600 m along each of two tributary streams of the Río Sirena, to the north of Estación Sirena. Stream 1 intersects Sendero Pavo 3.3 km north of the station, and Stream 2 intersects the trail approximately 2 km north of the station.

Following the suggestions of Braden et al. (2001), we marked transects in the morning and surveyed in the afternoon when lizards are most active. Starting approximately 200 m upstream of the mouth of the Río Claro, we marked 24 contiguous 50 m transects on both sides of the river. We measured river width at the beginning and end of each transect, and made qualitative descriptions of the bank. On both Stream 1 and Stream 2, we established 12 contiguous 50 m transects heading upstream from their intersections with Sendero Pavo.

On 6 February, from 1300 to 1630, we surveyed the Río Claro population by walking upstream with two researchers on each bank. Each pair searched each transect on their respective bank for up to eight minutes, poking bushes with

sticks, and searching as far back as 5 m from the water's edge, before moving on to the next transect. We estimated the size class of each observed basilisk, the lizard's distance from the water's edge, and whether it was initially detected in an "open" or "covered" habitat. Cover was a subjective assessment of the immediate habitat surrounding a lizard and included overhead roots, foliage, or fallen trees. We also estimated distance from this cover to the water's edge. Because most basilisks fled when they saw us, we took care to avoid recounting individuals. We sampled the Río Claro again during the afternoon of 7 February, beginning with the most upstream transect and searching downstream towards the mouth. The size class proportions and total counts for Río Claro are comparable between days (61 lizards on day 1, 59 lizards on day 2); we used the larger sample for population modeling and statistical tests.

We sampled the two small streams at 1000 on 7 February, ca. 2 hr after establishing transects. Two researchers sampled each stream by walking down the streambed and searching each transect for up to 8 min. We surveyed the small stream transects only once.

Modeling and statistics

In our modeling exercise, we used a stage-based population model (Lefkovich matrix) to project the population out to a stable age distribution (Braden et al. 2001). We used published survival probabilities from a basilisk population in Guanacaste (Van Devender 1986) to esti-

mate survival of hatchlings to stage 1 (0.15) and stage 3 lizards to the next year (0.40). We estimated survival probabilities from stage 1 to 2 and stage 2 to 3 based on a Type III survivorship curve that we assumed typical of lizards, with a high initial mortality that decreases with age. Following the methods from Berg et al. (1998), we estimated adult contribution to stage 1 by multiplying fecundity (10 eggs by 5 clutches per year) × survival to stage 1 (0.15) (Van Devender 1986).

We tested for differences in lizard abundance by size class between open and covered habitat. We used a Spearman's test to test for effects of river width, and distance from river edge to forest, on basilisk abundance. All statistical analyses were conducted using JMP 7.0 (SAS Institute, Inc. 2007).

RESULTS

Population

A total of 61 basilisks were observed on the Río Claro, 12 basilisks on stream 1, and 9 basilisks on stream 2 (Table 1 and Fig. 1). The Río Claro population appears to have declined from the most recent count in 2001 while the stream populations (based on our small samples) appear to have remained at the same level (Fig. 1). The Lefkovich matrix based on our life cycle model, using a mix of Guanacaste and Corcovado data (Fig. 2), projects that the Río Claro population would reach a stable age distribution with 111 total individuals (Stage 1 = 0.72, Stage 2 = 0.18, Stage 3 = 0.10), while streams 1 and

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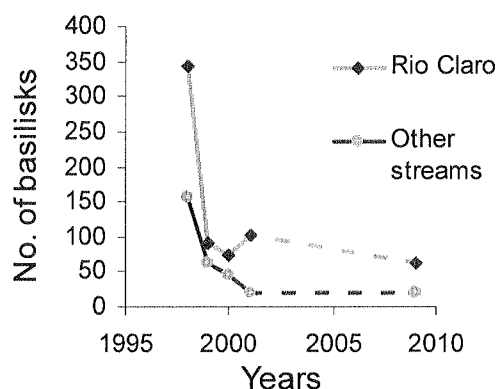
FIG. 1. Number of basilisks found in the Río Claro and two streams using identical sampling methods from 1998 to 2009 in Corcovado National Park, Costa Rica. Dashed line indicates years with no survey data.

2 together could reach a stable age distribution with approximately 37 individuals (Stage 1 = 0.72, Stage 2 = 0.18, Stage 3 = 0.10). Note that the projected stable stage class distributions are identical for the Río Claro and the streams because we assumed the transitional probabilities from Van Devender (1986) were identical in both populations.

Habitat

We found that large basilisks on the Río Claro were more often under cover and that small ones were more often in open habitat (χ^2_2 = 6.7, P = 0.035; Fig. 3). On the Río Claro, we observed no significant correlations for the following relationships: size class and the distance that basilisks were found from water's edge

(P = 0.97), basilisk abundance and river width (P = 0.16), and basilisk abundance and distance from cover to water's edge (P = 0.09).

DISCUSSION

Our population survey data show a continued downward trend in basilisk population numbers along the Río Claro. We offer several tentative explanations for this trend as starting points for future directions of this long-term population monitoring project.

We emphasize that our projections of stable stage structures are only a modeling exercise, since we have no basis for assuming Guanacaste demographic data are applicable to Corcovado basilisks. Lefkovich matrix models also have many inherent limitations for exploring population dynamics using short survey data. Most notably, they are limited to projections of exponential decline or increase (except in the special case of 1 = 1) after the population has reached stable age distribution. Therefore, they are only useful for exploring the implications of current estimates of population structure and transition probabilities for short-term population trajectories, rather than for projecting what might happen to a population over the long-term.

TABLE 1. Proportion of basilisks in three stage classes in three riparian habitats in Corcovado National Park, Costa Rica. Total number sampled each year is shown in the bottom row. Stage 1 = 0-20 cm, Stage 2 = 20-40 cm, Stage 3 = 40+ cm.

	Rio Claro					Stream 1					Stream 2				
	'98	'99	'00	'01	'09	'98	'99	'00	'01	'09	'98	'99	'00	'01	'09
Stage 1	0.66	0.55	0.76	0.47	0.54	0.56	0.49	0.28	0.10	0.58	0.58	0.56	0.57	0.18	0.44
Stage 2	0.22	0.34	0.20	0.46	0.30	0.31	0.40	0.52	0.50	0.33	0.28	0.36	0.21	0.46	0.33
Stage 3	0.12	0.11	0.04	0.07	0.16	0.13	0.11	0.20	0.40	0.08	0.14	0.08	0.21	0.36	0.22
#Indiv.	343	92	74	102	61	105	37	25	10	12	50	25	19	11	9

The field data from previous studies indicate an abrupt ca. 50% decrease in population size from 1998 to 1999 (Braden et al. 2001). The population since then has continued to decrease, but much more gradually (Fig. 1). Based on our 2009 field observations, we suspect the greater abundance in 1998 may be the result of high microhabitat availability. We found pockets of high basilisk density along the Río Claro, where fallen trees and mangroves housed up to 20 lizards in a ca. 20 m section of river and other sections of the bank were uninhabited. Habitat availability created by tree falls depends on annually variable environmental conditions and thus may explain the variability of population estimates between years. Without data before 1998, it is impossible to conclude

whether 1998 was an anomalously high year (relative to previous years) or if the population actually crashed in 1999 from consistently high historical population levels (Fig. 1). By quantifying both suitable habitat and yearly microhabitat availability, future studies may gain a better understanding of what drives basilisk population trends.

Finally, it is possible that increased trail traffic along banks near the mouth of the Río Claro could be driving basilisk population further upstream. A survey of the stretch of the Río Claro that we sampled in this study compared to additional sections upriver could uncover whether the population is actually declining in time or has simply shifted in space (i.e. upriver).

Our finding that large basilisks tend
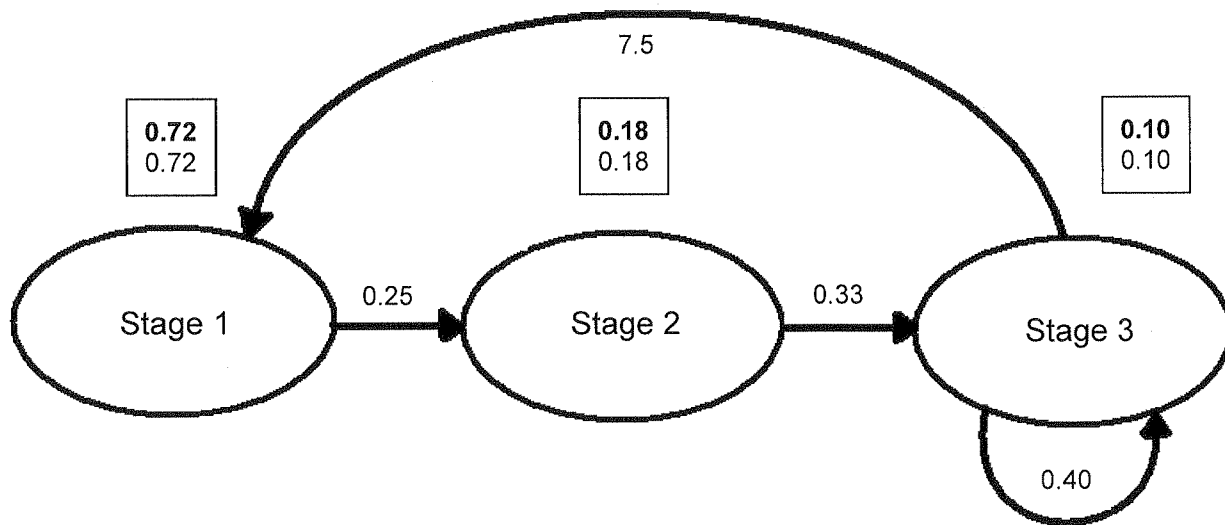
FIG. 2. Life cycle diagram of survivorship and fecundity for two basilisk subpopulations (Río Claro and the combined two small streams) in Corcovado National Park, Costa Rica. Arrows are labeled with proportional survivorship between stage classes; numbers are estimates from 2009 Corcovado data combined with Guanacaste data (Van Devender 1986). Numbers in boxes represent proportion of lizards in each stage class at Stable Age Distribution in our modeling exercise (bold for Río Claro, regular for streams 1 and 2 combined). Stage class proportions are identical for Río Claro and streams 1 and 2 because the estimated survivorship between stages is identical for the two populations for the purpose of this modeling exercise. Stage 1 = 0-20 cm, Stage 2 = 20-40 cm, Stage 3 = 40+ cm.
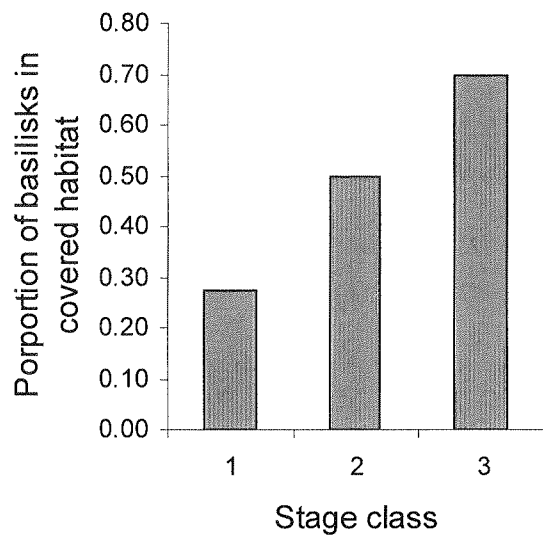
FIG. 3. Proportion of basilisks for each size class found in covered habitat during a population survey in Corcovado National Park, Costa Rica. Cover was a subjective assessment of the immediate habitat surrounding the observed lizard and included overhanging roots, foliage, or fallen trees (n = 61).

to occupy covered areas while small basilisks tend to occupy open areas is consistent with Braden et al. (2001), who attributed this pattern to a social dominance hierarchy. But we observed many unoccupied covered habitats along the riverbank, suggesting the population is not habitat-limited. We propose, as an alternative explanation based on life history observations by Van Devender (1986), that young lizards are capable of running farther on water than older lizards. However, older, reproductive-age lizards may be less vulnerable to potential ground predators due to their larger size (Van Devender 1986). Therefore we propose that young lizards are found more in the open because they can forage more efficiently there, and can use water to escape from predators. As lizards age, we sug-

gest it becomes advantageous to seek cover to protect potential nesting sites and avoid aerial predation.

In summary, a study of microhabitats along the Río Claro could help to determine how annual microhabitat variation and availability influence basilisk distribution. Population data from upstream habitats will help clarify whether the temporal decline is limited to habitats near the mouth of the stream.

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Effects of Fragmentation on Forest Structure in Corcovado National Park

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Faculty Editor: David R. Peart

Abstract: Fragmentation can strongly affect forest structure. We compared two tropical forest sites that both experienced understory clearing in the 1970s: one site that was left surrounded by forest and one fragment that was surrounded by pastures that have since been allowed to regrow. As expected, the fragment, which is likely to have experienced more edge-related disturbance than the unfragmented site, had fewer large trees and an overall lower basal area.

Key words: undercutting, succession, edge effects

Efectos de la fragmentación en la estructura del bosque en el Parque Nacional Corcovado

Resumen: La fragmentación puede afectar considerablemente la estructura del bosque. Comparamos dos sitios de bosque tropical cuyo sotobosque fue desmontado en los años 1970s: El primero quedó rodeado por bosque y el otro permaneció rodeado de potreros a los que posteriormente se les permitió regenerarse. Como esperábamos, el fragmento aislado, que posiblemente ha experimentado mayor perturbación relacionada al borde en relación al sitio sin fragmentar, tenía menos arboles grandes y una área basal total menor.

Palabras clave: desmonte del sotobosque, sucesión, efecto de borde

Introduction

Human land use impacts forests beyond the areas directly affected by human activities. Forest fragmentation causes edge effects (Oliveira-Filho et al. 1997), such as increased light penetration and greater wind exposure (Laurance et al. 1999), that lead to high tree turnover rates (Laurance et al. 2006).

We assessed two forest stands in Corcovado National Park as the start of a long-term study on forest response to human land use. The two sites, located near the Espaveles and Sirena trails, were both undercut in the mid-1970s (E. Deinert, pers. comm.). A 1980 aerial photo of the area showed similar tree canopy sizes and densities for both stands (Phillips 1989). However, the Espaveles sample site was surrounded by forest of similar apparent structure, while the area around the Sirena sample site was clearcut for pasture (Phillips 1989). Despite their similar land use histories, we expected these two stands to have different structures due to the edge effects of fragmentation. Specifically, we predicted that there would be greater basal area and more canopy cover in the Espaveles site.
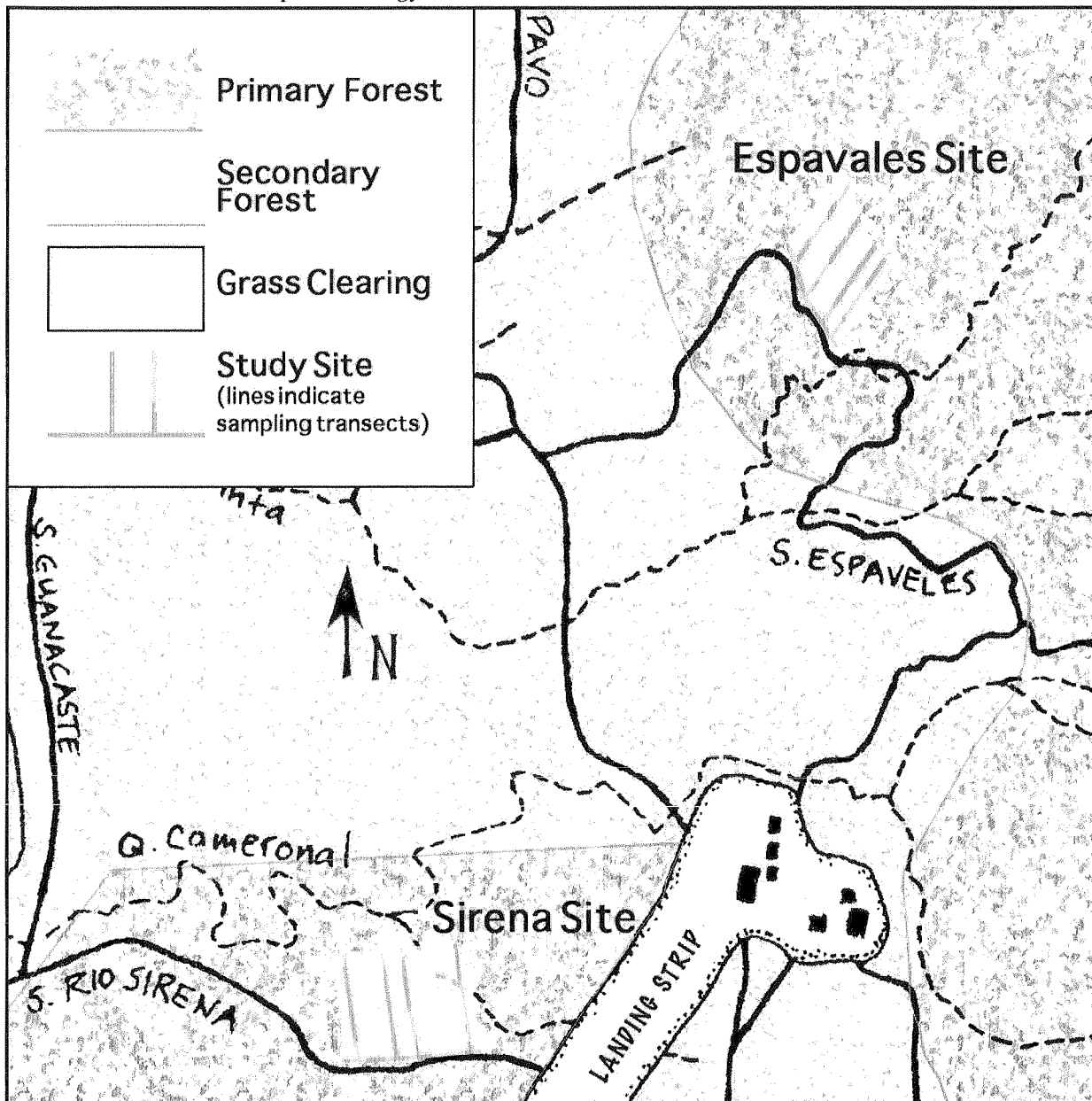
FIG. 1. Map of the area around Sirena Biological Station, Corcovado National Park, showing the two sites at which we sampled forest structure. Note the area of clearcutting around the Sirena site. Trail map by P. Valverde, M. Swartz, K. Warkentin, L. Gilbert, and D. Westcott; primary vs. secondary forest taken from Phillips 1989.

We also predicted that there would be fewer large trees and more small trees at the Sirena site due to more tree falls and subsequent regeneration.

METHODS

We sampled along the Espaveles and Sirena trails near the Sirena Biological Station, in Corcovado National Park, Costa Rica (Fig. 1). The Espaveles site was located in a large patch of primary forest behind the station that is bordered to the southeast by a ridge. The Sirena site was within 1 km of the Pacific Ocean,

and most of the land surrounding it was cut and maintained as pasture in the 1960s (Phillips 1989). Both were primary forest that was undercut in the early 1970s before being preserved by the formation of Corcovado National Park in 1975 (E. Deinert, pers. comm.). However, the Sirena site has been a forest fragment for ca. four decades, with secondary forest developing around it since the establishment of the park.

For each site, we used a stratified random sampling scheme. We marked points every 10 m along the trail for 100
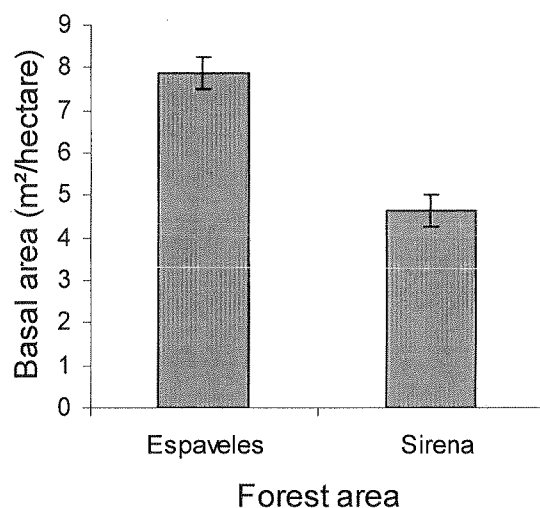
FIG. 2. In forest near the Sirena Biological Station, Corcovado National Park, basal area was higher in an area of continuous forest (Espaveles) than in a forest fragment (Sirena) (n = 32 plots). Bars are means ± 1 S.E.

m and randomly chose four of them to begin transect lines. From each of these points, we moved 10m into the forest to avoid effects of the trail, and selected four additional random numbers, from 1-100, to determine where to locate the four sample points along that transect line.

We traveled at 30°N from the Espaveles trail and 340°N from the Sirena trail in order to stay approximately perpendicular to the trail and not encounter any streams. At each site, we repeated this four times for 16 total stratified random sample points.

At each sample point, we estimated total stand basal area using a 2.5 metric basal area prism and evaluated canopy openness facing north, east, south, and west with a spherical densiometer, both from 1.5 m above the ground. We counted trees and lianas in a 10 m x 4 m belt centered on the sample point, oriented lengthwise along the 30°N transects in the Espaveles site and 340°N transects in the Sirena site. We counted trees in three size classes: 10-20 cm diameter at breast height (DBH), 20-30 cm DBH, and over 30 cm DBH. Lianas were
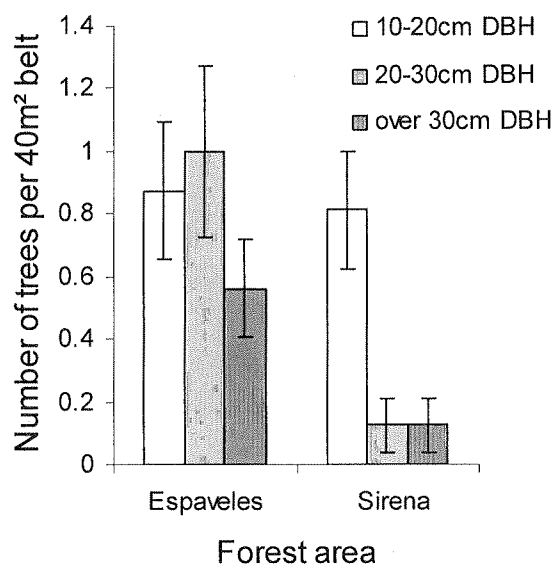
FIG. 3. In Corcovado National Park, the area of continuous forest (Espaveles) had significantly more medium and large trees than did the forest fragment area (Sirena) (n = 32 plots). Bars are means ± 1 S.E.

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classed as 2-5 cm DBH or over 5 cm DBH.

RESULTS

Stand basal area was 1.7 times higher at the Espaveles site than at the Sirena site (t_{30} = 6.22, P < 0.01; Fig. 2). The Espaveles site also had a higher density
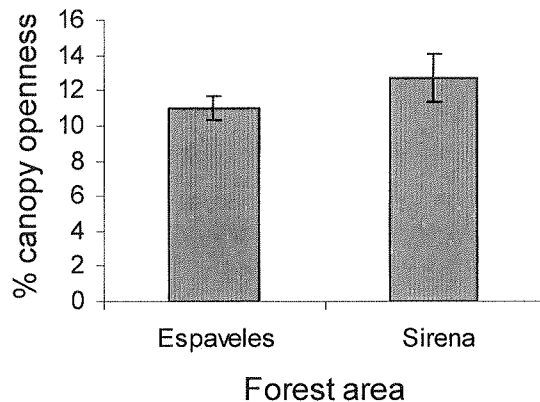
FIG. 4. There was no difference in canopy openness between the area of continuous forest (Espaveles) and the forest fragment area (Sirena) (n = 32 plots). Bars are means ± 1 S.E.

of trees over 30 cm DBH (t_{30} = 2.44, P = 0.02) and between 20-30 cm DBH (t_{30} = 3.05, P < 0.01) than the Sirena site (Fig. 3). However, there was no difference in density of trees 10-20 cm DBH (Fig. 3; t_{30} = 0.22, P = 0.83) or in canopy cover (Fig. 4; $t_{21.9}$ = 1.13, P = 0.27) between sites.

DISCUSSION

The lower basal area (Fig. 2) and fewer large trees (Fig. 3) in the Sirena fragment relative to the Espaveles site is consistent with fragmentation and edge effects found in Amazon forests by Laurance et al. (2006). We noted (without quantification) that the understory of the Sirena site was densely packed with

light-demanding species like *Calathea* spp. and *Acacia* spp., as well as *Bromelia* spp., which prefers dry soils. This is consistent with Oliveira-Filho et al.'s finding that forest fragments favor sun-loving and early successional species (1997). In the Espaveles site, understory plants were sparser and included many shade-tolerant palms and woody plants.

Soil and landscape position may exacerbate the effects of forest fragmentation (Laurance et al. 1999). The Sirena site's sandy soil may result in superficial tree roots, making the trees more susceptible to windfall, as well as favoring plants like *Bromelia* sp., noted above, that perform well in dry soils. The site's proximity to the ocean probably subjects it to stronger winds, increasing the likelihood of blowdowns. In contrast, Espaveles is located on richer alluvial deposits and buffered from winds by a ridge, and therefore probably less prone to wind-driven treefalls. Current differences in forest structure between the two sites may also be, in part, due to differences in the original primary forest that existed at each site before undercutting.

Continuing to monitor forest structure at these two sites will allow for greater understanding of how land use has impacted the forest and how re-growth and succession are proceeding after land protection. This information would offer predictions of forest species population dynamics through time and thus help guide priorities for conservation. A detailed floristic census, measurements of light and wind intensity, and

evaluation of soil characteristics would clarify many of the differences between the two sites implied by our quantitative findings and anecdotal observations. Extending long term monitoring to other stands near the Sirena station, such as unaltered primary forest and former pasture or plantation sites, would increase our understanding of forest successional patterns following the variety of anthropogenic effects in the area.

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Maternal foraging behavior and diet composition of squirrel monkeys (*Saimiri oerstedii*)

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Faculty Editor: David R. Peart

Abstract: We investigated the foraging behavior and diet composition of female *Saimirii oerstedii*. Considering the nutritional and energy requirements of rearing offspring, we predicted (1) that mothers would eat more food items and forage for less time, resulting in a higher foraging rate compared to adult non-mothers and (2) that mothers would consume proportionally more invertebrates because of increased protein demand. From 85 one-minute focal observations comparing a mother to a non-mother, recording food items consumed and behavioral time allotments, we found that mothers did not have a higher foraging rate but did include more protein-rich food items.

Key words: maternal care, time budget tradeoffs, dietary requirements, foraging efficiency

Comportamiento de forrajeo materno y composición de la dieta del mono ardilla (*Saimiri oerstedii*)

Resumen: Investigamos el comportamiento de forrajeo y la composición de la dieta de las hembras de *Saimiri oerstedii*. Considerando los requerimientos de energía del periodo de crianza, nuestras predicciones son (1) que las madres comerían más porciones de alimento y emplearían menos tiempo en forrajear, resultando en una tasa de forrajeo mayor que las hembras adultas que no son madres y (2) que las madres consumirían proporcionalmente más invertebrados en respuesta a una elevada demanda de proteínas. De 85 observaciones focales de 1 min comparando madres y no-madres, el registro de los porciones de alimento consumidos y el empleo de tiempo en estas conductas, encontramos que las madres no tienen una tasa de forrajeo mayor, pero si incluyen porciones de alimento más ricos en proteínas.

Palabras clave: cuidado maternal, compensación, presupuestos de tiempo, requerimientos de dieta, eficiencia de forrajeo

INTRODUCTION

Producing milk and carrying young require primate mothers to consume more protein and calories (Herrera and Heymann 2004). To meet increased nutritional needs mothers face many tradeoffs and must change their behavior to ensure their infants' survival (McCabe and Fedi-gan 2007). We compared *Saimiri oerstedii* (squirrel monkeys) to determine if these tradeoffs are reflected in changes in diet and foraging behavior of mothers compared to females without babies (non-mothers).

We predicted that mothers would address these tradeoffs by eating more food in less time than non-mothers. We also

predicted that mothers would consume a higher proportion of invertebrates than non-mothers as invertebrates are particularly protein-rich (McCabe and Fedigan 2007).

METHODS

Study Site

Our study was conducted on 6 and 7 February 2009 in Corcovado National Park near the Sirena Biological Station. We followed troops of *Saimiri oerstedii* (squirrel monkeys) near Sendero Naranjo and Sendero Río Sirena through secondary forest, the squirrel monkeys' preferred habitat (Emmons 1990). Our study site also included a small amount of primary forest that had been undercut in the 1970s.

Experimental Design

We conducted paired one-minute focal observations (n = 85), observing one mother and one non-mother, to control for time of day, weather, troop dynamics, and food availability. We followed two troops that included three to four mothers each carrying a single offspring. Squirrel monkeys have synchronous breeding periods (Wainwright 2002), so all infants were of similar ages, likely making similar nutritional and physical demands on their mothers. We selected one visible mother, chose the nearest visible female non-mother, and performed as many focal observations on these same individuals as possible. Ideally, we would have made a series of focal observations on a particular mother/non-mother pair, and then replicated that protocol across several different pairs to obtain independence. However, this was not feasible since we could not keep track of focal individuals for more than several minutes at a time.

We noted the number of hand-to-
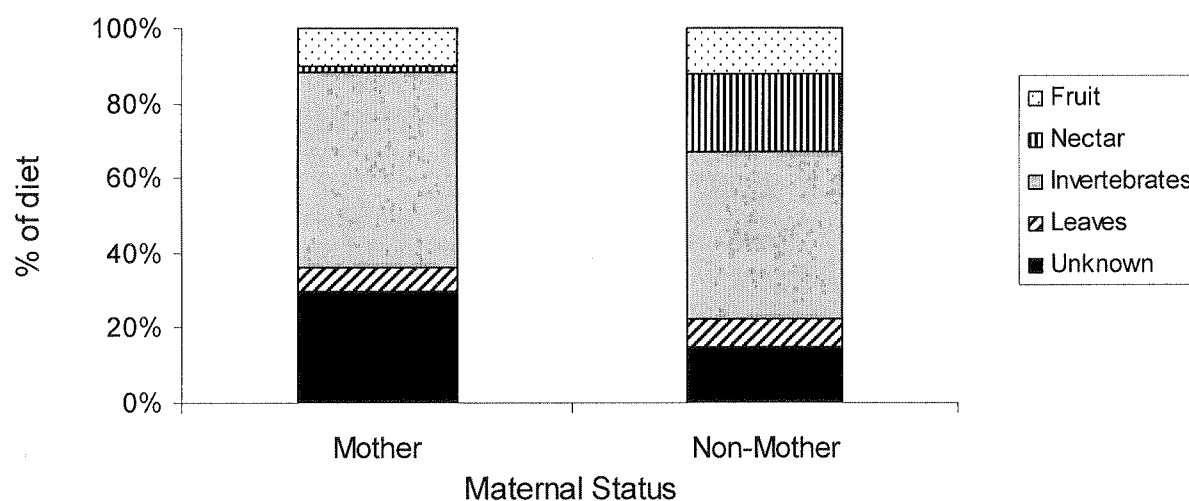
FIG. 1. Average proportion of diet for mother and non-mother squirrel monkey (*Saimiri oerstedii*) individuals. Mothers: 10% fruit, 2% nectar, 52% invertebrates, 6% leaves, and 30% unknown. Non-mothers: 12% fruit, 21% nectar, 44% invertebrates, 8% leaves, and 15% unknown. From a sample of 81 pairs of mother and non-mother squirrel monkey individuals in Corcovado National Park, Costa Rica on 6 and 7 February 2009.

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mouth movements each individual made during the one-minute observation periods, and classified each food item consumed as fruit, nectar, invertebrate, leaf, or unknown. The nectar came solely from *Aphelandra golfodulcensis* (Acanthaceae), an understory plant with red, tubular flowers that are hummingbird-pollinated. We assumed that each hand-to-mouth movement contained the same quantity of food and the same nutritional and caloric value within a type of food. We also recorded the time spent by each individual foraging, resting, and moving. Foraging was defined as consuming or searching for food items. Moving was defined as movement when they were clearly not looking around for food, and resting was defined as lying down, or sitting without chewing.

Data Analysis

Although our trials were not independent due to repeated sampling of mothers, we nevertheless assumed independence for all statistics. We analyzed the total amount eaten and the total amount of foraging time for pairs of mothers and non-mothers using a Wilcoxon signed-rank matched pairs test, due to non-normality. We calculated foraging rates for every individual by dividing the total number of foraging events by the number of seconds spent foraging in each focal observation period. For normality, we log-transformed foraging rate data before doing a matched pairs test. Finally, to test for the difference in foraging between mothers and non-mothers on both invertebrates and nectar, we per-

formed Fisher's Exact Tests for both food types. We used JMP v. 7.0 (SAS Institute, Inc. 2007) for all analyses.

RESULTS

There was no significant difference in the total amount eaten by mothers and non-mothers (z_{84} = -195.00, P = 0.1933), but non-mothers spent an average of 8 more seconds foraging per bout (z_{84} = -618.00, P < 0.0001). However, the foraging rates for mothers and non-mothers were similar (t_{27} = -1.201, P = 0.2401). Invertebrates composed proportionally more of the mother's diets than non-mothers'—52% and 46% respectively (P = 0.0008)—while non-mothers' diets contained ten times as much nectar as mothers' (P < 0.0001, Fig. 1). Finally, it appears
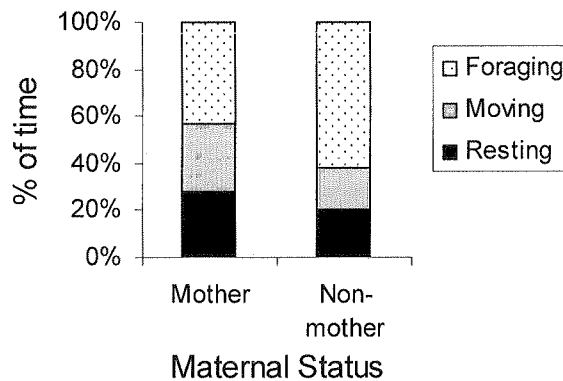
FIG. 2. Average proportion of time spent foraging, moving, and resting for mother and non-mother squirrel monkey (*Saimiri oerstedii*) individuals (n = 81 pairs) in Corcovado National Park, Costa Rica on 6 and 7 February 2009. Mothers: 43% foraging, 29% moving, and 28% resting. Non-mothers: 62% foraging, 17% moving, and 21% resting.

that mothers and non-mothers allocate their time differently; non-mothers spend a greater proportion of time foraging (t_{80}

= -3.73, P = 0.0004) while mothers spend more time moving (t_{80} = 2.67, P = 0.009; Fig. 2).

DISCUSSION

Mother squirrel monkeys increased their foraging efficiency, not by eating more food in less time than non-mothers, but by consuming higher quality food (protein-rich invertebrates) in less time. Because mothers spent less time foraging, we suggest there is a tradeoff between foraging and caring for offspring.

Mothers foraged less than non-mothers on protein-poor nectar, supporting our conclusion that mothers prefer a high protein diet. We suggest that by not foraging in the understory (where *A. golfodulcensis* nectar-bearing flowers are abundant), mothers may reduce predation risk.

Ideally, we would have kept all samples independent, but this would require finding more mothers, and the ability to recognize focal individuals. To compare quantitatively the energy intake between mothers and non-mothers, it would be necessary to measure the caloric content of an item of each food type, and assess the average number of hand-to-mouth movements required to consume each type of food item. Future studies could also compare mothers' foraging behaviors across primate species to determine if our conclusions apply more widely.

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SPATIAL AND TEMPORAL VARIATION IN ACTIVITY AMONG TROPICAL UNDERSTORY BIRDS OF DIFFERENT FORAGING GUILDS

KARL GRUNSEICH AND ROBIN M. MEYERS

Faculty Editor: David R. Peart

Abstract: We used mist-nets to examine how bird activity varies (1) among habitats of different understory stem densities, and (2) between morning and afternoon. We predicted most captures in areas of intermediate stem density (with sufficient habitat structure and also sufficient flying space). We also predicted highest insectivore capture rate in the morning and a relatively constant capture rate of other feeding guilds. The distribution of birds among nets departed from the random Poisson expectation (with marginal significance), but was not associated with understory stem density. The foraging guild capture rate varied as predicted (though our limited data did not allow for statistical tests). We make specific recommendations for using mist-nets to compare activity patterns among foraging guilds.

Key words: mist-net, insectivores, stem density

VARIACIÓN ESPACIO-TEMPORAL EN LA ACTIVIDAD DE LAS AVES DEL SOTOBOSQUE ENTRE DIFERENTES GREMIOS DE FORRAJEO

Resumen: Utilizamos redes ornitológicas para examinar cómo la actividad de las aves varía (1) entre hábitats de diferentes densidades de tallos en el sotobosque y (2) entre la mañana y la tarde. Nuestra predicción fue que la mayoría de las capturas se encontrarían en áreas de densidad intermedia de tallos (con suficiente complejidad estructural y también suficiente espacio para volar). También esperábamos una mayor tasa de capturas de insectívoros en la mañana y una tasa de capturas relativamente constante para otros gremios de forrajeo. La distribución de las aves entre redes es diferente a la esperada distribución de Poisson (marginalmente significativa), pero no estaba asociada a la densidad de tallos del sotobosque. La tasa de capturas por gremio varió como en nuestra predicción. Hacemos recomendaciones específicas para el uso de redes ornitológicas para comparar patrones de actividad entre gremios de forrajeo.

Palabras clave: redes ornitológicas, insectívoros, densidad de tallos.

INTRODUCTION

Mist-netting can be used to examine the species composition and abundance of understory birds and to examine how activities of species or guilds change over time. One difficulty with mist-netting is obtaining sufficient data for statistical inference. In this study we experienced this limitation, so we present some of our results as "apparent trends" that could be tested in a more extensive study.

We examined temporal variation in activity of understory birds of different feeding guilds in a tropical lowland forest. We predicted that the capture rate of insectivores would be highest in the early morning due to high food availability

and would decrease over the day. We predicted that birds from other feeding guilds would be captured at a constant rate across the day because there is little to no variation in their food availability (mainly fruits and seeds). Although nectar availability varies, we did not make specific predictions about nectarivore activity and captured few hummingbirds.

We also tested for effects of forest structure on spatial variability in bird activity. We predicted that open areas with low understory stem density would be relatively poor habitats for birds, while high understory stem density would be a difficult habitat to navigate while foraging. Thus we predicted the highest capture rate in habitats of intermediate stem density.

Finally, we conclude with an examination of possible factors that influence variation in the number of captures for different nets, and what measures could overcome bias caused by this variation.

METHODS

We placed 10 mist-nets along a 1 km stretch of Sendero Pavo beginning just past the intersection with Sendero Guanacaste and extending further north (away from the Sirena Biological Station) in Corcovado National Park, Costa Rica. Corcovado is lowland tropical forest and our net array ran through second growth. Each net had at least 40 m of trail separating it from the nearest net. On 6 and 7 February 2009, nets were open from ca. 0600 to 1015 and 1335 to 1640. Nets were checked at ca. 40 min intervals. We iden-

tified each bird species captured and classified it as either predominantly insectivorous or other (nectarivores, fruigivores, and granivores) using information in Stiles and Skutch (1989). To estimate stem density of trees in a 13 m x 13 m area near each net, we established two 6.5 m x 2 m belt transects that ran from points on the net 4 m from each pole, and extending perpendicularly outwards on opposite sides of the net (Fig. 1). We counted stems less than 5 cm DBH
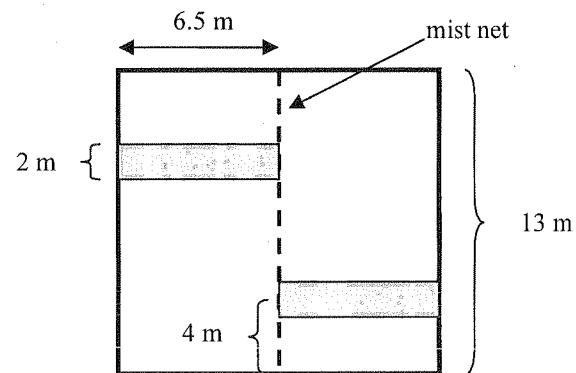
FIG. 1. Layout of belt transects (gray bars) used to estimate density of small (< 5 cm DBH) stems in the understory of secondary forest at Corcovado Natl. Park.

in each belt, classifying each as either woody or non-woody. Trees with DBH greater than 5 cm were counted in the entire 13 m x 13 m area surrounding the net.

Statistical Methods

We used a Poisson distribution and χ^2 test to determine whether the distribution of bird captures among nets was different from random. We used EcoSim v. 7.72 to generate a species richness accumulation curve for all species caught (Acquired Intelligence Inc. 2005). To test

our prediction that the highest number of captures would occur at intermediate stem densities we used a quadratic regression. We also tested this relationship with a linear regression and determined that a quadratic regression better fit the data. We conducted the regression analysis in JMP v 7.0 (SAS Institute, Inc. 2007). We limited the interpretation of temporal variation in capture rate to a graphical analysis, as our study spanned only two days.

RESULTS

We captured 56 birds of 24 species (Table 1) over 147.5 mist-net hours. Some may have been recaptures. The species richness accumulation curve did not reach saturation (Fig. 2), so we were unable to estimate a total species richness of understory birds. Birds caught per net ranged from 2 to 10. However, the difference between the distribution of captures among nets and a corresponding Poisson distribution (the random expectation)

TABLE 1. Understory birds captured in mist-nets over two days (147.5 mistnet-hrs) in secondary forest at Corcovado National Park. Species are listed in order by number of individuals captured. Feeding guilds are listed as used in this study.

Latin Name		Common Name	Feeding Guild	Captures
Eucometis	penicillata	Gray-headed Tanager	Insectivore	8
Phaethornis	longirostris	Long-billed Hermit	Other	6
Pipra	coronata	Blue-crowned Manakin	Other	5
Terenotriccus	erythrurus	Ruddy-tailed Flycatcher	Insectivore	4
Platyrinchus	coronatus	Golden-crowned Spadebill	Insectivore	4
Gymnopithys	leucaspis	Bicolored Antbird	Insectivore	3
Hylophilus	ochraceiceps	Tawny-crowned Greenlet	Insectivore	3
Thamnophilus	bridgesi	Black-hooded Antshrike	Insectivore	2
Mionectes	oleagineus	Ochre-bellied Flycatcher	Other	2
Hylocharis	eliciae	Blue-throated Goldentail	Other	2
Myiobius	sulphureipygius	Sulphur-rumped Flycatcher	Insectivore	2
Myrmotherula	schisticolor	Slaty Antwren	Insectivore	2
Archilochus	colubris	Ruby-throated Hummingbird	Other	2
Dendrocincla	anabatina	Tawny-winged Woodcreeper	Insectivore	1
Attila	spadiceus	Bright-rumped Attila	Insectivore	1
Thamnistes	anabatinus	Russet Antshrike	Insectivore	1
Phaethornis	striigularis	Stripe-throated Hermit	Other	1
Rhytipterna	holyerythra	Rufous Mourner	Insectivore	1
Arremon	aurantiirostris	Orange-billed Sparrow	Insectivore	1
Myrmeciza	exsul	Chestnut-backed Antbird	Insectivore	1
Malacoptila	panamensis	White-whiskered Puffbird	Insectivore	1
Xenops	minutus	Plain Xenops	Insectivore	1
Dendrocolaptes	sanctithomae	Northern Barred-Woodcreeper	Insectivore	1
Myiarchus	tuberculifer	Dusky-capped Flycatcher	Insectivore	1
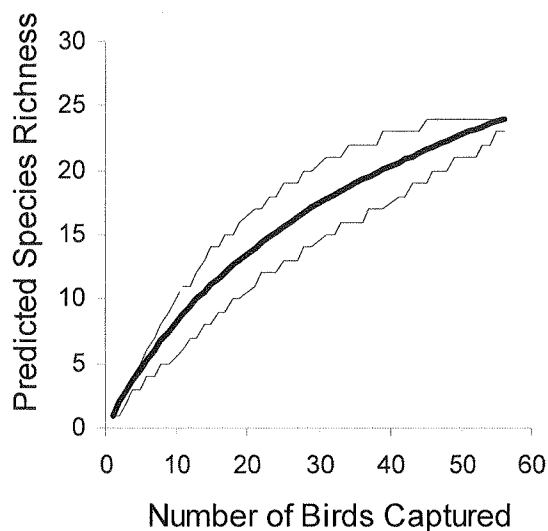
FIG. 2. Partial species richness accumulation curve for birds captured in secondary forest in Corcovado Natl. Park on 6-7 Feb 2009, based on samples described in Table 1. The curve, generated by EcoSim, indicates saturation was not reached, and our sampling did not capture the total richness of the area. Dotted lines indicate 95% confidence interval.

was only marginally significant ($\chi^2_{10} =$ 17.46, $P = 0.06$). Number of captures was not related to total stem density (quadratic; $r^2 = 0.02$, $F_{2,7} = 0.06$, $P = 0.94$, linear; $r^2 = 0.00$, $F_{1,8} = 0.01$, $P = 0.92$). For the following results, due to limitations in the data, we could not use statistical inference. However, we believe there are interesting and suggestive patterns in the data. Based on pooled data for both days, the average capture rate decreased over the course of the day (Fig. 3). This apparent trend was driven by insectivores, which greatly decreased, from 0.45 to 0.11 captures per mist-net hr, throughout the day. Capture rate of the other foraging guilds remained relatively constant throughout the day. The total capture rate dropped from 0.50 to 0.26 captures per mist-net hour from day one to day two.
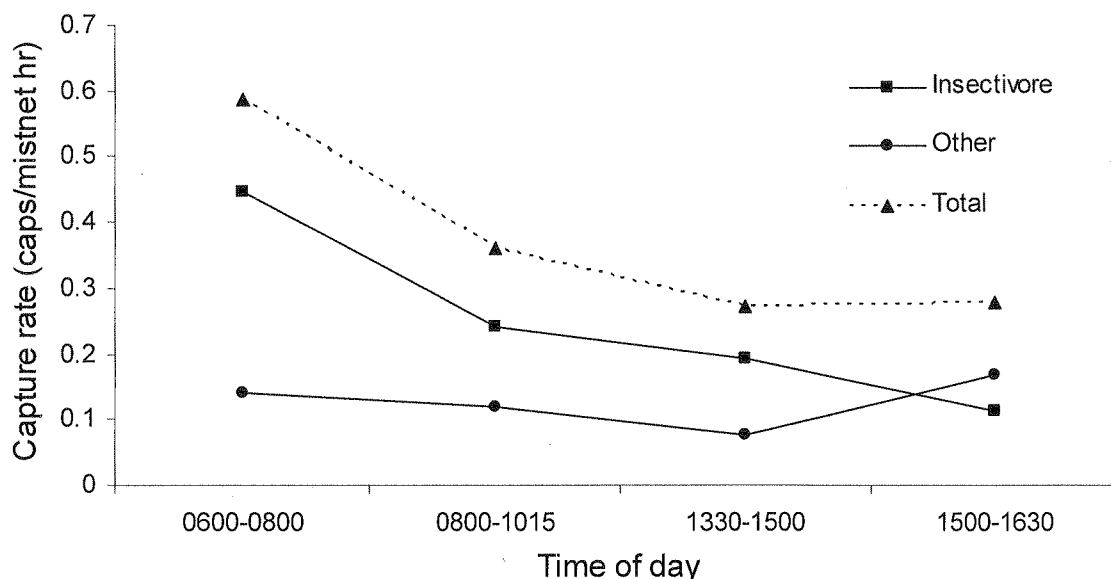
FIG. 3. Capture rate for two avian foraging guilds across different times of day in secondary forest at Corcovado National Park on 6-7 Feb 2009. Insectivore capture rate decreased while species of other guilds remained relatively constant. With only two days of data we could not test these trends statistically. (Times listed are approximate due to slight variation in sampling times for each day.)

DISCUSSION

Contrary to our main predictions, understory stem density was not related to mist-net bird captures. Other descriptors of understory vegetation such as plant species composition may be superior predictors of capture rate, and our samples may not have encompassed a sufficient range of understory bird habitats to influence the capture rate of birds.

During the two days of our study, capture rate was greater among insectivorous birds in the morning than in the afternoon, while birds of other foraging guilds were caught at similar rates morning and afternoon, as we predicted. Insect availability peaks in the morning and declines over the day (Flaspohler 1998), while fruit and seed availability does not.

On day 2, capture rate decreased, without change in weather conditions, possibly due to net shyness resulting from captures on day 1. Net shyness is more pronounced among tropical birds than temperate birds (MacArthur and MacArthur 1974).

It would be useful if future studies could statistically test these apparent trends in bird capture rates, by feeding guild and over time. Based on our data, studies aiming to have high capture rates of insectivores or total birds should set nets during the morning hours while those examining birds from other foraging guilds could set nets at any time of day (Fig. 2). Relocating nets periodically to avoid the effect of net shyness could also lead to higher capture rates. Finally, setting nets to encompass the full range of secondary forest habitat diversity would make mist-net results more broadly applicable.

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Evaluation of Mist-Netting as a Method to Examine Seed Content in Feces from Tropical Understory Birds

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Abstract: We examined seed content in feces of frugivorous tropical understory birds by mist-netting in the successional plots at La Selva Biological Station, Costa Rica. In 110 mist-net hours, we obtained fecal samples containing seeds from 18 individuals of five frugivorous species, including 11 White-collared Manakins (*Manacus candei*). Seed morphotypes present varied greatly among fecal samples, and the low overlap between individuals of the same species indicates we would need larger samples to characterize species' seed/fruit diets and to test for differences among species. Based on our data, we suggest a sample size and layout of mist-nets that could yield the necessary data.

Key words: ornithology, mutualism, seed viability

Evaluación del Uso de Redes como un Método para Examinar el Contenido de Semillas en las Heces de Aves Tropicales del Sotobosque

Resumen: Examinamos el contenido de semillas en las heces de aves tropicales frugívoras de sotobosque a través de capturas en redes en las parcelas sucesionales de la Estación Biológica La Selva, Costa Rica. En 110 horas/red, obtuvimos muestras fecales de 16 individuos de cinco especies frugívoras, incluidos 11 individuos de *Manacus candei*. Los morfotipos de semillas exhiben gran variación entre muestras fecales y el reducido traslape entre individuos de la misma especie indica que requeriríamos de tamaños de muestra mayores para caracterizar las dietas de frutas de las especies y encontrar diferencias entre las especies. En base a nuestros datos, sugerimos un tamaño de muestra y una distribución de redes que podría generar los datos necesarios.

Palabras clave: ornitología, mutualismo, viabilidad de semillas

Introduction

Frugivorous birds are important seed dispersers in tropical forests (Loiselle and Blake 1999). Our goal was to characterize the seed content in feces from mist-netted understory frugivorous birds in successional forest plots at La Selva. We expected but did not observe substantial overlap in seed morphotypes among fecal samples from individuals of the same species. Thus, it became clear that we would need larger samples to characterize species' seed/fruit diets, and to test for differences among species. Rather than attempting to draw strong conclusions from a limited data set, we simply summarize our results and use them to inform specific recommendations for future studies of avian seed/fruit diets using mist-net captures.

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METHODS

Study Site

We conducted our study in the tropical wet forest near the Organization for Tropical Studies La Selva Biological Station. La Selva has sections of pasture along with primary and secondary forest. Our mist-nets were located alongside six successional experimental plots (0-1 years to 4-5 years since cutting), off the Sendero Sábalo-Esquina (Fig. 1).

cate during handling, we placed it in a paper-lined cardboard box for up to 30 min to collect a fecal sample.

We counted the seeds (if any) in each fecal sample, separating seeds into 22 morphotypes. Where possible, we matched seed morphotypes to seeds from fruits collected from the successional plots. Finally, each seed morphotype was verified by Orlando Vargas (La Selva Biological Station assistant director) to be a distinct species, though the

FIG. 1. Map of the mist-net array (nets 1-10) in the successional plots at La Selva Biological Station, Costa Rica.

Experimental Design

We mist-netted understory birds (n = 87) on 16 and 17 February 2009 from 0600–1130, using ten nets checked ca. every 30 min (110 mist-net hrs; Fig. 1). We identified each bird to species, and where possible, to sex. For species that eat fruit (Stiles and Skutch 1989), we collected fecal matter if the bird defecated during handling. If the bird did not defe-

species was not identified in all cases. We assumed that all intact seeds were viable.

RESULTS

We found 22 seed morphotypes in fecal samples from five bird species: White-collared Manakin (*Manacus candei*, "WCMA," n = 11 birds), Buff-throated Saltator (*Saltator maximus*, "BTSA," n = 2 birds), Ochre-bellied Flycatcher
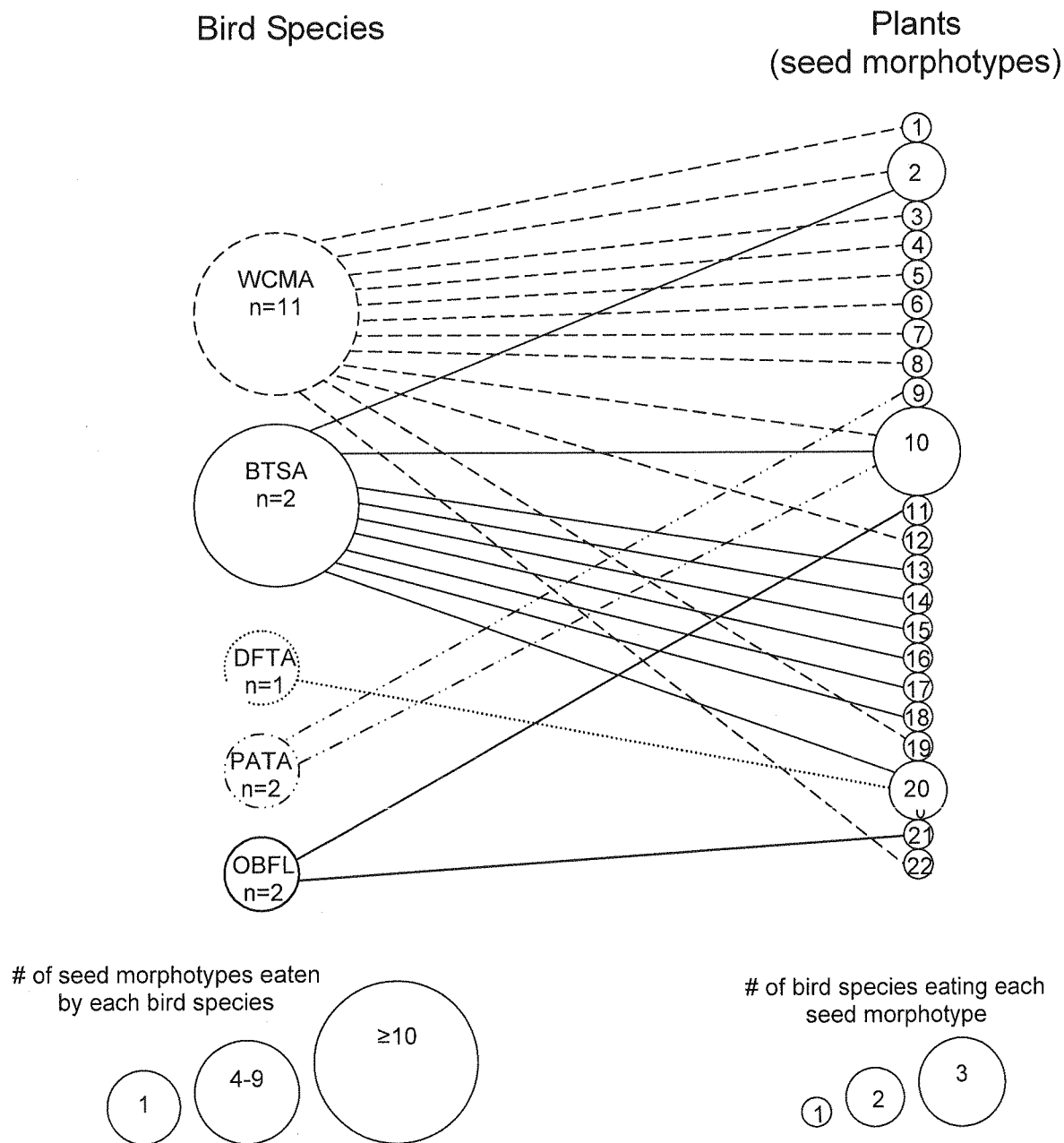
FIG. 2. Relationships between the 22 seed morphotypes found in fecal samples and the five understory bird species that defecated them at La Selva Biological Station, Costa Rica. WCMA: White-collared Manakin (*Manacus candei*). BTSA: Buff-throated Saltator (*Saltator maximus*). OBFL: Ochre-bellied Flycatcher (*Mionectes oleaginous*). PATA: Passerini's Tanager (*Ramphocelus passerinii*). DFTA: Dusky Faced Tanager (*Mitrospingus cassinii*). Line styles differentiate between bird species.

(*Mionectes oleaginous*, "OBFL," n = 2 birds), Passerini's Tanager (*Ramphocelus passerinii*, "PATA," n = 2 birds), and Dusky-faced Tanager (*Mitrospingus cas-sinii*, "DFTA," n = 1 bird). WCMA ate 12 different seed morphotypes, BTSA ate nine, OBFL and PATA ate two morpho-types each, and DFTA ate one (Fig. 2).

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Most of the seed morphotypes in fecal samples were eaten by a single species in our sample: two seed morphotypes were eaten by two bird species, and one was eaten by three bird species.

Altogether, the 11 WCMA passed 12 seed morphotypes, 10 of which were unique to WCMA in our limited sample (Fig. 3). Three out of seven males, as well as two out of four females, passed two or
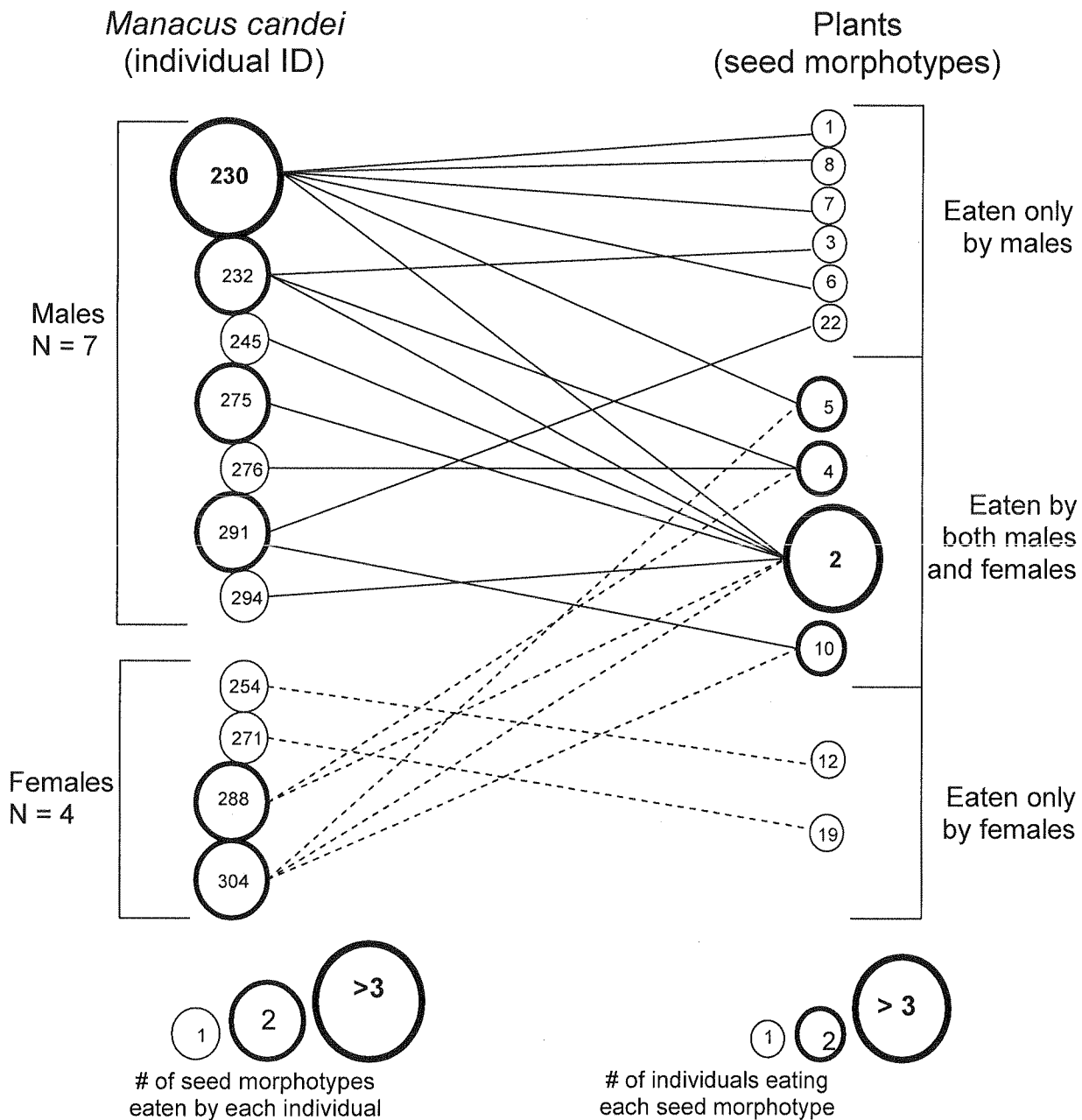
FIG. 3. Relationship between the 12 seed morphotypes found in fecal samples and the 11 White-collared Manakins (*Manacus candei*) that defecated them at La Selva Biological Station, Costa Rica. Numbers in circles indicate the bird and seed morphotype number. Line styles differentiate between males and females.

more seed morphotypes. Six seed morphotypes were unique to males, two were unique to females, and four were passed by both males and females.

DISCUSSION

We found a wide range of seed morphotypes in the fecal samples of the frugivorous birds we caught. However, the seeds in each sample provided only a snapshot of each bird's diet; this, combined with our small sample size, means that we cannot draw strong conclusions. The birds removed a wider variety of seeds than we expected (given that birds carry seeds only from plant species with ripe fruit). Further, since many fecal samples contained seeds and insect parts, omnivorous birds clearly play a role as seed removers.

WCMA passed twelve different seed morphotypes and was the only strictly frugivorous bird species caught (n = 11 birds). Because of the low overlap of seed morphotypes between individual WCMA, we expect that we did not reach "saturation" in our sample; this species probably removes seeds of many more morphotypes than we observed. Our data also suggest differences between the seed carrying tendencies of males and females. However, we have insufficient data to adequately describe the dietary differences between the sexes, or determine the breadth of WCMA's diet, or compare WCMA to other species.

Mist-netting provides an opportunity to study birds up close, and fecal samples can provide essential information about the seeds they potentially disperse. However, to make strong conclusions from mist-net data, sample sizes would have to be increased. It is important to select a study site that has a high density of birds. Of the sites visited on the Dartmouth Foreign Study Program, only La Selva had a high enough capture rate from mist-nets to make such a project feasible. Fifteen nets would increase captures by 50% and still be manageable for a small group. Finally, the sampling time could be increased from two to four days (doubling the sample size), but this may require shifting the nets at least once to reduce the effects of "net shyness" (avoidance of nets by birds previously captured). In combination, these modifications could increase sample size three-fold. Based on our sample, this could result in more than 30 manakins and 300 total birds. With a sample of that size, it may be possible to approach seed morphotype saturation for abundant bird species, and draw stronger conclusions about the comparative seed removal effectiveness of bird species in these successional plots.

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"Fig"uring it out: An evaluation of differential seed removal by frugivorous avifauna

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Faculty Editor: David R. Peart

Abstract: To assess differential seed removal by four size classes of frugivorous birds, we observed birds feeding on a fruiting fig tree in La Selva Biological Station, Costa Rica. We recorded three aspects of foraging behavior as a proxy for seed dispersal effectiveness: rate of fruit removal, time foraging per visit, and distance flown after leaving the tree. We predicted (and found) that seed removal would increase with bird size because larger birds ingest more seeds. Large birds also flew further than small birds immediately after leaving the tree.

Key words: foraging behavior, seed dispersal

Una evaluación de remoción diferencial de semillas por aves frugívoras

Resumen: Para determinar la remoción diferencial de semillas por aves frugívoras de cuatro clases de tamaños, observamos aves alimentándose de una higuera fructificando en la Estación Biológica La Selva, Costa Rica. Registramos tres aspectos del comportamiento de forrajeo como indicadores de efectividad en la dispersión de semillas: tasa de remoción de frutos, tiempo de forrajeo por visita y distancia a la que volaron después de dejar la higuera. Nuestra predicción (y hallazgo), fue que la remoción de semillas incrementaría con el tamaño del ave porque las aves de tamaño más grande ingieren más semillas. Inmediatamente después de dejar el árbol, las aves más grandes volaron distancias mayores que las aves pequeñas.

Palabras clave: comportamiento de forrajeo, dispersión de semillas

Introduction

Some avian frugivores ingest fruits and defecate seeds, potentially acting as effective dispersal agents. Fruit removal effectiveness depends on visitation and fruit removal rates (Stoner and Henry undated). Birds that carry seeds farther from the tree before defecating contribute more to seed dispersal. We could not evaluate seed dispersal in terms of distance carried or microhabitat placement, but estimated fruit removal rate, time spent foraging, and distance flown when leaving the tree, as possible indicators of seed dispersal effectiveness.

We observed foraging birds in a fruiting fig tree at La Selva Biological Station, Costa Rica. Our hypotheses were organized around bird size classes because we were unable to identify some birds to species. It would have been preferable to test hypotheses according to species or higher taxonomic categories. Instead, we hypothesized that larger birds would be more effective seed removers than small

birds. We predicted that birds would spend similar amounts of time foraging, but that small birds would drop more seeds at the tree because they have more trouble ingesting them. Knowing that small birds are often the most abundant size class in tropical forests (Terborgh et al. 1990), we predicted that small birds would make the most visits. We also tested whether different size classes of birds flew different distances after feeding in the tree. We had no prior prediction regarding distances traveled by birds of different sizes.

METHODS

On 16 and 17 February 2009, we observed birds visiting a *Ficus colubrinae* tree near the Camino Experimental Sur/ Sendero Tres Rios trailhead at Estación Biológica La Selva, Costa Rica. We sampled from 0830 to 1030 on both days and 1400 to 1600 on the first day.

We observed three aspects of bird foraging behavior. First, we ran two-minute focal samples, counting the number of figs taken from the tree by a bird, how many figs were dropped before processing, how many were processed to remove seeds before consumption, and how many were consumed whole. The focal individuals were haphazardly chosen from birds observed foraging at the tree. All birds used in the foraging rate focal samples were later identified to species. For the two sampling methods described below, birds were placed into size classes based on visual estimates: small (<20 cm), medium (20-40 cm), large (40-60 cm), and extra-large (>60cm). Eleven small, nine medium, six large, and four extra-large birds were observed in the focal samples.

Second, we observed birds during their whole visit to the fig tree, timing how long they spent in the tree and how
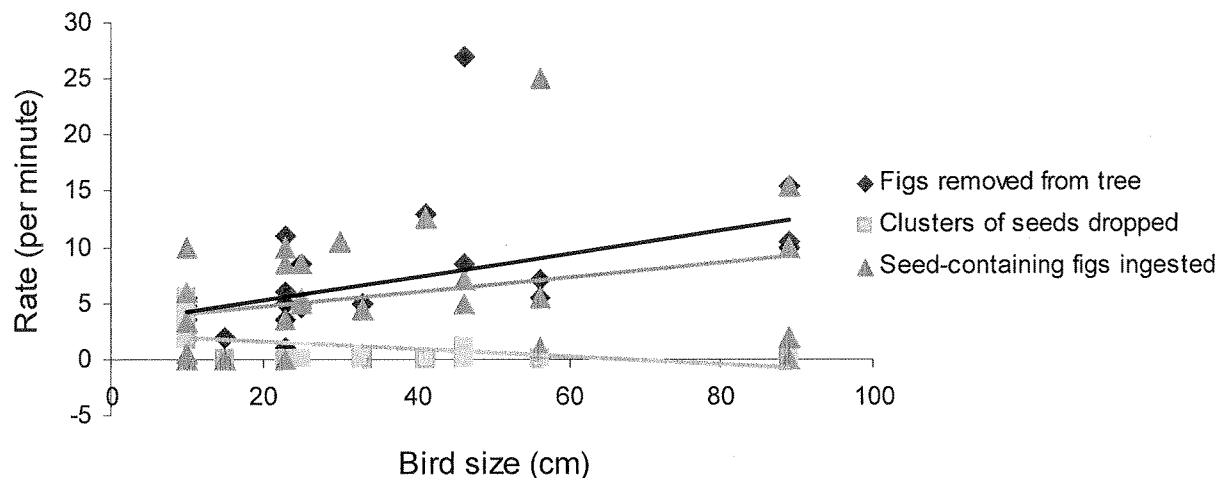
FIG. 1. Birds were observed feeding on a *Ficus colubrinae* tree in La Selva National Park for two minutes. Each point represents the rate of the given behavior for one observed bird. Some birds would process figs before eating them, dropping a cluster of seeds per fig, so units of clusters were used to measure seed-dropping. Per minute, smaller birds took significantly fewer figs and dropped significantly more seeds at the tree than larger birds, meaning that overall they ingested significantly fewer seed-containing figs (n = 30 birds).
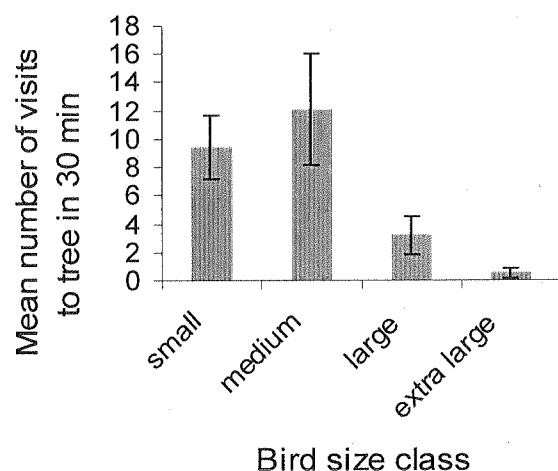
FIG. 2. Significantly more small and medium birds visited a single *Ficus colubrinae* tree in La Selva National Park over a 4 hr study period than large or extra-large birds (n = 252 birds). Bars are means ± 1 S.E. .

much time they spent foraging. When the first focal individual left, the next individual to arrive at the tree was observed, and so on, until observations were completed. We observed a total of 32 small, 26 medium, 16 large, and one extra-large bird over 6 hours of observations.

Third, we observed departing birds' first flight from the tree, noting which clump of trees they went to and visually estimating a distance class. Distance classes were short (5-10 m), medium (10-50 m), and far (>50 m). We observed the first flights of 83 small birds, 115 medium birds, 28 large birds, and 2 extra large birds. We excluded extra large birds in

our analysis due to small sample size.

All statistical analyses were performed using JMP v. 7 (SAS Institute, Inc. 2007).

RESULTS

Birds of all size classes spent similar amounts of time foraging (χ^2_3 = 5.44, P = 0.14). However, larger birds removed more figs per unit foraging time (Spearman's r = 0.75, P < 0.01), and smaller birds dropped more seeds per unit foraging time (Spearman's r = -0.76, P < 0.01). Thus, smaller birds ingested fewer seeds per unit foraging time (Spearman's r = 0.88, P < 0.01; Fig. 1).

Large birds visited the tree less often than medium (χ^2_1 = 5.38, P = 0.02) or small (χ^2_1 = 5.07, P = 0.02) birds. There was no difference between the numbers of visits by medium and small birds (χ^2_1 = 0.01, P = 0.94; Fig 2).

By combining foraging time per visit and foraging rate, we found that large birds took 3.8 times as many figs per visit as medium birds and 57.9 times as many figs as small birds (Table 1). By considering number of visits by each size class, we calculated that large birds as a class took 1.5 times as many figs as medium birds and 28.2 times as many figs as

TABLE 1. We observed four size classes of birds feeding on a *Ficus colubrinae* tree at La Selva Biological Station. Larger birds ingested more figs, but small and medium birds visited the tree more often. Thus, as a size class, medium and large birds ingested the most seed-containing figs per hour.

Size Class	Figs/individual visit	Total visits	Seed-containing figs ingested per hour
S (<20cm)	0.43	94	11.1
M (20-40cm)	6.49	121	204
L (40-60cm)	24.9	32	314
XL (>60 cm)	45.6	5	57.9

small birds (Table 1).

Large birds flew farther upon leaving the tree than medium or small birds did ($\chi^2_4 = 33.17$, $P < 0.01$; Fig 3).

DISCUSSION

Medium and large sized birds removed the most seeds. Both sizes ate many figs and were quite abundant. In contrast, small birds dropped most seeds, carrying few ingested seeds away. Individual extra large birds ate many seeds, but were too rare for this size class to remove many seeds.

Although large birds flew farther on their first flight from the tree, we could not follow birds until they excreted seeds. Medium birds may play a large role in scattering seeds because there were many individuals, who might fly in different directions.

Our study assumes similar behaviors by species within a size class. This may not be so. For example, Passerini's Tanager consumed entire figs without dropping seeds, unlike other small birds. The large Montezuma Oropendolas visited the tree often, but only one sampled individual foraged. The extra-large Crested Guans ate many figs, but stayed so long in the tree that they defecated there, without dispersing seeds. However, the difficulty of identifying some bird species made use of size classes necessary.

Seed dispersal is crucial for trees. Our data indicate that in general, medium and large birds may be important in dispersing *F. colubrinae* seeds, while small and extra-large birds often remove figs without providing dispersal benefits.

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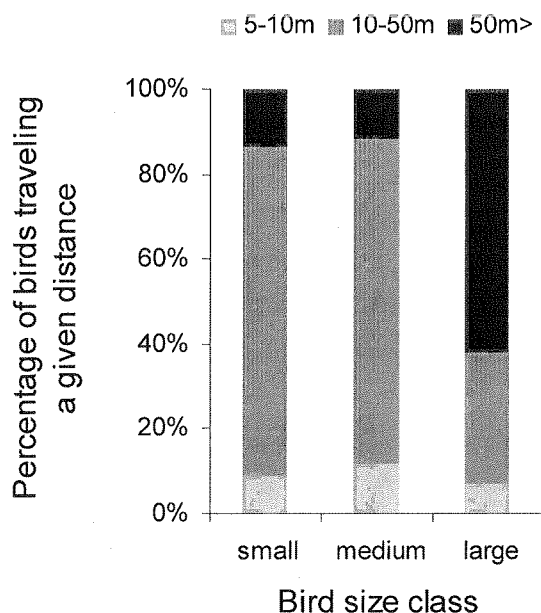
FIG. 3. Visual estimates of distances birds traveled immediately after leaving a focal *Ficus colubrinae* tree in La Selva National Park. Large birds flew significantly further than small or medium birds (n = 223 birds).

The effect of local fruiting synchrony
on seed predation in *Dipteryx panamensis*

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Abstract: We investigated how the timing of nearby conspecific tree fruiting affects mammalian seed predation in *Dipteryx panamensis*. We quantified seed predation at the bases of two classes of fruiting *D. panamensis* individuals: those with synchronously fruiting conspecific neighbors and those with conspecifics neighbors that had already fruited. We found less seed predation under synchronously fruiting focal trees. It may be advantageous to fruit synchronously because high seed availability may satiate predators. Further, because seed predators return to areas where seeds had recently been abundant, it may be detrimental to fruit after a neighboring conspecific. Our results point to positive density dependence in seed survivorship and may help explain the abundance and spatial distribution of *D. panamensis* at La Selva.

Key words: La Selva, seed dispersal, post-dispersal seed predation.

El efecto de la sincronía local en la fructificación
en la depredación de semillas de *Dipteryx panamensis*

Resumen: Investigamos cómo la temporalidad de la fructificación de árboles conspecíficos vecinos afecta la depredación de semillas por mamíferos en *Dipteryx panamensis*. Determinamos la proporción de semillas depredadas en parcelas situadas al pie de individuos fructificantes de *D. panamensis* y las clasificamos en dos tipos, como fructificante en sincronía o con conspecíficos vecinos que fructificaron en el pasado. Encontramos una menor depredación de semillas bajo árboles focales que fructifican en sincronía, lo que sugiere que los depredadores estaban saciados por una mayor disponibilidad de semillas o que la fructificación reciente de los vecinos cercanos hizo que los depredadores regresaran a las áreas donde la densidad de semillas fue alta. Nuestros resultados señalan una dependencia de la densidad positiva en la sobrevivencia de semillas que puede explicar la abundancia y distribución espacial de *D. panamensis* en La Selva.

Palabras clave: La Selva, dispersión de semillas, depredación de semillas después de la dispersión

Introduction

Seed predation and dispersal by vertebrates greatly influence tree distribution and abundance in the tropics (Romo et al. 2004). We investigated the effects of local fruiting synchrony on seed predation in *Dipteryx panamensis* (Fabaceae).

The fleshy fruit surrounding *D. panamensis* seeds is an abundant food source for many birds and mammals. Frugivorous bats are the primary seed dispersers, while the main seed predators are ground mammals, such as agoutis and peccaries (Bonaccorso et al. 1980).

Neighboring *D. panamensis* often fruit synchronously, which may satiate predators and allow a higher proportion of seeds to survive (Kemp et al. 2004). In contrast, for trees fruiting at different times, seed predators may be able to eat a higher proportion of seeds (if they discover them) because there are fewer seeds at a given place and time. In addition, some seed predators are likely to return to an area where seeds were available from nearby trees that had recently fruited (Romo et al. 2004).

Because synchronously fruiting *D. panamensis* trees (hereafter referred to as synchronous fruiters) may satiate predators, we predicted that synchronous fruiters would have lower seed predation (higher per-seed survival rate) than trees whose nearby conspecifics had just finished fruiting (late fruiters), where predators are more likely to return to forage.

METHODS

We conducted our study on 16 and 17 February 2009 at the La Selva Biological Station, Costa Rica, in primary forest along the CCC, CCL, SUR, CEN, CES, and SCH trails. We selected ten focal trees haphazardly with the criteria that each was 1) currently fruiting, 2) visible from the trail, and 3) at least 100 m from other focal trees, to avoid overlapping sampling areas. For each focal tree, we set three 2 m by 1 m seed count plots, extending North, Southwest, and Southeast. Each plot extended radially from the tree, starting 2 m from the trunk and extending outward to 4 m. In each plot, we counted all seeds on the ground surface. By a visual inspection, we noted if each seed remained viable (seed case was intact) or was damaged due to vertebrate predation.

We also noted if any *D. panamensis* within a 50 m radius of each focal tree were past fruiting or currently fruiting, by examining the ground for recent seed fall and the canopy for mature seeds.

All statistical analyses were conducted using JMP 7.0 (SAS Institute, Inc. 2007).

RESULTS

Synchronously fruiting *D. panamensis* trees experienced a lower level of seed predation than late fruiting trees (Student's t-test, $t_{5.81}= -2.85$, $P = 0.03$, Fig. 1).

DISCUSSION

Seed survivorship in synchronously fruiting trees was twice as high as for late fruiting trees, suggesting that predator satiation occurred in synchronously fruiting trees. Previous studies have also found that predator satiation reduces seed predation for *D. panamensis* (Forget 1993; Romo et al. 2004). Seeds of late fruiting individual trees are easy targets for seed predators, which remember and return to abundant seed sites (Romo et al. 2004).

Thus, negative density dependent factors, such as decreased seedling survival near parent trees (Clark and Clark 1984), may not be the only density dependent factors driving the distribution and abun-

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dance of *D. panamensis*. Since the advantages of synchronous fruiting accrue only to individuals in aggregations, our results suggest an advantage to aggregation, and thus positive density dependence in seed survival. Because neither seed nor seedling survival alone give an accurate picture of survival to adulthood (DeSteven and Putz 1984) it would be informative to estimate how seed and seedling survival influence overall survival to adulthood, and how those influences vary with local *D. panamensis* density.

We were not able to estimate how many seeds were cached by seed preda-

FIG. 1: Proportion of seeds killed by predation for focal *D. panamensis* trees with at least one nearby conspecific fruiting at the same time (synchronous fruiters) and for focal *D. panamensis* trees with at least one nearby conspecific that recently finished fruiting (late fruiters) at La Selva Biological Station (n = 10). Bars show means ± 1 S.E.

tors such as agoutis. Forget (1993) found increased per-seed caching rates with increasing seed availability, suggesting that the higher seed availability in synchronous fruiting trees would be more susceptible to seed caching than the later fruiting trees. It would be useful to directly examine the extent of seed caching for synchronous and late fruiting trees and furthermore to examine seed predation rates in trees without any conspecifics nearby.

While the Janzen-Connell model explains the occurrence of many rare species in tropical forests by negative density dependence in seedling survival, positive density dependence in seed survival could explain why some tree species, such as *D. panamensis*, are more common than others. Of course, some negatively density dependent pressure on survivorship must exist in later life stages to counteract positive density dependence at the seed stage, or a species population would grow without limit.

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Water Status and Number of Flower Buds Govern Bract Filling Rate in *Heliconia Wagneriana*

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Faculty Editor: David R. Peart

Abstract: Like many *Heliconia* species with upright inflorescences, *Heliconia wagneriana* fills its bracts with a fluid secretion that protects fruits and flowers from herbivory. However, *H. wagneriana* is unusual in that it flowers during the dry season. We examine how *H. wagneriana* manages and is affected by potentially limited water availability. As we hypothesized, *H. wagneriana* secreted more bract fluid during the night, when xylem water potential is higher, and secreted fluid more quickly in bracts with more buds, which most effectively protects its reproductive structures. Because the strength of our inferences is reduced by limited replication across plants, we recommend that the study be repeated with greater replication.

Key words: transpiration, inflorescence

El estado del agua y el número de retoños regulan la tasa de llenado de las brácteas de *Heliconia wagneriana*

Resumen: Como muchas especies de *Heliconia* con inflorescencias erectas, *Heliconia wagneriana* llena sus brácteas con un una secreción fluida que protege de herbivoría a frutos y flores. Sin embargo, *H. wagneriana* es inusual porque florea durante la temporada seca. Examinamos cómo *H. wagneriana* maneja y es afectada por una potencial limitación en la disponibilidad de agua. Como en nuestra hipótesis, *H. wagneriana* secretó más fluido de brácteas durante la noche, cuando el potencial de agua del xilema es más alto, y secretó fluido más rápidamente en brácteas con más retoños, que protegen sus estructuras reproductivas de manera más efectiva. Debido a que nuestras inferencias están limitadas por el escaso número de individuos, recomendamos repetir este estudio con más réplicas.

Palabras clave: transpiración, inflorescencia

INTRODUCTION

Some species of *Heliconia* produce upright inflorescences with bracts that secrete and contain fluid (Bronstein 1986), which surrounds and protects flowers and developing fruits from herbivorous insects (Wootton and Sun 1990). *Heliconia wagneriana* is unusual among Costa Rican heliconias in flowering during the dry season (Zuchowski 2005), which may make it more difficult to maintain bract fluids. Wootton and Sun (1990) reported that bract fluid replenishment rate is unrelated to geographic location of plants, previous day's rainfall, number of plant leaves, and number of bracts. We studied two additional aspects of the water economy of *H. wagneriana*. First we examined whether rate of bract fluid secretion differs between late afternoon and evening, vs. night and early morning. We ex-

pected that bract fluid production rate would be higher during the night than during the same afternoon due to higher xylem water potential at night.

We also tested whether *H. wagneriana* fills some bracts more quickly than others within an inflorescence. Since bract fluid directly impacts the plant's fitness by protecting reproductive structures, bract fluid should be allocated in a way that maximizes protection. Thus, if flowers of a certain age are most vulnerable, we would expect bracts at a particular height within the inflorescence to fill at a faster rate (bracts at the bottom of an inflorescence mature first). If flowers of all ages are equally vulnerable, the plant may instead allocate more fluid to bracts with more flowers, buds, or both, to maximize the protection.

Alternatively, the physiology of replenishing the fluid may dictate the rate at which bracts get filled. For example, low bracts might get filled more quickly, simply because the water pressure inside the xylem decreases with height and it may be more physically difficult to pump water into the higher bracts.

METHODS

We set up two experiments at La Selva Biological Station in Costa Rica on 16 and 17 February 2009. In the first, we measured temporal differences in fluid secretion rate using two *H. wagneriana* plants near the station buildings. For each plant, we measured and emptied the volume of liquid in the lowest two bracts in each of eight inflorescences:

four for the afternoon (1330 to 2050) and four for the overnight (2215 to 545) time periods. At the end of each time period we measured the amount of new fluid in each bract.

In the second experiment, we manipulated six inflorescences on a third *H. wagneriana* plant at the station. We chose inflorescences with a similar number of open bracts (6-7) and number of total bracts (8-10). For the open bracts in each inflorescence, we emptied and measured the fluid and counted the number of open flowers and buds therein. The bracts were allowed to replenish fluid from 1600 on 16 February to 800 on 17 February In both experiments, inflorescences were covered with plastic bags between measurements, to prevent rain water from filling bracts.
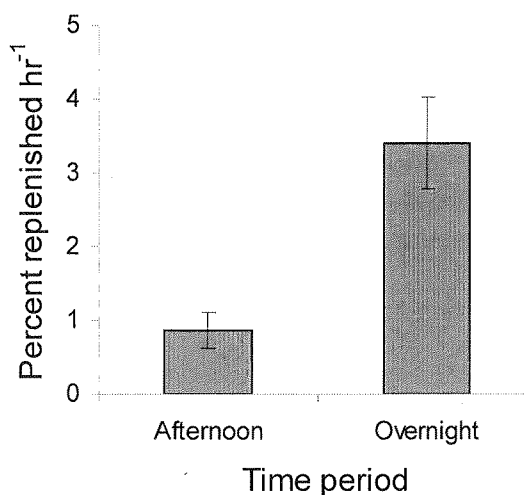
FIG. 1. Fluid from the lowest two bracts of *Heliconia wagneriana* inflorescences was drained and allowed to refill during either the afternoon (1330 to 2050) or overnight (2215 to 545) at La Selva Biological Station. The percent of original bract volume replenished per hour in *Heliconia wagneriana* was greater at nighttime than in the afternoon (n = 16 inflorescences, 8 on each of two plants). Bars are mean ± 1 SE.

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For each experiment we calculated the percentage of the original volume replenished per hour. In the first experiment, the average hourly replenishment rate within each inflorescence was used for statistical analyses. In the second experiment, we excluded bract 1 of inflorescence 6 because it regained more than its original volume. We believe this was because the plastic bag covering this inflorescence did not fully cover this first bract. We used JMP v 7.0 (SAS Institute, Inc. 2007) for statistical analyses.

RESULTS

In the first experiments, we found that the percentage of original bract fluid replenished per hour was almost four times higher during the overnight period than during the daytime period (2-sample-t: $t_{14} = 3.81$, $P = 0.001$; Fig. 1). In the second experiment, we found that volume replenished per hour was not related to bract position ($r^2 = 0.02$, $F_{1,38} = 0.92$, $P = 0.34$). There was a weak positive relationship between percentage replenished per hour and bract position ($r^2 = 0.19$, $F_{1,38} = 8.88$, $P = 0.005$). We had no basis for excluding the three outliers (Fig. 2) from this analysis, yet we consider the trend suspect because the outliers drove the relationship. Bracts with four buds had a fluid secretion rate of 0.25 ml hr^{-1} while those with only two buds had a secretion rate of 0.13 ml hr^{-1} (ANOVA: $F_{2,37} = 3.12$, $P = 0.06$; Linear Contrast 4 > 2: $F_{1,37} = 6.06$, $P = 0.02$; Fig. 3). We compared bracts with four and two buds because we expected those with four (the greatest number of observed buds in a bract) would
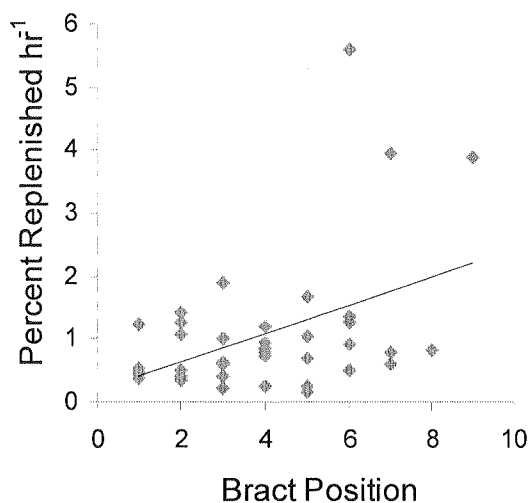
FIG. 2. Fluid from all 40 open bracts, in 6 *Heliconia wagneriana* inflorescences on a single plant, was drained and allowed to refill for 16 hours overnight, at La Selva Biological Station. Replenishment rate is significantly positively correlated with bract position. Because three outliers drove the relationship, we discounted this result (see text).

ber of observed buds in a bract) would refill more quickly than those with two (the lowest number of buds observed in a bract). Fluid secretion rate was not related to number of open flowers ($r^2 = 0.07$, $F_{1,38} = 2.85$, $P = 0.10$).

DISCUSSION

Bract fluid replenishment rate was lower during the afternoon and evening than during the night and early morning, probably due to diurnal trends in plant water status (xylem water potential). During the day, plants lose water through transpiration and deplete water in soil interstitial space. The change in plant water status appears to lower its ability to produce bract fluid, even in the moist conditions of La Selva. When xylem water potential is restored at night,
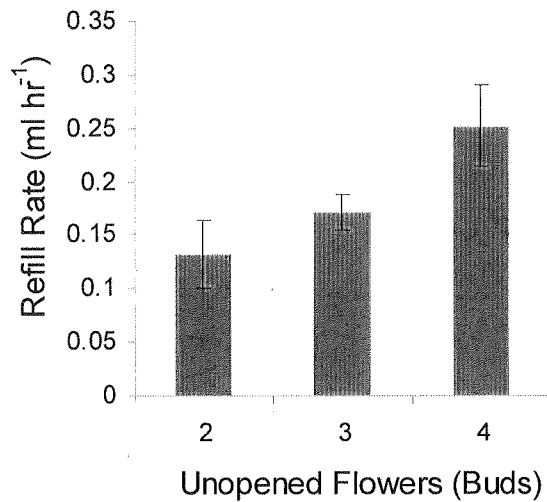
Fig. 3. Fluid from all 40 open bracts, in six *Heliconia wagneriana* inflorescences on a single plant, was drained and allowed to refill for 16 hours overnight, at La Selva Biological Station. Bracts containing four buds refilled at a greater rate than those with two. Bars are mean ± 1 S.E.

H. wagneriana produces bract fluid at a greater rate. Given this finding, it is surprising that Wootton and Sun (1990) found no relationship between bract fluid replenishment rate and the previous day's rainfall; however, their study was not primarily concerned with water status, and there may have been little variation in rainfall over the three days of their study.

Filling rate was weakly correlated with height of the bract within the inflorescence. This suggests that plants may allocate bract fluid production according to inflorescence age, or according to location within inflorescence. However, as noted above, we are not confident in drawing inferences from those data (Fig. 2).

We also found that bracts with four flower buds filled significantly faster than those with two buds. The plant's increased investment in these bracts may eventually yield greater fitness. Bract fluid may be more effective at protecting buds than flowers because buds are fully submerged, while flowers are only partially submerged (Fig. 4). If this is the case, *H. wagneriana* may have experienced a selective pressure to allocate water according to the number of buds rather than number of mature flowers.

A weakness of our study is that we only tested across three individual plants: two for our finding of day-night differences and one for the relationship between replenishment rate and flower development stage. For the day-night comparison we treated inflorescences as independent replicates (though they were on only two plants), and for the relationship between replenishment and flower stage we treated 40 bracts as independent replicates (from six inflorescences on a single plant). Strictly, the latter relationship can be inferred only for the single focal plant. The finding would be
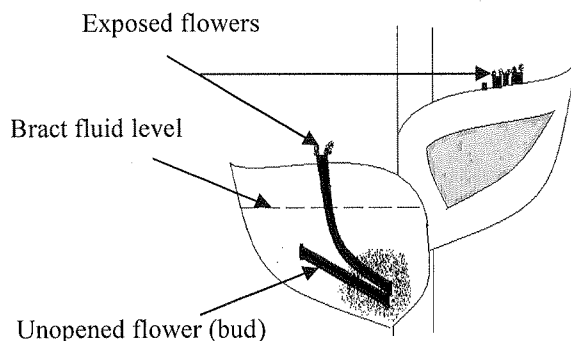
FIG. 4. Structure of *Heliconia wagneriana* bracts. Flowers develop under fluid and emerge when they are mature. After pollination the flower dies and falls back into the fluid while the fruit develops. When the fruit is ripe it is pushed back above the water surface (Zuchowski 2005).

strengthened if the study were repeated with replication across plants.

The physiological processes by which the plant refills bracts are not well understood (Bronstein 1986). Perhaps the presence of buds directly induces bract filling. Future research on the mechanisms would clarify how the plant allocates water resources among bracts.

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Patterns of bird abundance, diversity, and foraging guild composition among five sites in Costa Rica

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Project Design: Ernesto Ruelas Inzunza. Faculty Editor: David R. Peart

Abstract: We evaluated bird abundance, diversity, and foraging guild structure at five sites in Costa Rica, predicting higher abundance and diversity at the two lowland rainforest sites and similar proportional abundance of birds in each foraging guild across all sites. Abundance and diversity were higher at the cloud forest and rainforest sites than at the high-altitude and seasonally dry sites. Although all guilds were present at all sites, relative abundance of individuals in foraging guilds differed statistically among sites, with insectivore abundance lowest at the high-altitude site and highest at the Pacific rainforest site.

Key words: community structure

Patrones de diversidad, abundancia y composición de gremios de forrajeo en las aves de cinco sitios en Costa Rica

Resumen: Evaluamos la abundancia, diversidad y estructura de gremios de forrajeo de las aves en cinco sitios en Costa Rica. Nuestra predicción fue que encontraríamos mayor abundancia y diversidad en los dos sitios de selvas húmedas en tierras bajas y una abundancia proporcional similar en cada gremio de forrajeo a lo largo de todos los sitios. La abundancia y la diversidad fueron mayores en los sitios con bosque de niebla y selvas húmedas que en los sitios de mayor altitud y en el estacionalmente secos. Aunque todos los gremios estuvieron presentes en todos los sitios, la abundancia relativa de individuos por gremio de forrajeo difiere estadísticamente entre éstos, con una abundancia de insectívoros menor en sitio de mayor altitud y mayor en el sitio de selvas húmedas en el Pacífico.

Palabras clave: estructura de la comunidad

Introduction

Birds play important ecosystem roles based on well-defined "foraging guilds," such as seed dispersal by frugivores, pollination by nectarivores, and invertebrate predation by insectivores (Şekercioğlu et al. 2004). These guilds, and the role of birds in ecosystems as a whole, are thought to remain approximately constant across localities with similar habitat types (Holmes et al. 1986, Terborgh et al. 1990). We assumed secondary forest was a similar habitat type across five sites in Costa Rica, though those sites varied greatly in elevation, seasonality and rainfall.

We mist-netted birds and classified them into foraging guilds in secondary forest at Palo Verde, a tropical dry forest; Monteverde, a tropical lower montane wet forest; Cuericí, a tropical montane wet forest; Corcovado, a Pacific tropical wet forest; and La Selva, an Atlantic

TABLE 1. Number of birds and species captured across five sites in Costa Rica. We sampled over three mornings using 10 mist-nets at five sites across Costa Rica. Due to uneven sampling effort (total mist-net hours), particularly at Cuericí where we only sampled for two mornings, total captures and number of species are not comparable for bird abundances. Indices were rarefied to 29 samples with 10,000 replicates using EcoSim v. 7.72 (Acquired Intelligence, Inc. 2005).

Site	Palo Verde	Monteverde	Cuericí	Corcovado	La Selva
Mist-net Hours	128.33	126.25	83.33	129.17	140.00
Total Captures	29	81	32	51	116
# Species	16	27	11	24	32
Capt/Mist-net Hour	0.23	0.64	0.38	0.39	0.83
Rarefied Richness	16.00	16.98	10.43	17.49	15.33
Rarefied S-W Diversity	2.53	2.68	2.00	2.70	2.51
Rarefied Evenness	0.91	0.95	0.85	0.94	0.92

tropical wet forest (Hartshorn 1983). We hypothesized that abundance and diversity would differ among sites, but that foraging guild structure (the relative abundances of individuals and species across guilds) would be similar among sites. We predicted higher total abundance and richness at the two rainforest locations, which Stiles (1983) states are very similar in their avifauna as well as climate and habitat.

METHODS

At each of the five sites we set up 10 mist-nets, each 2.5 m x 12 m, with 25 mm mesh, spaced ca. 50 m apart in the understory. We sampled from ca. 0600-1020 for three mornings at each site (ca. 130 mist-net hours) except at Cuericí where we sampled for only two mornings (ca. 80 mnh).

At Palo Verde, nets were located on the Mapache trail which loops off the main road, ca. 50 m to the east of the biological station. At Monteverde, nets were located on Sendero el Targuá, approximately a 5-min walk downhill from the biological station. At Cuericí, nets were located on the loop trail, starting after the farm, a ca. 10-min walk to the east of the biological station. At Corcovado, the nets were located on Sendero Pavo a 25-min walk from the biological station. Finally, at La Selva the nets were located a 30-min walk from the biological station in successional plots (0-1 years to 4-5 years since cutting), off the Sendero Sábalo-Esquina. For maps and exact net locations seek project metadata from the authors and FSP faculty.

Upon capture, we identified each bird to species, and where possible, to sex. Hummingbirds were released after identification to species due to their fragility. For all other birds we measured wing, culmen and total weight and noted in which net they were caught.

We later determined the foraging guild for each bird species using Stiles and Skutch (1989). No birds are strict frugivores, but birds that would preferentially feed on fruit were considered frugivores for our analyses.

Statistical Methods

We analyzed differences in diversity among sites by using two statistical methods. First, we rarefied data down to the number of captures at the site with the lowest abundance to compare species richness, Shannon-Weiner diversity, and evenness across sites. The rarefaction was performed with 10,000 replicates using EcoSim v. 7.72 (Acquired Intelligence Inc. 2005). Second, we compared Shannon-Weiner diversity between all pairs of sites using the statistical method described in Hutcheson (1970, *in* Zar 1984), designed to compare this index between unreplicated samples among sites based on species frequencies. Unlike rarefac-

tion, this statistical method assumes a constant sampling effort across sites. Therefore, we excluded Cuericí, where we sampled for fewer days.

We tested whether the frequency of captures for each foraging guild differed among sites, i.e. if the proportions individuals or species in foraging guilds was different among sites. We did this using contingency tables for both total individuals caught in each foraging guild by site, as well as total species sampled in each foraging guild by site.

We could not test some of our results statistically (e.g. differences among sites in total abundance) due to lack of replication.
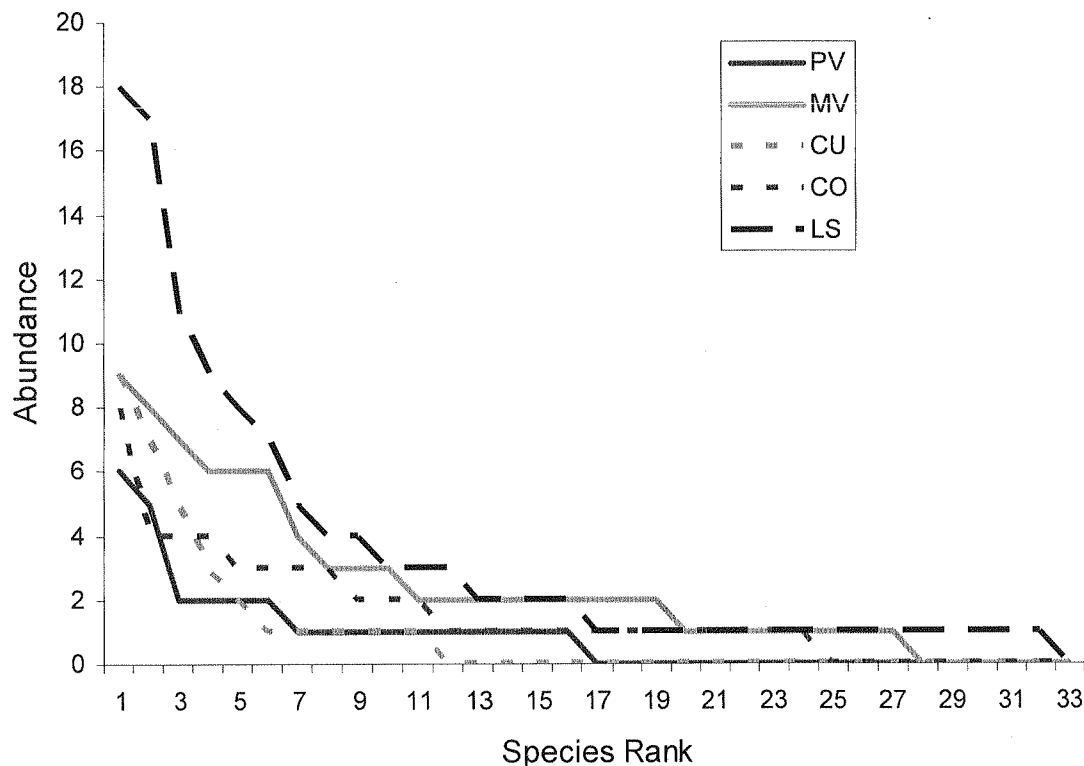
FIG. 1. Rank-Abundance relationships of birds sampled (as in Table 1) across 5 sites in Costa Rica (PV = Palo Verde, MV = Monteverde, CU = Cuericí, CO = Corcovado, LS = La Selva) show a log-series distribution. Steeper slopes indicate less evenness of bird community diversity. See Table 1 for total sample sizes by site.

RESULTS

We captured 309 birds of 99 species (Appendix A) in four foraging guilds—insectivores, frugivores, nectarivores, and others. "Other" included one granivore, one carnivore, and an unidentified bird; "other" was excluded from χ^2 analyses due to small sample size.

Bird capture rate was highest at La Selva and Monteverde; Corcovado and Cuericí had similar bird capture rates, while Palo Verde's was the lowest (Table 1). While we had no way to test differences in abundance statistically, we suggest tjat the differences in total captures across sites are so great (with equal sampling effort) that the probability of underlying differences in local abundances is high. Rank-abundance curves for each site show a log-series distribution, with highest evenness at Monteverde and Corcovado (Fig. 1). Rarefaction analysis and Hutcheson's (1970) statistical comparison of Shannon-Weiner diversity index between sites gave different results. Rarefaction gave the highest diversity for Monteverde and Corcovado, then La Selva and Cuericí, and the lowest for Palo Verde. Analyses using Hutcheson's

t-tests showed marginal differences in diversity between Monteverde and Corcovado and between Monteverde and La Selva and large differences between Palo Verde and all other sites (Table 2). However, the relatively large number of site comparisons (n = 6) increases our probability of finding false positive results in these tests, and only Palo Verde showed strong differences in diversity.

The proportions of species in each foraging guild were the same across sites ($\chi^2_8 = 10.08$, $P = 0.26$). However, the proportions of total individuals in guilds did vary significantly across sites ($\chi^2_8 = 45.77$, $P < 0.001$; Fig. 2), with abundance of insectivores being very high at Corcovado and very low at Cuericí. Total biomass of each foraging guild across sites is shown in Fig. 3.

DISCUSSION

Our capture data, expressed per mist-net hour, suggest there are real differences in total bird abundance among sites (though we could not test this statistically), with most birds caught at La Selva, a lowland rainforest site. The capture rate was only half as high at Corcovado, the other lowland site, but the high

TABLE 2. Shannon-Weiner diversity of sampled bird species (as in Table 1) across four sites in Costa Rica (excluding Cuericí due to reduced sampling effort). Sites are listed in order of decreasing H` from left to right. Site diversities were compared pairwise using the method described in Hutcheson (1970). We report Hutcheson's t, df, and P-values. Values in bold indicate a significant difference in diversity between pairs of sites.

Site	Monteverde	Corcovado	La Selva	Palo Verde
H`	3.034	2.939	2.933	2.528
Corcovado	$t_{109} = 1.74$ $p = 0.08$			
La Selva	$t_{197} = 1.93$ $p = 0.05$	$t_{138} = 0.11$ $P = 0.91$		
Palo Verde	$t_{49} = 7.43$ $p < 0.0001$	$t_{58} = 5.65$ $p < 0.0001$	$T_{58} = 5.68$ $P < 0.0001$	

trail traffic along the Sendero Pavo compared to all other sites may have reduced captures.

The high elevation at Cuericí and seasonal dryness at Palo Verde may have caused lower abundances and diversity at these sites, respectively. The elevation of our mist-nets at Cuericí was ca. 2600 masl and well-documented relationships predict lower species richness at higher elevations (e.g. Hunter and Yonzon 1992, *in* Begon et al 1996). In addition, high winds on sampling days, typical of the dry season in Guanacaste (Coen 1983), may have driven lower capture rates and diversity at Palo Verde. Birds may also migrate away from dry forest to riparian

habitat during the dry season because of both insect and plant resource limitation in forested areas (Stiles 1983). Species diversity was not significantly different between the two rainforest sites, but surprisingly, was significantly higher at Monteverde, the cloud forest site, than at La Selva. The high diversity at Monteverde may have been a localized effect, i.e. the result of more varied habitat close to the net locations (more nets adjacent to forest edges).

The lack of significant difference in the number of species in each guild among sites suggests that all guilds are represented to a similar degree, so birds may be filling the same range of basic
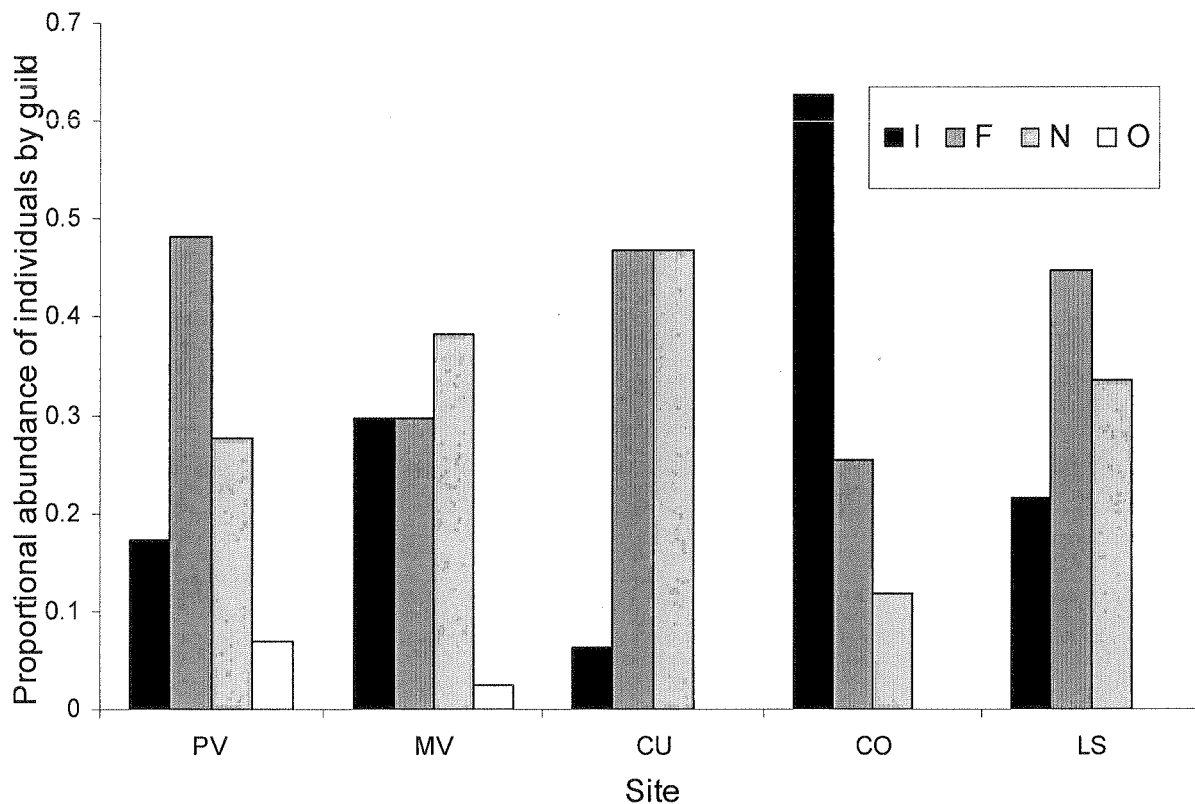
FIG. 2. Proportional abundance of individuals representing different foraging guilds (I = insectivore, F = frugivore, N = nectarivore, O = other) determined by this study's decision rules and based on information in Stiles and Skutch (1989), sampled (as in Table 1) across five sites in Costa Rica (abbreviations as in Fig. 1).
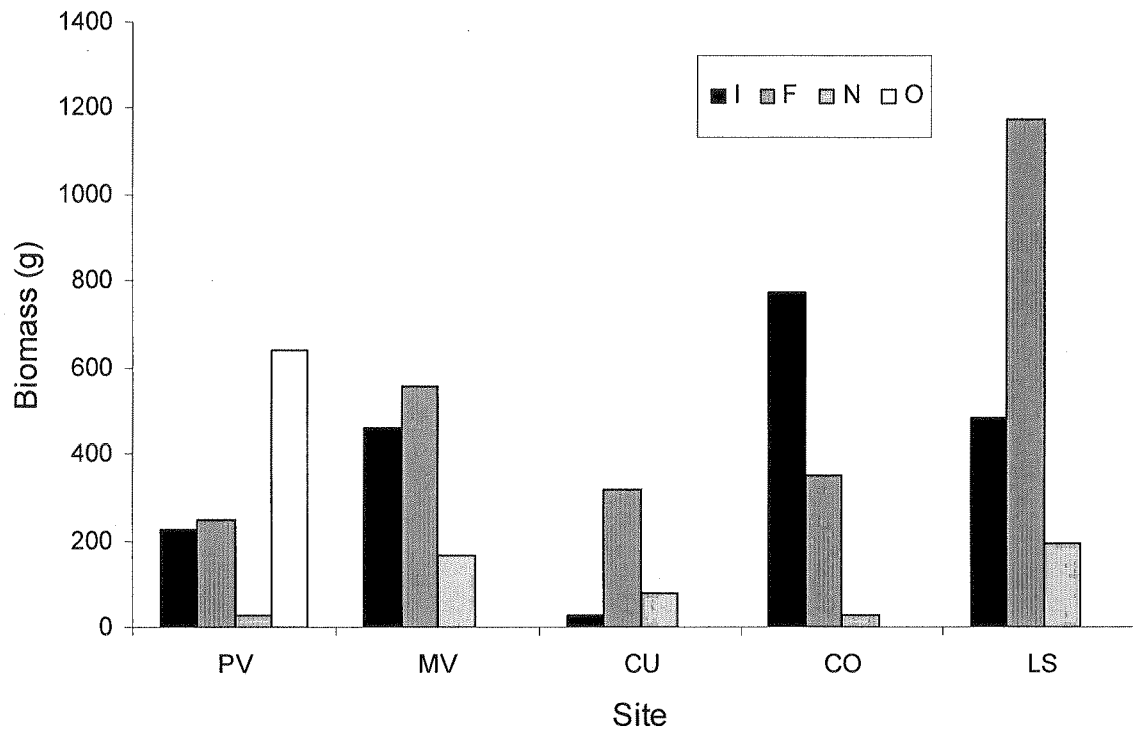
FIG. 3. Total biomass of birds in each foraging guild (Fig. 2) sampled (as in Table 1) across five sites in Costa Rica (abbreviations as in Fig. 1). Individual bird mass data are from our field measurements if available, and otherwise from Stiles and Skutch (1989).

ecosystem functions across sites. This result is consistent with findings of guild-structured bird communities across different habitats by Holmes et al. (1986) and Terborgh et al. (1990). However, the proportional abundance of birds in each guild did not remain constant across sites, suggesting that sites may provide different amounts of particular resources. In particular, Cuericí had significantly fewer insectivores, possibly because of lower insect abundance. It is reasonable to assume that insect abundance will be relatively lower at this high elevation because insects are poikilothermic. In addition, there is a greater diversity of insects at Corcovado. For example, Chirripó National Park near Cuericí hosts only 30 species of breeding butterflies, while Corcovado hosts 220 species (Janzen 1983). This may also explain why we netted more insectivorous individuals and species at Corcovado, because higher insect abundance and diversity could support more specialized insectivores that exploit the insect population in different ways, e.g. birds that glean insects off vegetation and active searchers that catch insects in flight.

Unfortunately, the areas of forest sampled across sites were not always equivalent. For example, the successional forest at the La Selva was much younger than at other sites (maximum age of 5 years), which may explain the high bird abundance since secondary forest often

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has a higher abundance of birds (Ernesto Ruelas, pers. comm.). Unlike any of the other sites, Cuericí included areas of meadow with abundant flowers, which may explain the relatively high proportion of nectarivores netted at this site. We also had a slightly lower sampling effort at Cuericí due to scheduling conflicts. Future studies should continue to use our standardized methods, but choose more homogenous habitats among sites if possible.

Having sampled in four different Holdridge Life Zones (Hartshorn 1983), our analysis of bird community composition found a high variance in abundance, diversity, and foraging guilds, probably due to the range of climatic conditions in our five sites and its effect on relative food abundances.

ACKNOWLEDGMENTS

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APPENDIX A. BIRD SPECIES CAPTURED IN MIST-NETS

List of bird species sampled at five sites in Costa Rica with capture frequencies by site (PV = Palo Verde, MV = Monteverde, CU = Cuericí, CO = Corcovado, LS = La Selva). Foraging Guild (FG) of bird (I = insectivore, F = frugivore, N = nectarivore, O = other) classified using a decision rule created for this study and based on information in Stiles and Skutch (1989). Mass was based on our field measurements when available, and otherwise on data in Stiles and Skutch (1989).

Family	Common Name	Scientific Name	FG	Mass (g)	PV	MV	CU	CO	LS	Total
Accipitridae	Broad-winged Hawk	*Buteo platypterus*	O	480	1	0	0	0	0	1
Columbidae	White-tipped Dove	*Leptotila verreauxi*	O	158	1	0	0	0	0	1
Cuculidae	Mangrove Cuckoo	*Coccyzus minor*	I	68	1	0	0	0	0	1
Caprimulgidae	Common Pauraque	*Nyctidromus albicollis*	I	55	0	1	0	0	0	1
Trochilidae	Bronzy Hermit	*Glaucis aeneus*	N	5	0	0	0	0	7	7
	Band-tailed Barbthroat	*Threnetes ruckeri*	I	6	0	0	0	0	1	1
	Green Hermit	*Phaethornis guy*	N	6	0	4	0	0	0	4
	Long-billed Hermit	*Phaethornis longirostris*	N	6	0	0	0	3	18	21
	White-tipped Sicklebill	*Eutoxeres aquila*	N	11	0	0	0	0	1	1
	Green Violetear	*Colibri thalassinus*	N	5	0	0	5	0	0	5
	Green-breasted Mango	*Anthracothorax prevostii*	I	8	0	0	0	0	1	1
	Canivet's Emerald	*Chlorostilbon canivetii*	N	3	5	0	0	0	0	5
	Violet-crowned Woodnymph	*Thalurania colombica*	N	5	0	0	0	0	1	1
	Blue-throated Goldentail	*Hylocharis eliciae*	N	4	1	0	0	2	0	3
	Cinnamon Hummingbird	*Amazilia rutila*	N	5	2	0	0	0	0	2
	Stripe-tailed Hummingbird	*Eupherusa eximia*	N	4	0	9	0	0	0	9
	Coppery-headed Emerald	*Elvira cupreiceps*	N	3	0	6	0	0	0	6
	Bronze-tailed Plumeleteer	*Chalybura urochrysia*	N	7	0	0	0	0	1	1
	Purple-throated Mountain-gem	*Lampornis calolaemus*	N	6	0	8	0	0	0	8
	White-throated Mountain-gem	*Lampornis castaneoventris*	N	6	0	0	9	0	0	9
	Ruby-throated Hummingbird	*Archilochus colubris*	N	3	0	0	0	1	9	10
Momotidae	Blue-crowned Motmot	*Momotus momota*	I	120	0	1	0	0	0	1
	Broad-billed Motmot	*Electron platyrhynchum*	I	63	0	0	0	0	1	1

Family	Common Name	Scientific Name	FG	Mass (g)	PV	MV	CU	CO	LS	Total
Momotidae	Turquoise-browed Motmot	*Eumomota superciliosa*	I	64.5	2	0	0	0	0	2
Bucconidae	White-whiskered Puffbird	*Malacoptila panamensis*	I	50	0	0	0	1	0	1
Ramphastidae	Prong-billed Barbet	*Semnornis frantzii*	F	93	0	1	0	0	0	1
Furnariidae	Gray-throated Leaftosser	*Sclerurus albigularis*	I	35	0	1	0	0	0	1
	Spotted Barbtail	*Premnoplex brunnescens*	I	15	0	6	0	0	0	6
	Plain Xenops	*Xenops minutus*	I	11	0	0	0	1	0	1
	Tawny-winged Woodcreeper	*Dendrocincla anabatina*	I	40	0	0	0	3	0	3
	Olivaceous Woodcreeper	*Sittasomus griseicapillus*	I	14	0	2	0	0	0	2
	Wedge-billed Woodcreeper	*Glyphorynchus spirurus*	I	16	0	0	0	0	2	2
	Strong-billed Woodcreeper	*Xiphocolaptes promeropirhynchus*	I	15	0	0	0	1	0	1
	Northern Barred-Woodcreeper	*Dendrocolaptes sanctithomae*	I	70.5	0	0	0	3	0	3
	Cocoa Woodcreeper	*Xiphorhynchus susurrans*	I	42	0	0	0	0	1	1
Thamnophilidae	Black-hooded Antshrike	*Thamnophilus bridgesi*	I	27	0	0	0	2	0	2
	Plain Antvireo	*Dysithamnus mentalis*	I	14	0	2	0	0	0	2
	Slaty Antwren	*Myrmotherula schisticolor*	I	9	0	3	0	1	0	4
	Dusky Antbird	*Cercomacra tyrannina*	I	16.5	0	0	0	0	2	2
	Chestnut-backed Antbird	*Myrmeciza exsul*	I	27	0	0	0	1	0	1
	Bicolored Antbird	*Gymnopithys leucaspis*	I	27	0	0	0	4	0	4
Tyrannidae	Mountain Elaenia	*Elaenia frantzii*	F	20	0	2	0	0	0	2
	Olive-striped Flycatcher	*Mionectes olivaceus*	F	13.6	0	6	0	0	0	6
	Ochre-bellied Flycatcher	*Mionectes oleagineus*	F	11.7	0	1	0	1	11	13
	Northern Bentbill	*Oncostoma cinereigulare*	I	7	0	0	0	0	1	1
	Stub-tailed Spadebill	*Platyrinchus cancrominus*	I	9	0	2	0	0	0	2
	Golden-crowned Spadebill	*Platyrinchus coronatus*	I	9.5	0	0	0	4	0	4
	Ruddy-tailed Flycatcher	*Terenotriccus erythrurus*	I	7	0	0	0	1	0	1
	Sulphur-rumped Flycatcher	*Myiobius sulphureipygius*	I	12	0	0	0	3	0	3
	Yellow-bellied Flycatcher	*Empidonax flaviventris*	F	10	1	0	0	0	0	1

Family	Common Name	Scientific Name	FG	Mass (g)	PV	MV	CU	CO	LS	Total
Tyrannidae	Yellowish Fly-catcher	*Empidonax flavescens*	F	12	0	1	0	0	0	1
	Bright-rumped Attila	*Attila spadiceus*	F	32.5	0	0	0	1	1	2
Pipridae	White-collared Manakin	*Manacus candei*	F	19	0	0	0	0	17	17
	Long-tailed Ma-nakin	*Chiroxiphia linearis*	F	17.3	6	0	0	0	0	6
	Blue-crowned Ma-nakin	*Pipra coronata*	I	14.5	0	0	0	4	0	4
	Red-capped Ma-nakin	*Pipra mentalis*	F	15	0	0	0	0	1	1
Vireonidae	Philadelphia Vireo	*Vireo philadel-phicus*	F	11	1	0	0	0	0	1
	Tawny-crowned Greenlet	*Hylophilus ochraceiceps*	F	12	0	0	0	2	0	2
Corvidae	Azure-hooded Jay	*Cyanolyca cu-cullata*	F	82	0	1	0	0	0	1
Troglodyti-dae	Black-throated Wren	*Thryothorus atrogularis*	I	23	0	0	0	0	4	4
	Stripe-breasted Wren	*Thryothorus thoracicus*	I	17	0	0	0	0	1	1
	Banded Wren	*Thryothorus pleurostictus*	I	20.5	1	0	0	0	3	4
	Ochraceous Wren	*Troglodytes ochraceus*	I	10	0	1	0	0	0	1
	White-breasted Wood-Wren	*Henicorhina leucosticte*	I	16	0	0	0	0	1	1
Turdidae	Black-faced Soli-taire	*Myadestes melanops*	F	30	0	2	0	0	0	2
	Black-billed Night-ingale-Thrush	*Catharus gracilirostris*	F	19.3	0	0	3	0	0	3
	Slaty-backed Nightingale-Thrush	*Catharus fus-cater*	F	35	0	3	0	0	0	3
	Ruddy-capped Nightingale-Thrush	*Catharus frantzii*	F	30	0	0	2	0	0	2
Turdidae	Wood Thrush	*Hylocichla mus-telina*	F	47.3	1	0	0	0	2	3
Parulidae	Golden-winged Warbler	*Vermivora chrysoptera*	I	7.5	0	0	0	0	1	1
	Yellow Warbler	*Dendroica pete-chia*	I	8	1	0	0	0	0	1
	Chestnut-sided Warbler	*Dendroica pen-sylvanica*	F	8.5	0	0	0	0	3	3
	Kentucky Warbler	*Oporornis for-mosus*	I	13.5	0	0	0	0	5	5
	Wilson's Warbler	*Wilsonia pusilla*	I	7	0	0	1	0	0	1
	Slate-throated Red-start	*Myioborus miniatus*	I	8.5	0	3	0	0	0	3
	Collared Redstart	*Myioborus tor-quatus*	I	21	0	0	1	0	0	1

Family	Common Name	Scientific Name	FG	Mass (g)	PV	MV	CU	CO	LS	Total
Parulidae	Golden-crowned Warbler	*Basileuterus culicivorus*	F	10	0	7	0	0	0	7
	Rufous-capped Warbler	*Basileuterus rufifrons*	F	9.5	2	0	0	0	0	2
	Black-cheeked Warbler	*Basileuterus melanogenys*	F	13.3	0	0	7	0	0	7
	Three-striped Warbler	*Basileuterus tristriatus*	I	12	0	2	0	0	0	2
Thraupidae	Common Bush-Tanager	*Chlorospingus ophthalmicus*	N	20	0	2	0	0	0	2
	Sooty-capped Bush-Tanager	*Chlorospingus pileatus*	F	20	0	0	1	0	0	1
	Dusky-faced Tanager	*Mitrospingus cassinii*	F	42	0	0	0	0	1	1
	Gray-headed Tanager	*Eucometis penicillata*	F	31	0	0	0	8	0	8
	White-throated Shrike-Tanager	*Lanio leucothorax*	I	30	0	0	0	1	0	1
	Passerini's Tanager	*Ramphocelus passerinii*	F	28	0	0	0	0	8	8
Emberizidae	Thick-billed Seed-Finch	*Oryzoborus funereus*	F	11	0	0	0	0	3	3
	Yellow-thighed Finch	*Pselliophorus tibialis*	F	31	0	0	1	0	0	1
	Large-footed Finch	*Pezopetes capitalis*	F	55	0	0	1	0	0	1
	Orange-billed Sparrow	*Arremon aurantiirostris*	F	35	0	0	0	1	0	1
	Olive Sparrow	*Arremonops rufivirgatus*	F	22.5	2	0	0	0	0	2
Cardinalidae	Buff-throated Saltator	*Saltator maximus*	F	46.5	0	0	0	0	4	4
	Blue-black Grosbeak	*Cyanocompsa cyanoides*	I	32	0	0	0	0	1	1
	Painted Bunting	*Passerina ciris*	F	15	1	0	0	0	0	1
Icteridae	Yellow-billed Cacique	*Amblycercus holosericeus*	F	71	0	0	0	0	1	1
	UNID		O		0	2	0	0	0	2
	UNID – Antbird		I		0	0	0	1	0	1
	UNID – Hummingbird		N		0	2	1	0	2	5
	UNID – Woodcreeper		I		0	0	0	1	0	1
		Total			29	81	32	51	116	309
		# Spp.			16	27	11	24	32	99

LONG-TERM CORAL AND ALGAE ASSESSMENT: CONTINUATION AND INVESTIGATION OF METHODS

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Abstract: We contributed to a long-term study on the coral and algal species composition and abundance on the back reef behind the Little Cayman Research Center. Due to practical difficulties, we only partially re-censused permanent plots, and focused instead on improving methods that can be more easily and rigorously repeated in the future. Using photographs of 10 of the 20 plots established in 2008, we qualitatively compared coral and algal abundances between 2008 and 2009. We were unable to compare visual estimates of cover quantitatively due to non-standardized methods. There were changes in coral and algae in some plots, but we could not determine if this was due to the recent hurricane, Paloma. We suggest that methods should be overhauled. Standard, repeatable methods, including photographic records, are most easily applied in deeper water where current, waves and turbidity are less. However, the back reef is a distinct habitat and merits its own study. Sampling in the physically dynamic back reef can be improved by taking photographs for qualitative analysis and ensuring that all observers are calibrated to make accurate visual estimates.

Key words: global coral decline

INTRODUCTION

Coral reefs have been declining at an alarming rate around the world due to anthropogenic effects (Pandolfi et al. 2003). Long-term studies on coral ecosystem dynamics are important to understand how coral health and community structure might change in the future (Hughes and Tanner 2000; Guzner et al. 2007). The coral reefs surrounding Little Cayman Island are considered some of the healthiest in the Caribbean, and have recently been carefully documented (Coelho and Manfrino 2007). However, little work has been done on the shallow reef crests, back reefs or lagoons surrounding the island (Manfrino et al. 2000).

We began by continuing a study started in 2008 (Thomas et al. 2008) to monitor coral and algal dynamics in permanent plots on the back reef. We were confronted with methodological challenges of sampling in this habitat which had been addressed, but not fully resolved, in 2008. We reconsidered the question of how best to create a long-term replicable study in a back reef environment. In the first part of this paper we describe our continuation of the long-term study. In the second part, we consider methodological options and make recommendations for changes.

PART I: CONTINUATION OF LONG-TERM STUDY

Thomas et al. (2008) laid foundations

TABLE 1. GPS-derived coordinates for the first 10 (of 20 total) plots, for the long-term study of coral and algae cover on the back reef near Little Cayman Research Center on Little Cayman Island. Compass orientation shows the direction of the line joining center of the bottom to the center of the top of the frame (Fig. 1).

Plot	North Coordinate	West Coordinate	Compass orientation
1	19° 41.809	80° 3.622	0
2	19° 41.812	80° 3.626	20
3	19° 41.810	80° 3.629	20
4	19° 41.805	80° 3.633	90
5	19° 41.807	80° 3.637	200
6	19° 41.805	80° 3.645	310
7	19° 41.800	80° 3.650	260
8	19° 41.797	80° 3.655	0
9	19° 41.795	80° 3.661	290
10	19° 41.795	80° 3.666	300

for a long term study of changes in coral and algal cover in the back reef. Although only one year had elapsed since 2008, we expected changes in cover due to a recent category 4 hurricane, Paloma, that caused severe damage on the island in November 2008.

Methods

On February 27, we returned to the first 10 study plots described by Thomas et al. (2008) to make visual estimates on coral and algal cover, photograph the plots, and take more precise information on plot locations.

In 2008, Thomas et al. placed a cinder block at their first plot and recorded GPS coordinates. They used compass bearings and distances from this first plot to locate later plots. Following Thomas et al. (2008), we placed the same ca. 1 m x 1 m frame used in 2008 around each plot (frame constructed out of PVC pipe; outside edge 99.4 cm x 94.0 cm; inside edge 99.0 cm x 93.6 cm). The frame was divided into four quadrants by two strings. We consulted photos of each plot in Thomas et al. (2008) to confirm locations and to orient the frame as in 2008, using coral colonies and other conspicuous small scale landmarks. Exactly reproducing the frame's 2008 position was not possible because the photographs were not sufficient to determine the exact orientation of the frame, and no means of precisely relocating the corners of the plot had been established.

FIG. 1. Photographs of plot 1 in 2008 (left) and 2009 (right), angled arrows indicate qualitative changes in algal cover on the back reef north of Little Cayman Research Center. Numbering of quadrants also shown, along with the direction of the compass bearing taken for each plot.

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We made visual estimates of algal and coral cover within the frame, incorporating two major changes in methods from Thomas et al (2008), fully explained in Part II. First, we estimated total projected area (three-dimensional coral and algae structures visualized from above as a two-dimensional plane) covered by coral and algal species instead of basal area of attachment, because basal area estimates are hard to reproduce, and we believe they are less representative of coral and algae growth than projected cover. Second, to increase precision of estimates, we had two observers independently estimate algal cover and a different pair estimate coral cover, instead of having just one observer for each, as

TABLE 2. Visual estimates of coral cover from 2008 and 2009 for three permanent plots on the back reef behind Little Cayman Research Center on Little Cayman Island. Calculated differences between years are shown. 2008 values were estimates of basal area while estimates from 2009 were percent cover estimates. TL = top left quadrant, TR = top right, BR = bottom right, BL = bottom left. Top, bottom, left, right as viewed with quadrant 1 and 2 on top, usually facing the ocean (see Fig. 1).

Plot	Quadrant	Montastrea annularis	Siderastrea siderea	Porites asteroides	Porites porites	Diploria strigosa	Agaricia humilus	Millepora complanta	Knobby Sea Rod	Corky Sea Finger	Total Coral Cover
					2008						
1	TL (1)	0	0	9	0	0	0	22	0	20	51
1	TR (2)	0	0	2	6	6	0	16	0	14	44
1	BR (3)	0	55	0	0	7	0	0	0	0	62
1	BL (4)	0	15	0	0	35	0	0	0	0	50
2	TL (1)	42	0	0	0	16	0	0	0	0	58
2	TR (2)	0	0	0	0	0	0	79	0	0	79
2	BR (3)	0	0	0	0	0	0	6	0	0	6
2	BL (4)	23	0	0	0	0	0	11	0	0	34
3	BL (1)	0	0	0	0	0	0	0	0	0	0
3	TL (2)	0	0	0	0	0	12	0	0	16	28
3	TR (3)	0	0	0	0	0	18	0	0	12	30
3	BR (4)	0	0	0	0	0	0	0	0	0	0
					2009						
1	1	0	0	4.5	0	0	0	11	0	7.5	23
1	2	0	0	1.5	0	0	2	9.5	0	4.5	17.5
1	3	0	53.5	0	0	7.5	1	0	0	0	62
1	4	0	0	0	0	25	0	0	0	3	28
2	1	19.5	0	0	1	6.5	2	1	0	0	30
2	2	0	0	0	3	0	1	55	0	0	59
2	3	0	0	0	0	0	1.5	3.5	0.5	0	5.5
2	4	11.5	0	0	0	0	0	5	0	0	16.5
3	1	0	0	0	0	0	0	0	0	2.5	2.5
3	2	0	0	0	0	0	0	0	0	6	6
3	3	0	0	1	1	0	3.5	0	0	4	9.5
3	4	0	0	0	0	0	1	0	0	1	2

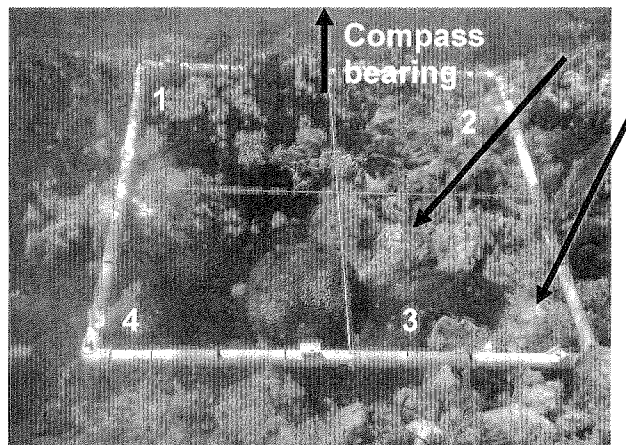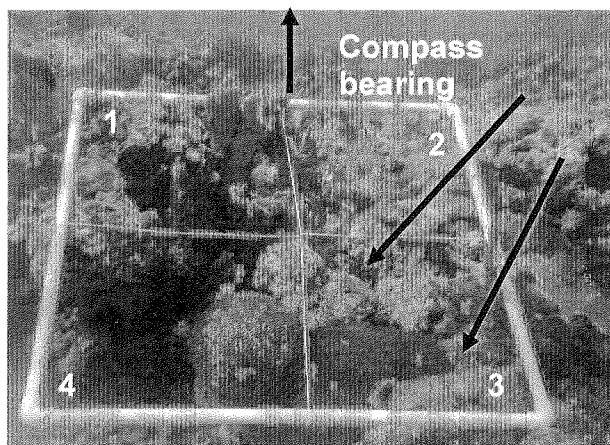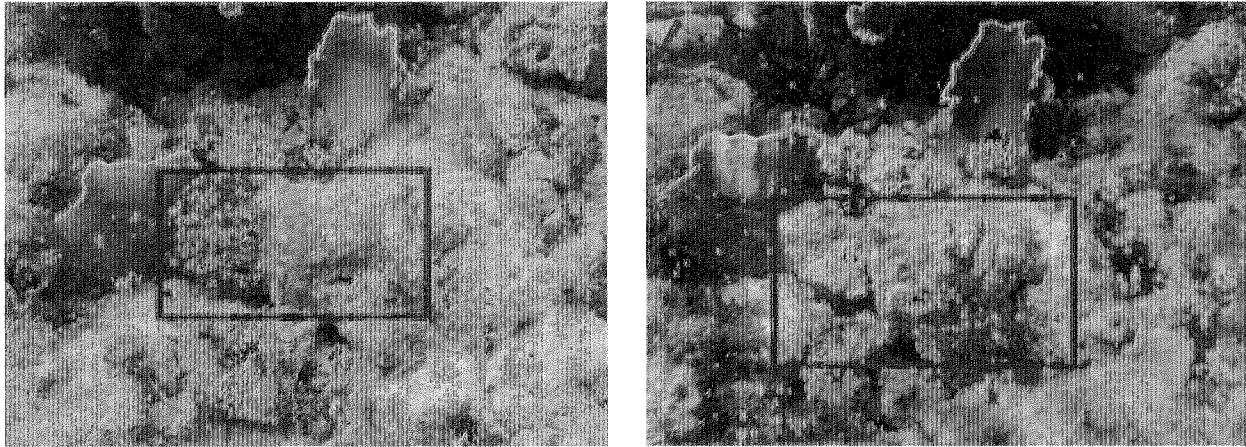FIG. 2. Close-up photographs of plot 2 in 2008 (left) and 2009 (right) indicate qualitative changes in algal and coral cover on the back reef north of Little Cayman Research Center. Note the disappearance of brown algae and growth of Knobby Sea Rod within the superimposed rectangle, and the growth of fire coral to the lower right of the rectangle.

basal area estimates were made in 2008.

We estimated the proportion of every quadrant covered by each of the coral species and algal genera present for only the first three plots due to time constraints. The observer pairs estimating algal or coral cover did so simultaneously, attempting to view the frame perpendicularly when possible. Details on the angles of frame orientation were not

given in the previous study, but we recorded approximate values used in 2009 for the first 10 plots (Table 1). Observers consulted each other on the identification of algae and corals before making cover estimates.

For each of the 10 plots, we recorded GPS coordinates using a Garmin GPSmap76 owned by the Central Caribbean Marine Institute, which we carried

TABLE 2, continued.

Plot	Quadrant	Montastrea annularis	Siderastrea siderea	Porites asteroides	Porites porites	Diploria strigosa	Agaricia humilus	Millepora complanta	Knobby Sea Rod	Corky Sea Finger	Total Coral Cover
					Difference (2009-2008)						
1	1	0	0	-4.5	0	0	0	-11	0	-12.5	-28
1	2	0	0	-0.5	-6	-6	2	-6.5	0	-9.5	-26.5
1	3	0	-1.5	0	0	0.5	1	0	0	0	0
1	4	0	-15	0	0	-10	0	0	0	3	-22
2	1	-22.5	0	0	1	-9.5	2	1	0	0	-28
2	2	0	0	0	3	0	1	-24	0	0	-20
2	3	0	0	0	0	0	1.5	-2.5	0.5	0	-0.5
2	4	-11.5	0	0	0	0	0	-6	0	0	-17.5
3	1	0	0	0	0	0	0	0	0	2.5	2.5
3	2	0	0	0	0	0	-12	0	0	-10	-22
3	3	0	0	1	1	0	-14.5	0	0	-8	-20.5
3	4	0	0	0	0	0	1	0	0	1	2

TABLE 3. Visual estimates of algal cover (genus level) from 2008 and 2009, for three permanent plots on the back reef behind Little Cayman Research Center on Little Cayman Island. Calculated differences between years are shown. 2008 values were estimates of basal area while estimates from 2009 were percent projected cover estimates. TL= top left quadrant, TR= top right, BR=bottom right, BL=bottom left. Top, bottom, left, right as viewed with quadrant 1 and 2 on top, usually facing the ocean (see Fig. 1). Encrusting orange refers to an unidentifiable orange encrusting Rhodophyta alga.

Plot	Quadrant	*Halimeda*	*Galaxaura*	*Dictyota*	*Ceramium*	*Valonia*	*Liagora*	Encrusting Orange	Total Algal Cover
					2008				
1	TL (1)	0	0	5	5	0	0	40	50
1	TR (2)	0	20	10	0	0	0	0	30
1	BR (3)	0	0	0	0	0	0	0	0
1	BL (4)	0	0	15	5	0	0	0	20
2	TL (1)	0	0	5	0	0	5	10	20
2	TR (2)	5	0	10	0	0	10	5	30
2	BR (3)	5	5	15	0	0	0	0	25
2	BL (4)	5	0	15	0	2	0	2	24
3	BL (1)	5	0	0	0	0	0	0	5
3	TL (2)	20	0	0	0	0	0	0	20
3	TR (3)	25	5	0	5	0	0	0	35
3	BR (4)	0	0	0	35	0	0	0	35
					2009				
1	1	2.5	0	0	1	0	7.5	25.5	36.5
1	2	4	0	2.5	0	0	0	10.5	17
1	3	0.5	12	6.5	0	0	0.5	0	19.5
1	4	0	0	3	0	0	3	7	13
2	1	0	0	5	0	0	0	0	5
2	2	5	0	2.5	0.5	0	0	0	8
2	3	6	0	11	0.5	0	1	5.5	24
2	4	9.5	0	9.5	0	0	1	4	24
3	1	3.5	0	0.5	0	0	0	1.5	5.5
3	2	7	0	0.5	4	0	0	3	14.5
3	3	4.5	1.5	2	0.5	0	0	9	17.5
3	4	4	0	4	4.5	0	1	6.5	20

in a plastic jar sealed with duct tape. The frame quadrants were numbered 1-4 starting with the upper left, as viewed facing North and progressing clockwise, and the exact compass bearing of the North-South center line was taken (Fig. 1). We then took five photos using a Canon Powershot SD 1000 at maximum focal length ("zoomed out"). One photo was taken of the entire frame from a similar angle to the previous study, and four more photos were taken to detail each quadrant. We kept the camera underwater and as perpendicular as possi-

TABLE 3, continued.

Plot	Quadrant	*Halimeda*	*Galaxaura*	*Dictyota*	*Ceramium*	*Valonia*	*Liagora*	Encrusting Orange	Total Algal Cover
				Difference (2009-2008)					
1	1	2.5	0	-5	-4	0	7.5	-14.5	-13.5
1	2	4	-20	-7.5	0	0	0	10.5	-13
1	3	0.5	12	6.5	0	0	0.5	0	19.5
1	4	0	0	-12	-5	0	3	7	-7
2	1	0	0	0	0	0	-5	-10	-15
2	2	0	0	-7.5	0.5	0	-10	-5	-22
2	3	1	-5	-4	0.5	0	1	5.5	-1
2	4	4.5	0	-5.5	0	-2	1	2	0
3	1	-1.5	0	0.5	0	0	0	1.5	0.5
3	2	-13	0	0.5	4	0	0	3	-5.5
3	3	-20.5	-3.5	2	-4.5	0	0	9	-17.5
3	4	4	0	4	-30.5	0	1	6.5	-15

ble to the frame, while still capturing the entire quadrant area. But in most cases, the camera angle was < 90° to the plane of the frame, due to water depth. Despite the variable camera angle, some of the photos of quadrants were analyzed using Photoshop CS3 Extended to estimate the projected area of each species of coral and genus of algae. In Photoshop, we outlined each cover type and used the Image Analysis feature to calculate the areas of each cover compared to total area of the quadrant.

Results

We found small qualitative changes in plots from 2008 to 2009 (Figs. 1 and 2). There were generally more changes in algal than coral cover. Based on quantitative visual estimates, projected cover of some algal and coral species in some quadrants were over 20 percentage points less than the estimated basal area in 2008 (Tables 2 and 3). However, these large differences lack credibility, not only because of the different type of data collected, but also because such large changes were not apparent when we compared the photos between 2008 and 2009. We also found differences within our 2009 data between visual estimates and computer estimates of projected cover. Differences were calculated between the cover estimates, and ranged from 0 to 19%. In some cases visual estimates were double those from image analysis (Table 4).

Discussion

The differences in visual estimates of cover between 2008 and 2009 are most likely due to our use of projected area (2009) rather than basal area (2008) and to differences between observers between the two years. While a comparison of photos between 2008 and 2009 also suffers from lack of truly replicable methods, evidence of large changes in cover

TABLE 4. Visual estimates of % projected cover by two individuals, compared to the photo estimation for both coral and algal cover (see text for details) in two permanent plots on the back reef behind Little Cayman Research Center. The difference between the visual estimators and photo estimation is shown, as a proxy for the accuracy of visual estimations. N.D. designates photographs where the cover was not visible due to the angle from which it was taken. Need to explain 1.1, 1.2 etc—different scheme from table 3

Coral Species and Algae Genera	Visual Estimator 1	Visual Estimator 2	Average of Two Visual Estimates	Photo Estimation	Difference (two-person-avg minus photo)
Plot 1.1					
Coral	Karl	Sarah			
Porites asteroides	5	4	4.5	1	3.5
Millepora complanata	10	12	11	11	0
Corky Sea Finger	7	8	7.5	1	6.5
total	22	24	23	13	10
Algae	Jeremy	Jon			
Halimeda	3	2	2.5	0	2.5
Ceramium	0	2	1	1	0
Liagora	7	8	7.5	3	4.5
Encrusting Orange	30	21	25.5	16	9.5
Wrangelia	3	8	5.5	1	4.5
total	43	41	42	21	21
Plot 1.2					
Coral	Karl	Sarah			
Agaricia humilus	2	2	2	3	-1
Porites asteroides	2	1	1.5	0	1.5
Millepora complanata	10	9	9.5	7	2.5
Corky Sea Finger	6	3	4.5	2	2.5
total	20	15	17.5	13	4.5
Algae	Jeremy	Jon			
Halimeda	4	4	4	1	3
Dictyota	2	3	2.5	1	1.5
Encrusting Orange	12	9	10.5	2	8.5
Wrangelia	0	1	0.5	N.D	0.5
Brown Encrust	3	0	1.5	N.D	1.5
Stopopodium	0	2	1	N.D	1
total	21	19	20	4	16

would be visible in the images, where even small changes can sometimes be clearly seen (Fig. 1, Fig. 2). Large changes in the cover of corals and algae did not

TABLE 4, continued.

Coral Species and Algae Genera	Visual Estimator 1	Visual Estimator 2	Average of Two Visual Estimates	Photo Estimation	Difference (two-person-avg minus photo)
Plot 1.3					
Coral	Karl	Sarah			
Siderastrea siderea	60	47	53.5	34	19.5
Agaricia humilus	2	0	1	0	1
Diploria strigosa	8	7	7.5	5	2.5
total	70	54	62	39	23
Algae	Jeremy	Jon			
Halimeda	1	0	0.5	N.D	0.5
Galaxaura	12	12	12	8	4
Dictyota	5	8	6.5	5	1.5
Liagora	1	0	0.5	N.D	0.5
Stopopodium	2	1	1.5	0	1.5
total	21	21	21	12	9
Plot 1.4					
Coral	Karl	Sarah			
Siderastrea siderea	4	2	3	7	-4
Diploria strigosa	25	25	25	22	3
total	29	27	28	29	-1
Algae	Jeremy	Jon			
Dictyota	4	2	3	2	1
Liagora	3	3	3	N.D	3
Encrusting Orange	5	9	7	2	5
Green Encrusting	7	8	7.5	4	3.5
total	19	22	20.5	8	12.5

occur.

Changes in algal cover may just be a regular part of the dynamics of the back reef, or the recent hurricane may be partially responsible for some of the small changes apparent. The substantial differences in 2009 between estimates of cover obtained visually and from image analysis are probably due to error by the visual estimators and our inability to standardize the angle from which photos were taken. Changes to the methods are essential to ensure that estimates, photographs, and plot placements are consistent, precise, and reliable from one year to the next.

TABLE 4, continued.

Coral Species and Algae Genera	Visual Estimator 1	Visual Estimator 2	Average of Two Visual Estimates	Photo Estimation	Difference (two-person-avg minus photo)
		Plot 2.1			
Coral	Karl	Sarah			
Montastrea	18	21	19.5	8	11.5
Siderastrea radiens	2	1	1.5	1	0.5
Agaricia humilus	3	1	2	0	2
Porites porites	1	1	1	5	-4
Millepora Complanta	1	1	1	N.D.	1
Diploria strigosa	6	7	6.5	N.D.	6.5
total	31	32	31.5	15	16.5
Algae	Jeremy	Jon			
Dictyota	2	8	5	5	0
Wrangelia	4	0	2	4	-2
Penicillus	1	2	1.5	1	0.5
total	7	10	8.5	9	-0.5
		Plot 2.2			
Coral	Karl	Sarah			
Agaricia humilus	1	1	1	N.D.	1
Porites porites	3	3	3	N.D.	3
Millepora Complanta	50	60	55	73	-18
total	54	64	59	73	-14
Algae	Jeremy	Jon			
Halimeda	2	8	5	4	1
Dictyota	1	4	2.5	N.D.	2.5
Ceramium	1	0	0.5	N.D.	0.5
total	4	12	8	4	4

PART II:
RECOMMENDATIONS FOR METHODS

There are many practical difficulties to be addressed when planning a long-term comparative study of coral and algae on a shallow back reef. Waves break over the crest, creating currents, turbulence and turbidity that are all more problematic than in the deeper fore reefs, where most long-term coral monitoring has been done at Little Cayman and elsewhere. Despite these challenges, back reefs deserve their own careful study because they are one of the major reef habitats and support a distinct marine benthic community.

TABLE 4, continued.

Coral Species and Algae Genera	Visual Estimator 1	Visual Estimator 2	Average of Two Visual Estimates	Photo Estimation	Difference (two-person-avg minus photo)
Plot 2.3					
Coral	Karl	Sarah			
Agaricia humilus	2	1	1.5	1	0.6
Millepora Complanta	3	4	3.5	11	-7.5
Knobby Sea Rod	1	0	0.5	0	0.5
total	6	5	5.5	13	-7.5
Algae	Jeremy	Jon			
Halimeda	4	8	6	3	3
Dictyota	12	10	11	5	6
Ceramium	1	0	0.5	1	-0.5
Liagora	1	1	1	N.D.	1
Encrusting Orange	7	4	5.5	3	2.5
Stopopodium	1	2	1.5	1	0.5
total	26	25	25.5	13	12.5
Plot 2.4					
Coral	Karl	Sarah			
Montastrea	10	13	11.5	18	-6.5
Millepora Complanta	5	5	5	6	-1
total	15	18	16.5	24	-7.5
Algae	Jeremy	Jon			
Halimeda	7	12	9.5	1	8.5
Dictyota	9	10	9.5	6	3.5
Liagora	0	2	1	N.D.	1
Encrusting Orange	5	3	4	1	3
Penicillus	1	2	1.5	0	1.5
Avrainvillea	1	1	1	1	0
total	23	30	26.5	10	16.5

Relocating plots on a back reef is difficult because of complex reef topography. GPS should be used to map precise locations; this is far easier and more reliable than following compass directions and using a measuring tape, especially in difficult weather conditions. To replicate frame position and orientation between years, accurate compass headings and angles of frame inclination are required, in addition to detailed photos from past years (Table 1). Permanently marking the

center or corners of plots is feasible but not advisable for very long term studies, because the presence and maintenance of a visible permanent marker would disrupt coral and algal growth.

Another serious limitation is inconsistency in species and genus identification from year to year, leading to incorrect inferences about changes in taxon-specific cover values. Even in the first two years there appear to be at least three discrepancies in identifications. In 2009, we found *Agaricia humilis* and *Siderastrea radians* present in several plots, but these were not documented in 2008, despite being apparent in 2008 photos. We also believe that the brain coral seen in most plots is *Diploria strigosa* rather than *Colpophyllia natans*. Familiarity of Dartmouth researchers with these species will increase over time, but for a long-term study it is imperative to establish correct baseline data as early as possible.

To this end, a preliminary edition of a comprehensive manual of coral species on the back reefs of Little Cayman has been prepared (Wengert 2009) with photographic records and basic information on local abundance, size range, habitat etc. A similar guide has been started for algae genera (Wachter and Wengert 2009). The resulting guides are designed to clarify identifications between years, and be refined when possible. They will supplement the published coral and algae guides for the Caribbean, which contain many species not found on the Little Cayman back reefs and lack some useful local information.

Visual Estimation

Visual estimation can be used successfully to assess coral and algal cover (Leujak and Ormond 2007). Thomas et al. (2008) visually estimated basal area for both coral and algae. However, the total basal area available on the substrate differs among plots and quadrants because of complex micro-topography. It is also difficult to standardize estimates of basal area of individual algae or coral colonies, because (1) basal areas are often not visible from above due to overhangs, and (2) because it is unclear how to calibrate basal area estimates to actual values based on field data. This is in contrast to projected cover, for which visual estimates can be calibrated using photography and image analysis. Estimations of projected cover eliminate the problems with basal area estimates as long as individuals view the plot perpendicular to the frame. Finally, basal area estimates are inadequate for species (e.g. Corky Sea Fingers) that can grow vertically and horizontally without changing their basal stem area.

Visual estimates of projected cover can attain high accuracy and precision, at least in the lab environment, if individuals calibrate their measurements. In the lab, we practiced estimating projected cover by placing various irregular shapes and objects, (representing coral and algal species) within the ca. 1 m² frame used in the field. After each observer made independent estimates in each trial, we photographed the quadrant perpendicular to the frame and used Adobe Photoshop

CS3 Extended to determine actual projected cover of each "taxon" in the quadrant; total projected cover ranged from 30% to 90%. During the first trial, our estimates were on average 2.8% away from those obtained by image processing, but by the fifth and last trial we were only 0.8% away. Using averages of percentages estimated independently by multiple individuals further reduces error. We calculated the differences of estimations from photographic analysis values, and

TABLE 5. This summary of the calibration data collected for five calibration trials shows the largest deviation of individual cover estimates from the photographic analysis and the largest difference between the average cover estimate from four observers and computer cover for each trial. Taking an average of individual estimates results in a smaller range of estimates.

Trial	Maximum Deviation for Individuals	Maximum Deviation for Averages
1	11	7
2	7	5
3	9	3.75
4	11	3.5
5	10	4.5

the largest deviation from photo analysis values for individual estimates was 11% while that for the average of four estimators was only 7% (Table 5). This exercise proved that it is possible to attain precise and accurate visual estimates of projected cover in laboratory conditions.

However, when we tried visual cover estimates on the back reef, accuracy and precision declined. Our estimates were an average of 2% away (calculated as a simple difference, by subtraction) from the photographic analysis but were

highly variable, ranging from 18% below to 19% above (Table 4). Because of waves, it was exceedingly difficult to position ourselves perpendicular to the quadrants to estimate projected cover. Individuals and colonies of algae and coral were often quite small, and easily missed, especially under difficult conditions. It was beneficial for all observers to discuss and identify species present before making cover estimates. Overall, visual estimation can be accurate in ideal conditions, but field conditions require much greater effort to ensure reliable estimates.

Photography

Using standardized photos to assess coral and algae cover can eliminate subjective assessments. However, errors can still be made in the interpretation of images, if species are not correctly identified, or in the outlining of the coral and algae to be analyzed by the software. Leujak and Ormond (2007) evaluated six different methods to survey coral reefs and concluded that photography and image analysis is the most efficient and reliable method; camera position can be standardized by building a rigid stand, and projected cover can be determined by using various software programs. We constructed a camera stand that was connected to a 0.45 m x 0.45 m quadrant frame, using PVC Pipe to hold the camera at a set distance perpendicular to the frame (construction details in Figs. 3 and 4). We mounted a Canon Power Shot SD1000 in a WP-DC13 waterproof case on top of this stand to take all photos in

the lab. There, the camera stand allowed us to take standardized photos of each 0.45 m x 0.45 m quadrant, and we obtained estimates of projected cover by analyzing the photos using Adobe Photoshop CS3 Extended.

However, underwater use presented three problems. First, although the camera mounted on the stand captured the entire quadrant when viewed through

FIG. 4. The camera fitting for top of camera stand. Constructed from a dive slate using a dremel. Specifically designed for Canon WP-DC13 Waterproof Case.

air, the higher refractive index of water magnified the image and we could no longer capture the entire quadrant. The stand (left at the lab in 2009 and potentially available in 2010) must be lengthened to mount the camera farther from the frame. Second, because some of the sites were shallow, the stand held the lens of the camera above the water, making it impossible to photograph the quadrant from the standardized position. The height of the stand also made it difficult to align with the quadrants of the permanent plots, due to water turbulence, and the effects of gravity when photographing vertically oriented plots. Third, clarity of the photos was an issue in rough conditions, because turbidity reduces image quality in proportion to the distance between the camera and the quadrant. Clear photos are critical for identification and analysis.

A possible alternative to a camera frame is a rod of appropriate length fixed to the camera frame, positioned perpen-
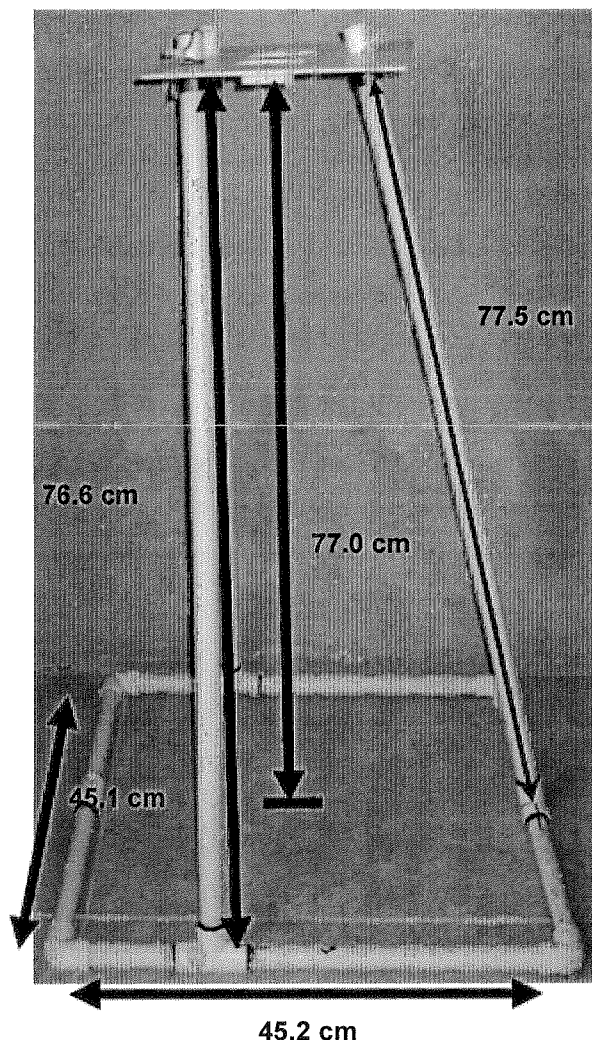

FIG. 3. This is the camera stand for standardized underwater quadrant photography. Measurements were taken from inside edges of PVC and to the floor for the center measurement. The height is incorrect for underwater photography, due to water magnification effects.
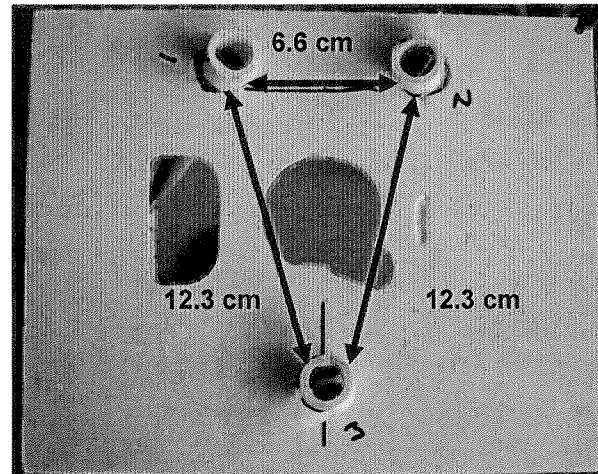
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dicularly to the quadrat. The rod standardizes the distance to the quadrant or substrate, and the image of the rod in the photo is a very small fraction of the total area, providing a narrow gauge rod is used and the photo is taken along the line of the rod. This method has been used in coral surveys around Little Cayman Island (Jonathan Clamp, pers.

comm.).

In spite of the many problems with photography on the back reef, it can be much more accurate and objective than visual estimations if conditions are favorable and methods are standardized.

Conclusion

Overall, we recommend that the long-

TABLE 6. Problems found and solutions suggested for a long-term study of coral and algae composition on the back reef near the Little Cayman Research Center on Little Cayman Island. See text for details of calibration. "Correctly proportioned for use underwater" refers to the difference in image size resulting from the different refractive indices of air and water; camera must be mounted farther from the frame in water to capture image of entire plot.

Problem	Solution
General	
Turbidity, current and waves	Unavoidable on back reef but minimized on calm days.
Relocation of plots	Use GPS, compass bearings, and photographs.
Replication of plot orientation and slope	Compass bearings and angle measurements combined with photographs.
Identification each year	Make comprehensive list of corals and algae in a plot and ensure that all observers can identify species. Develop a photographic and descriptive reference manual for corals, algae and other space-holding invertebrates on back reefs of Little Cayman.
Visual estimation	
Imprecision and inaccuracy of estimates	Calibrate observers, and have multiple observers estimating independently.
Inability to orient line of sight perpendicular to the frame	Take extra care and use calm days where possible.
Inaccurate identification or missing sections of plot	Talk to fellow observers to identify all species present, before estimating cover.
Photography	
Photo including whole plot (or defined quadrants)	Use camera mount frame proportioned for use under water . See text for alternative to camera mount frame.
Alignment of camera mount frame with quadrant	Use camera mount frame only in calm water or where it can be held steadily. Attach mount frame to quadrant frame if possible.
Camera positioned out of water	Use mount frame only in water that is deeper than mount frame height. For some existing plots in shallow water, only small portions of plots can be photographed perpendicular to quadrant plane. Take photos in high tide.
Poor photo quality	Take photos with enough light and minimal turbidity, at a high resolution. Where the purpose is a qualitative record, obtain close-up images showing sufficient detail, that can be located within images of the whole plot.

term study of coral and algae in permanently marked plots should be extended to deeper waters on the fore-reef. This would reduce the problems of current, waves and turbidity that interfere with photography and estimates on the back reef, and extend the long term study to another major habitat. The camera stand we constructed (or a similar one, or a rod as described above) should be used to take standardized photos that can be analyzed using proven software. In future years there are three potential fore-reef research sites near the Little Cayman Research Center, the NOAA ICON station to be installed directly offshore in 2009, and two dive sites a few hundred meters to the east ("Rock Bottom" and "Snapshot"), currently marked by white buoys attached to mooring anchors on the sea floor; in 2009, these buoys were clearly visible from the laboratory.

Continuing the long-term back reef project remains valuable, and the optimal study methods for this habitat would combine visual estimates with photography. Ideally, sampling would be conducted under calm conditions for photo clarity and ease of visual estimates. Using photos for image analysis of projected cover is not possible for all the long term plots established on the back reef, but it is possible for some. Further, as we did for 10 plots this year, sufficient photos should be taken every year at all plots, for qualitative analysis of presence and absence of corals. This would allow for studies of recruitment and survival. Visual estimates of projected cover

should be standardized by calibrating all individuals doing the sampling, and by having at least two people making estimates of each value.

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APPENDIX A: PHOTO ARCHIVE NOTES

Pictures are labeled in the format "Plot (plot #) – (quadrant # (or whole plot)) year." For example a photograph with the name "Plot 1-4 09.JPG" indicates quadrant 4 of plot 1 in 2009. Because we changed the orientation of plot 3, we took a whole plot picture from the new and old (2008) angles. This picture is followed with the tag "2008 view." Close up pictures within quadrants are followed by the label "close up." Lighting and turbidity make picture quality of some photos poor. It may therefore be necessary to consult the Thomas et al. (2008) photo archive when using photos to identify some plots in the future.

An Evaluation of Management for Sustainable Harvest in Queen Conch (*Strombus gigas*) Populations on Little Cayman Island

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Faculty Editor: David R. Peart

Abstract: We evaluated the effectiveness of the Little Cayman Islands government conch management strategy by comparing the abundance and size-class distribution between conch populations in adjacent protected and limited-harvest areas. Our data provide no indication of drastic population decline in the harvested area; conchs were similarly abundant in the protected and harvested areas. We found over 40 human-killed conchs in the harvested area and only three in the protected area, indicating that Little Cayman residents generally follow harvest regulations. Humans harvested the largest conchs, yet larger and older adult conchs were more abundant in the harvested area, possibly because large conchs migrate through the harvested area to get to deeper waters. Overall, the conchs are likely not being overharvested and it appears the local population is at no immediate risk.

Key words: replenishment zone, spillover effect

Introduction

The queen conch (*Strombus gigas*) is an economically and culturally important organism for island peoples throughout the Caribbean. Although it was once very abundant, overharvesting has caused conch populations to plummet and it is now listed as an endangered species under the Convention on International Trade in Endangered Species (Food and Agriculture Organization 2004). In the Cayman Islands, management to preserve declining conch populations began in 1978 (Department of Environment [DOE] 1978). Since 2006, harvesting has been allowed only in designated harvesting areas, from 1 May—31 October, and is limited to 5 conchs per person or a maximum of 10 conchs per boat per day (DOE 2006). Replenishment zones (hereafter referred to as protected areas) were also established throughout the is-

land and harvesting of conchs and lobsters is prohibited in these areas. One of these areas was established in South Hole Sound to provide habitat for conchs so they could supply recruits to the adjacent harvesting area. This approach to managing marine populations is based on the "spillover principle," whereby the larvae of organisms from protected areas may act as a source to offset overharvesting in unprotected populations (Collins 2007). The efficacy of this strategy has yet to be thoroughly evaluated on Little Cayman.

Furthermore, Manfrino and Brown (2006), based on recent surveys of other areas on the island, inferred that populations were declining, as they found more dead than live individuals and low conch densities overall. To determine the effectiveness of this "spillover" management strategy we compared the abundance and size-class distribution among conch

populations in adjacent protected and harvesting areas in South Hole Sound. We predicted there would be a higher density of conchs and more adults in the protected than the harvested area, because of human predation. In accordance with Collins and Harrison (2007) we also predicted that adult conchs would be smaller and younger in the harvested area, because of size-selective human predation.

METHODS

Study organism

Conchs grow by lengthening the shell until sexual maturity at 3.5 to 4 years (Collins 2007). They then stop growing

lengthwise and a flange develops on the lip of the shell, signaling the transition from the juvenile stage to adulthood (Martín-Mora et al. 1995). We used the presence/absence of this flange to classify conchs as juveniles or adults. The flange thickens for the rest of their adult life and can be used as a proxy for age (Collins 2007).

Sampling

We surveyed the conch population on 25-27 February 2009 in the adjacent protected and harvesting areas of South Hole Sound. We used three 60 m x10 m belt transects at each of 100, 300, and 500 m distances away from the dividing line, in each of the two areas, for a total of 18
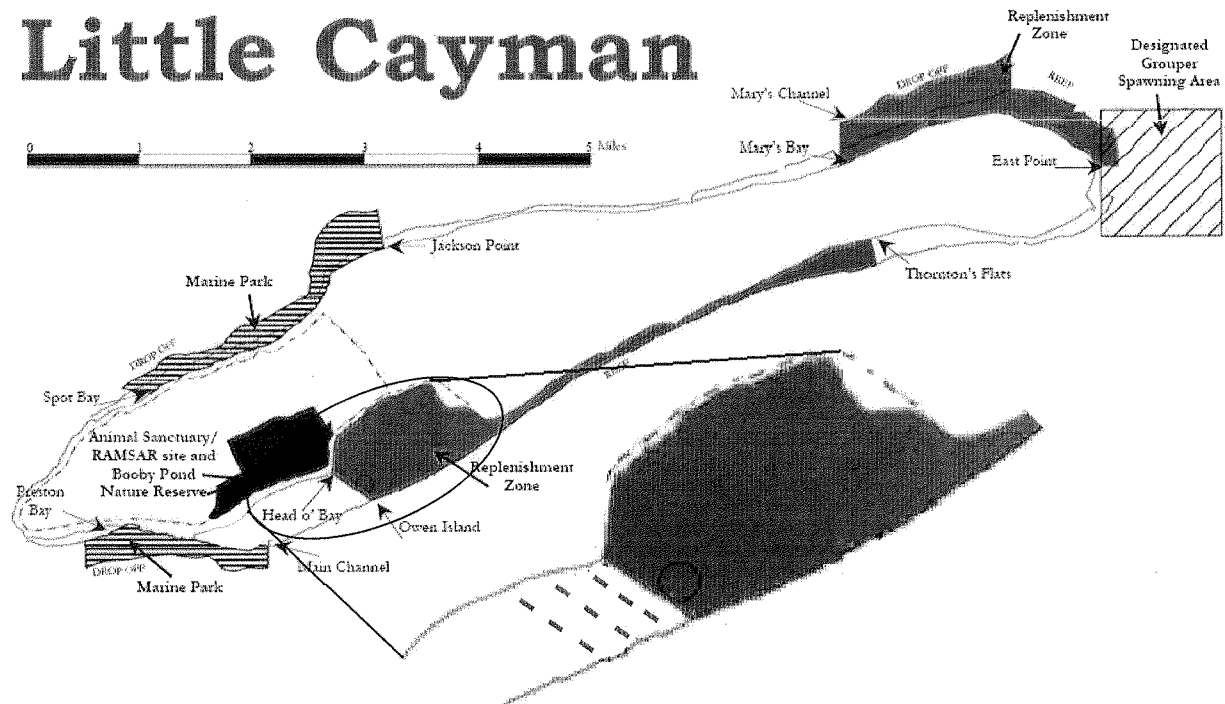
FIG. 1. Map of Little Cayman Island Conservation Management with South Hole Sound enlarged. The shaded area is protected, while harvesting is permitted in the non-shaded area. 18 60x10 m transects are marked on our study site, but are not to scale. There are near-shore, middle, and far transects at distances of 100m, 300m, and 500m on either side of the line dividing the two zones. Map used from the Cayman Island Department of the Environment (http://www.gov.ky/pls/portal/docs/PAGE/CIGHOME/FIND/ORGANISATIONS/AZAGENCIES/ENV//DOCUMENTS/BROCHUREDOE.PDF).

FIG. 2. Mature queen conch shell (*Strombus gigas*), displaying all measurements taken (Collins and Harrison 2007).

belts (Fig. 1). The three belts at each distance were separated by at least 50 m. Maximum water depth was 2.5 m and the harvested and protected sample areas contained approximately the same amount of turtle grass and open sand. For each conch shell in each belt we recorded shell length, lip thickness (Fig. 2), whether it was an adult or juvenile, if it was alive or dead, and if it had a chisel hole above the apical spiral (indicating human predation).
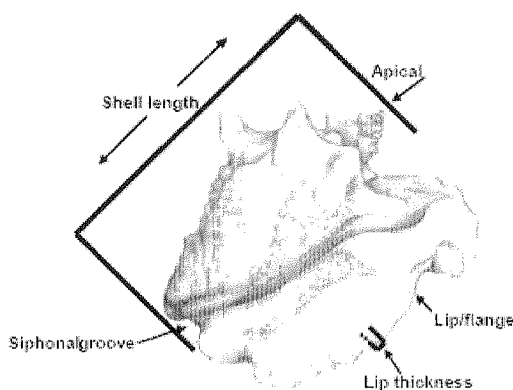
Statistics

We compared the mean abundance of total individuals, number of individuals with a chisel hole, adults, and juveniles in the protected and harvested area, using belts as replicates. We also compared adult age (using flange size as a proxy). We used an $\ln + 1$ transformation to normalize the data.

RESULTS

We found a total of 578 conch shells, 486 of which contained live individuals (349 in the protected area, 137 in the har-

vested area), over a total sampled area of 10,800 m² (1.08 ha). Mean conch density in the protected area was 0.065/m² while mean density in the harvested area was 0.025/m² (Fig. 3). However, this difference was not significant due to high variance in abundance among belt transects (one-tailed $t_{16} = 0.53$, $P = 0.30$; Fig. 3). There was also no difference in adult abundance (two-tailed $t_{16} = -0.17$, $P = 0.57$; Fig. 3) or juvenile abundance (two-tailed, $t_{16} = 0.94$, $P = 0.35$; Fig. 3) between the protected and harvested areas. Contrary to our prediction, adult conchs had a significantly larger flange in the harvested than in the protected area (two-tailed $t_{144} = -4.25$, $P = 0.001$), indicating that they were older in this area. On average, conchs in the harvested area had a flange that was 3.8 mm thicker than those in the protected area. The number of naturally dead individuals (not exhibiting a chisel hole) was not significantly different between the two areas (two-
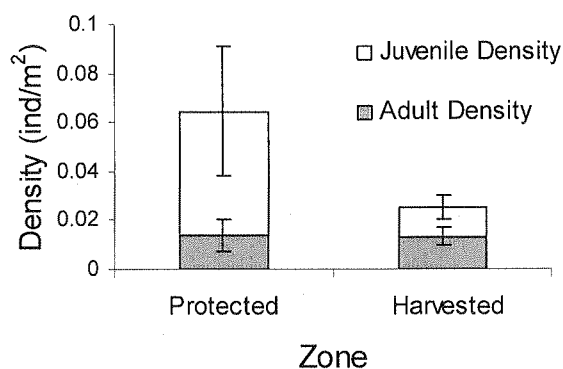

FIG. 3. Mean queen conch density in protected and harvested areas of South Hole Sound, Little Cayman Island. Bars indicate means ± 1 S.E. for juvenile and adult densities (n = 18 belt transects, each 60 m x 10 m; total number of alive conchs sampled = 486). Adults were defined by the presence of a flange on the shell lip (Fig. 2).

tailed $t_{16} = -0.54$, $P = 0.60$), while the number of conchs killed by human predation was greater in the harvested than the protected area (one-tailed $t_{16} = -2.15$, $P = 0.023$). We found forty-two conchs with chisel holes in the harvested area and three in the protected area.

DISCUSSION

As the conch population densities were not significantly different between the protected and harvested areas, our results provide no indication of population decline in the South Hole Sound harvested area. Furthermore, it appears that Cayman residents are following the management regulations, as we found over forty human-killed conchs in the harvested area and only three in the protected area. Contrary to our prediction, we found larger and older adult conchs in the harvested area compared to the protected area, even though humans selectively harvest the largest conchs. This may be explained by migration of adult conchs from the protected area through the harvesting area to reach deeper water to reproduce (Martín-Mora et al. 1995). The main boat channel links the harvested portion of the sound to the open ocean, and adult conchs could be responding to cues that drive them toward that channel.

Thus, aspects of the life history of conchs that are biologically interesting also complicate the inferences we can draw from our results. Pelagic conch larvae metamorphose into juveniles in shallows before migrating to deeper water as adults (Ray and Stoner 1995) and the shallow water conch populations we sampled may recruit from adjacent areas or from deeper waters (Roberts 1997). Studies examining differential survivorship and fecundity between the protected area, harvesting area, and deeper waters, as well as individual movements between these areas, could provide further insight into the conch population dynamics and also help inform management strategies. A follow-up study examining the same population would be helpful to determine how this population is changing over time.

As we believe our findings are directly relevant to conch population management, it is important to examine our population density data in more detail. We obtained large samples to maximize our statistical power to detect differences between the protected and harvested areas. We also tried to balance the number and size of the belt transects. Because conchs are known to have patchy distributions, we made the belt transects both long and wide in an effort to minimize variance among belts. Nevertheless, one dense aggregation of juvenile conchs in the protected area caused high variance among transects. Consequently, even with our large sample, and with mean conch density in the protected area more than double that in our harvested area samples, the difference was not statistically significant.

If large aggregations of conchs occurred more in either the protected or harvested areas, and were not repre-

sented in our belt samples, our comparison of population densities between the two areas may not reflect the true values. We had the opportunity to observe conch populations over much of the ca. 2 km² (200 ha) study area (Fig. 1) since we swam over 2 km in each of the harvested and protected zones. We noticed that major aggregations like the one we encountered in one of our protected area transects were rare across the entire study area, so we infer that most conchs in the area were not in major aggregations, which are notoriously difficult to sample adequately with transects.

In summary, we believe that if there had been a major difference in density resulting from conch harvesting, our large samples would have detected it. Nonetheless, we recommend that any follow-up study include a very extensive survey for conch aggregations in both protected and harvested areas, in addition to intensive sampling in plots or transect belts. The extensive survey could probably be done by boat in calm weather, recording the number of aggregations found and broad estimates of the numbers in each aggregation.

Overall, the results of our survey indicate that the conchs are likely not being overharvested and that the population is not immediately at risk.

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Residents' Attitudes About Environmental Issues on Little Cayman

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Abstract: I recorded Little Cayman residents' attitudes about the relative importance of environmental issues on the island in 12 interviews in February 2009. Using a series of questions about individuals' perceptions of environmental issues affecting the island, I found that global issues were ranked as less important, while waste disposal (a local issue) was mentioned by every interviewee, and ranked most important overall (Fig. 1). All interviewees agreed that change in an individual's behavior can make a difference. This suggests that efforts to improve waste disposal on Little Cayman may be well received and supported, and residents might alter behavior to reduce environmental impacts of waste disposal.

Key words: the Cayman Islands, public opinion, sustainability

INTRODUCTION

The Cayman Islands, located in the Caribbean between Cuba and Jamaica, are home to over 40,000 residents (Cayman Government 2009). World-renowned for their spectacular coral reefs, the three islands attract tens of thousands of overnight visitors and hundreds of thousands of day visitors from cruise ships every year (J. Clamp, pers. comm.). The less-known terrestrial ecosystems harbor numerous endemic species and subspecies, including birds, lizards, and snakes (Davies 1994). Development pressures can make it difficult to balance human growth with protecting the natural ecosystems upon which growth is based. In a strategic planning document published by the Cayman Government one of the goals for the Caymans is to be "a country which manages growth and maintains prosperity, while protecting our social and natural environment" (Cayman Government 1999).

Little Cayman is the smallest and least developed island, with a year-round population of just over 150 people (Cayman Government 2009). Little Cayman has experienced less development and environmental degradation than its sister islands, and continues to maintain its reputation for a pristine environment. Nonetheless, Little Cayman has grown rapidly in recent decades, with ca. 30% population increase since the last census in 1999 (Cayman Government 2009). Pressures on the island's natural resources and infrastructure are increasing along with its population. The values and actions of the inhabitants will determine Little Cayman's future trajectory. What is important to local residents is directly relevant to any efforts to protect the island's environment and promote sustainability.

TABLE 1. The series of questions, asked in the same sequence for each interview.

Sequence	Interview Questions
1	What do you consider the main environmental issues on Little Cayman?
2	Of these, what do you think is the most important to you/your family? (most urgent or biggest potential impact)
3	Do you currently experience the effect of any environmental problems?
4	Do you think you will within the next 10 yrs? Within your lifetime?
5	Which of the following environmental issues would you rank as most important to least important to you?: - waste disposal - water consumption/water quality - marine species - terrestrial species - shoreline development - reef decline - sea level rise - climate change
6	Is one of these particularly overlooked and not being addressed?
7	How urgently do you think this issue needs to be addressed?
8	How do you see island inhabitants' actions contributing to causing these environmental issues?
9	What do you think Little Cayman residents could do to reduce these environmental impacts?
10	Do you think that an individual resident choosing to change their behavior can make a real difference?
11	What do you currently do to reduce your personal environmental impacts?

METHODS

I interviewed 15 Little Cayman residents over three days, 25-27 February 2009. Interviewees spanned three generations and included life-long residents and recent arrivals. Occupations included resort management, local business, dive instruction, maintenance, finances, retirement, and employment with the Central Caribbean Marine Institute. I conducted twelve 30-60 min interviews using predetermined questions in a consistent sequence, designed to gauge residents' attitudes about environmental issues they perceived to be affecting them personally on Little Cayman (Table 1).

RESULTS

Residents identified waste disposal as an important environmental issue in every interview. Ten of the 12 interviewees included waste in their response to Question 1 (Table 1) and half ranked waste disposal as the single most important issue in Question 5. On the list of eight environmental issues in Question 5 (Table 1) waste was never ranked lower than fourth, and when rankings were averaged across interviews, waste was ranked highest (Fig. 1).

Closely related issues (lettered groupings in Fig. 1) were rated similarly. Water consumption (group B) was ranked second, followed by marine-related issues
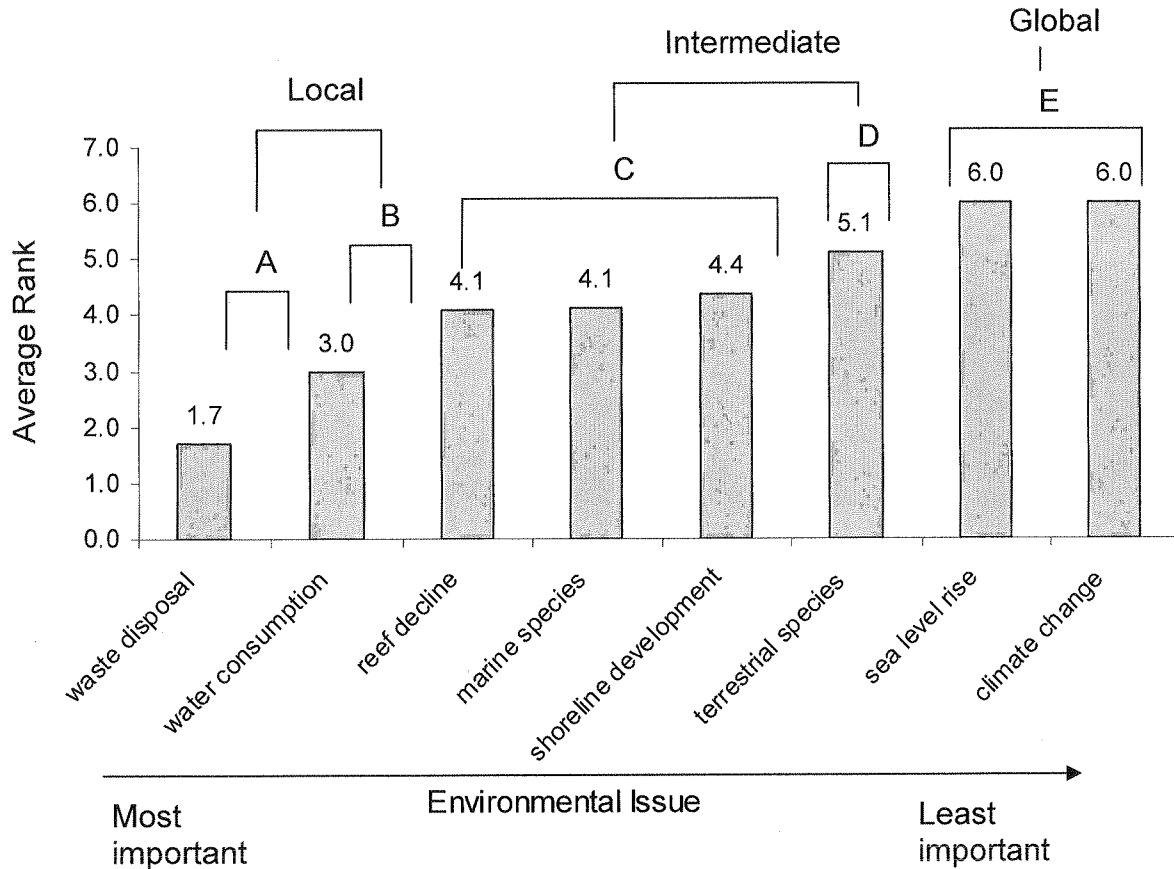
FIG. 1. Residents of Little Cayman (n = 12 interviewees with wide-ranging backgrounds) ranked waste as their most important environmental concern. Individuals were asked to rank (y-axis) eight environmental issues (x-axis), in order of importance to them personally, as a resident of Little Cayman, 1 being most important, 8 least. Lettered categories (A-E) identify related issues. A and B include the most local issues, C and D represent an intermediate scale, and E is global. Residents ranked local issues as more important.

(group C), then terrestrial species (group D), and finally issues related to global change (group E). Only five people thought that climate change is a serious concern for Little Cayman, two did not believe in climate change, and the remaining seven did not think climate change posed a significant threat to Little Cayman.

Every interviewee thought change in an individual's behavior could make a difference. Examples of ways interviewees currently reduce their environmental impact are listed in Table 2 and their sug-gestions to improve waste disposal are in Table 3.

DISCUSSION

Waste disposal was the most important environmental concern to interviewees. This issue is both highly visible and very local. There is only one disposal facility, so all the waste generated on the island is easily visible and residents personally experience the dump when they take their garbage there. I believe this fosters a widespread awareness of how individuals directly contribute to the is-

sue of waste disposal, which is reflected by residents' sentiment that changes in their behavior can make a difference. As one resident said, change happens "one pebble a time." Many people mentioned basic things they already do to reduce waste generation (Table 2). These findings suggest that efforts to improve waste disposal on Little Cayman would be well received and supported by the community.

Residents responded differently depending on the scale of the environmental issue. Their emphasis on local issues (Fig. 1) is likely influenced by Little Cayman's isolation, small size, and low population. Goods must be either produced on the island (which is rare) or shipped via barge or small airplane, mostly from Grand Cayman or the US. The logistics, costs, and frequent delays due to severe weather (especially hurricanes) make residents very aware of the resources they use. These factors, in combination with their direct interaction with the dump, help to explain residents' focus on the local waste disposal issue.

In contrast, residents rated more global concerns as less important (Fig. 1, group E). For these larger issues the same factors—Little Cayman's isolation, small size, and low population—may be acting to decrease residents' feelings of empowerment. Even interviewees who accept that humans are altering the climate said they gave climate change and sea level rise low rankings because they feel their contributions on Little Cayman are negligible, and that they are powerless to ef-

fect change, either through individual behavior or political action. Attitudes about coral reef decline were similar. Several interviewees assured me that the reefs around Little Cayman are still in good condition and the marine parks and other regulations are effective. However, even those who saw no immediate threats to the reefs emphasized the importance of preventive action through more government protection and regulation, should the need arise.

Residents may have limited access to recent scientific findings on the causes of climate change, and may be unaware of how the constraints of island life can contribute to residents' carbon footprints. None of the interviewees mentioned the emissions from air travel they depend upon, or the energy intensive food they consume (production, shipping, refrigeration, etc.) There may be potential to shift public attitudes by raising awareness of these factors. Translating that awareness into constructive action depends on (1) providing feedback to residents on their contributions to large-scale environmental issues, so that reductions in those contributions are apparent, and (2) helping to make alternative options available so that there are clear and reasonable choices that residents can make.

Compared to reducing waste, reducing one's carbon footprint is more abstract and more difficult to measure; the results are less visible and the benefits are dispersed across the globe. Recognizing these challenges, some strategies to address climate change focus on moni-

toring and benchmarking carbon emissions, so that changes in carbon footprints for individuals and communities are measurable and comparable. Creating direct feedback, by providing individuals with information about the amount of CO_2 they emit and how that compares to others, makes improvements quantifiable and more tangible.

One consultant organization that implements this three-tiered approach (measure, benchmark, report) is Earthcheck, which runs a benchmarking system for the Green Globe certification program (Earthcheck 2009). An example of how Little Cayman residents could approach the daunting task of reducing their contributions to climate change would be to monitor and reduce CO_2 emissions, with the assistance of this organization's consulting services. Gaining Green Globe status for the island could lead to many improvements, including better waste disposal and reduction of residents' CO_2 emissions. If residents felt part of an effort on the island to address

TABLE 2. Current practices of Little Cayman residents that help reduce their personal environmental impact (not an exhaustive list; only recommendations mentioned during the interview are listed).

Current Practices to reduce environmental impact	Category
Reuse various materials (boxes, jars, cans, etc)	Waste
Don't use disposable plates, cups, silverware, or napkins	Waste
Use biodegradable disposable plates, cups, silverware	Waste
Use biodegradable garbage bags	Waste
Print on both sides of paper, refill ink cartridges	Waste
Use refillable water bottle	Waste
Reusable water bottle issued to hotel guests to use for duration of stay instead of drinking bottled water	Waste
Encourage people to drink Caybrew beer so bottles can be reused	Waste
Put trash in trash cans; don't litter	Waste
Organize beach and roadside trash cleanups	Waste
Rain water catchment (tanks) for potable water, use brackish water for washing clothes and flushing toilets	Water
Plant native species for landscaping, minimizing need for water	Water
Passive solar hot water heater	Energy
Replace inefficient incandescent light bulbs with more efficient CFLs (Compact Fluorescent Light bulbs)	Energy
Reduce the number of bulbs in light fixtures	Energy
Wash linens and towels only when requested by hotel guests	Energy
Air dry laundry	Energy
Ask hotel guests to turn off air conditioner when not in room	Energy
Shades on windows to keep sun out and keep rooms cool	Energy
Solar heating rings to help heat swimming pool	Energy

global issues, current feelings of insignificance and apathy could be reversed, especially if residents perceived that progress was also being made on a larger scale through political commitments and international treaties.

Residents appeared well informed about and receptive to alternative energy sources. Passive solar hot water heaters are widely used as an alternative to costly, short-lived electric water heaters. Solar panels are cost-effective, with an average local payback time of ca. 4 years (J. Clamp, pers. comm.). Solar power generation would be more attractive if excess production could be sold to the power company, as on Grand Cayman. All interviewees thought wind turbines could be used both at a household and larger scale, except for two, who expressed strong objections because of potential impacts on birds and the vulnerability of turbines during storms. Because of the high cost of electricity on Little Cayman (ten times the average cost in the US), the payback time for alternative technologies is exceptionally quick (J. Clamp, pers. comm.). Two residents mentioned the potential of switching to alternative fuel sources. They said previous attempts to use waste vegetable oil to power boats were unsuccessful because of the oil's high viscosity, but that the biodiesel currently produced on Grand Cayman would work.

Half of the interviewees expressed concerns about continued growth on the island, recognizing that more people lead to more boats, more trash, and more

pressure on the island's limited infrastructure and resources. One resident who ranked "rapid growth" as her biggest environmental concern said, "there's a balance between keeping Little Cayman the way it is and sharing it." A resort general manager said, "I guess less is better in the Caymans, that's for sure." And a lifelong resident of Little Cayman said, "The island is growing now, and now is the time to put it [a new waste management system] in place." Even one resident who adamantly said he supports continued growth on the island stressed the importance of government regulation to help enforce responsible development standards on the island.

The findings of this study suggest that efforts to address environmental issues on Little Cayman should focus community-based initiatives on local issues like waste disposal, which residents feel is important and which they feel they can influence. Meanwhile, larger environmental issues might be approached from very different angles, for example through coordinated initiatives (like Green Globe) or government regulation and incentive programs in conjunction with community awareness/education campaigns.

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Slippery dickory docks, the goat kicks up the rocks: Mutualistic schooling of the Spotted Goatfish and the Slippery Dick

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Abstract: We investigated the interspecific association between the Spotted Goatfish (*Pseudupeneus maculatus*) and the Slippery Dick (*Halichoeres bivittatus*) near the back reef of Little Cayman Island. Goatfish had higher foraging rates and changed to cryptic coloration less often when in association with Slippery Dicks than when alone, which suggests that goatfish are less wary of predators when with Slippery Dicks. Slippery Dicks had similar foraging rates whether with goatfish or alone, but with goatfish they concentrated foraging attempts (bites) directly following goatfish foraging attempts. This suggests that the disturbance caused by goatfish foraging allows the Slippery Dick to forage more efficiently.

Key words: mixed-species schooling, foraging advantage, Little Cayman, back reef

Introduction

Mixed-species schooling is common among many Caribbean reef fishes; it may increase feeding efficiency and reduce predation risk (Ehrlich and Ehrlich 1972). We noticed small schools or pairs of the Spotted Goatfish, *Pseudupeneus maculatus*, hereafter referred to as "goatfish", and the Slippery Dick, *Halichoeres bivittatus*, foraging together on sandy flats near the back reef, directly offshore of the Little Cayman Research Center. We hypothesized that both the goatfish and Slippery Dick benefit from this association by foraging either more frequently or more efficiently.

To test this hypothesis, we first compared how goatfish and Slippery Dicks forage alone vs. together, with the prediction that when alone, both goatfish and Slippery Dicks would forage less. Second, we observed whether Slippery Dicks preferentially allocate their forag-

ing attempts to the time immediately after a goatfish foraging event. Such a behavior could be beneficial for Slippery Dicks, as goatfish use their barbels to locate prey items hidden in the substrate (Deloach and Humann 1999). Lastly, we imitated the substrate disturbance caused by foraging goatfish, with the prediction that the artificial disturbance would attract Slippery Dicks.

Methods

From 24 to 27 of February 2009, we observed several aspects of the foraging behavior of the Spotted Goatfish and the Slippery Dick in the back reef off the northern coast of Little Cayman Island, near the Little Cayman Research Center. We observed pairs of one Spotted Goatfish and one Slippery Dick; sometimes we found a pair foraging alone while other times we observed a pair within a small mixed-species school. We treated

individuals that were clearly foraging in close association as a pair (such pairs were apparent, even when there were several individuals in a foraging group). We also observed Spotted Goatfish and Slippery Dicks foraging solitarily.

During three-minute focal observations for each of 38 goatfish–Slippery Dick pairs (haphazardly chosen), we first recorded the number of foraging attempts (bites at the substrate) by the Slippery Dick for one minute. During the second minute, we recorded the number of foraging attempts (bites at the substrate) by the goatfish, as well as the amount of time spent disturbing the substrate with their barbels ("ruffling"). Finally, we scared the pair apart by swimming quickly towards them and making a wild hand gesture. During the third minute we recorded the (now solitary) goatfish's foraging attempts and time spent ruffling. For each minute, we qualitatively noted any coloration change by the goatfish. Goatfish often change to a cryptic coloration when threatened or inactive, so this observation gave us an indication of the goatfish's level of predator awareness.

We also made separate one-minute focal observations of 17 goatfish and 26 Slippery Dicks that we found swimming alone. Individuals were chosen haphazardly. For goatfish, we recorded the number of foraging attempts and the time spent ruffling; we also noted any coloration change. For Slippery Dicks, we recorded the number of foraging attempts.
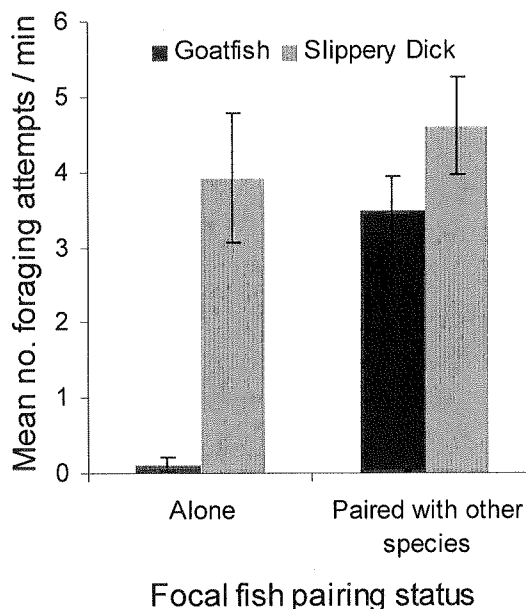

FIG. 1. Observations near the back reef at Little Cayman Research Center indicated that Spotted Goatfish (*Pseudupeneus maculatus*) had a lower foraging rate (foraging attempts per minute) when alone than when with Slippery Dicks (*Halichoeres bivittatus*). Slippery Dicks had similar foraging rates when alone and when paired with goatfish. Twenty-eight goatfish-Slippery Dick pairs, 17 goatfish alone, and 26 Slippery Dicks alone were observed. Bars show means ± 1 SE.

In separate observations of 28 goatfish-Slippery Dick pairs, we noted the number of Slippery Dick foraging attempts during a haphazardly chosen five-second time period of goatfish ruffling, and the five seconds immediately following a goatfish foraging attempt.

Finally, we dragged a piece of dead coral through the sandy substrate 20 times for two-minute periods, and recorded whether Slippery Dicks were attracted to the disturbance.

Data Analysis

We excluded 8 pairs from the comparison of paired vs. alone foraging attempts because the Slippery Dick left the pair. We excluded 16 pairs from the goat-

fish coloration change comparison because we were unable to scare the Slippery Dick and the goatfish apart, or because either the Slippery Dick or the goatfish left the pair before we finished the first observations.

RESULTS

When paired with a Slippery Dick, goatfish both ruffle more (t_{43}= 5.49, $P <$ 0.0001) and make more foraging attempts (t_{43}= 5.76, $P <$ 0.0001; Fig. 1) than when alone. We also found that goatfish used cryptic coloration more often when alone than when in association with a Slippery Dick, both when found alone and after being scared away from their Slippery Dick foraging partner (Contingency Table Analysis, χ^2_{57}= 24.130, $P <$ 0.0001; Fig. 2).
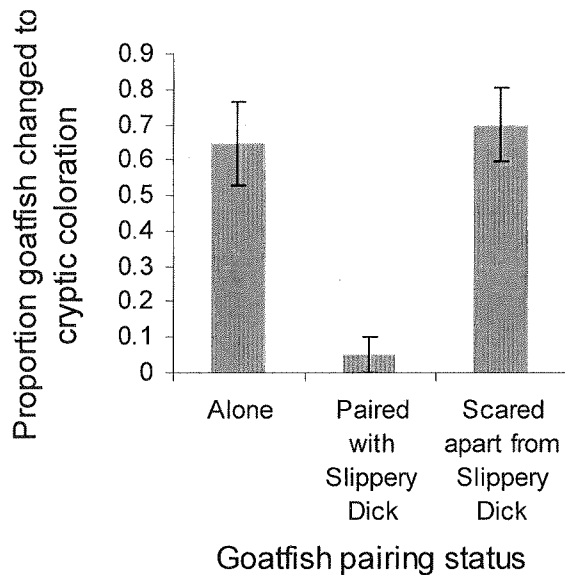

FIG. 2. Observations near the back reef at Little Cayman Research Center indicate that Spotted Goatfish (*Pseudupeneus maculatus*) have cryptic coloration less often when with a Slippery Dick (*Halichoeres bivittatus*) than when without a Slippery Dick, both when observed alone and when scared apart from a Slippery Dick. Bars show means ± 1 SE.
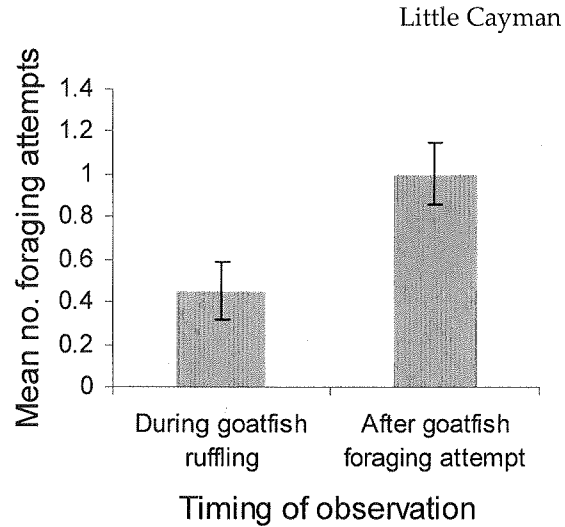

FIG. 3. Observations near the back reef at Little Cayman Research Center indicate that Slippery Dicks (*Halichoeres bivittatus*) have more foraging attempts directly following a foraging attempt by a Spotted Goatfish (*Pseudupeneus maculatus*) than during goatfish substrate ruffling time, a more general searching method. Twenty Slippery Dicks were observed. Bars show means ± 1 SE.

Slippery Dicks had similar numbers of foraging attempts when alone and when in association with a goatfish (t_{52}= 0.66, P = 0.51; Fig. 1). However, when they were with a goatfish, Slippery Dicks made more foraging attempts directly following a goatfish foraging attempt than during goatfish ruffling (t_{38} = -2.7729, P =0.0086; Fig. 3).

When we dragged pieces of coral along the sea floor, Slippery Dicks were attracted to the disturbance 20 out of 20 times, usually arriving in less than a minute (never more than two minutes). In nine of the trials, Slippery Dicks foraged in the area disturbed by the coral within a minute of arriving. In three trials, a large Slippery Dick appeared to defend the coral fragment, driving away other Slippery Dicks.

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DISCUSSION

Goatfish foraged more with Slippery Dicks than alone. We propose that goatfish may be using the Slippery Dick's predator vigilance to spend more time foraging. The fact that goatfish use cryptic coloration less when with a Slippery Dick further supports this hypothesis. It is also possible that both species benefit by reduced predation risk when in association, allowing each species to spend less time being vigilant.

Slippery Dicks do not make more foraging attempts when with goatfish. Instead, they preferentially allocate foraging attempts immediately following a goatfish foraging event. They may allocate attempts in this way because each attempt is more likely to be successful when the goatfish is locating prey items in the substrate. The fact that Slippery Dicks consistently gathered at and foraged near our artificial seafloor disturbance (and sometimes even defended it against conspecifics) also suggests that Slippery Dicks benefit from foraging near such disturbances. This result, in combination with the Slippery Dick foraging data, suggests that Slippery Dicks gain a foraging advantage by associating with goatfish.

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EFFECTS OF STRUCTURE SIZE, STRUCTURE DISTANCE, AND DAMSELFISH PRESENCE ON USE OF ARTIFICIAL REEFS BY JUVENILE DIURNAL FISH

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Abstract: Juvenile fish are often habitat-limited on coral reefs, so artificial reefs may be valuable in maintaining or increasing fish diversity and abundance. We examined early patterns of occupancy of small, artificial reefs by juvenile diurnal reef fishes. We predicted that larger artificial structures nearer the back reef would support more fish. However, there was no difference between fish abundance for structures of different sizes or at different distances. Damselfish abundance was negatively correlated with abundance of other herbivores, suggesting that species interactions may be important in the very early stages of development of these fish assemblages.

Key words: island biogeography, fish territoriality, spatial distribution, species interactions

INTRODUCTION

Juvenile fishes are often habitat-limited on coral reefs (Schmitt and Holbrook 1999; Jones et al. 2004), so artificial reefs may be valuable in alleviating competition among juvenile fishes (e.g. Strelcheck et al. 2005). We constructed artificial "patch reefs" in Grape Tree Bay directly behind Little Cayman Research Center to examine early assemblages of juvenile diurnal fishes in the context of the equilibrium theory of island biogeography. We assumed that the continuous back reef served as the mainland source, while our artificial structures served as either large or small islands, either near to or far from the source.

We hypothesized that use of a structure by juvenile fishes depends upon the suitability of the structure as shelter (Clarke 1988; Jones 1988) and upon the probability of encountering the structure.

Thus, in keeping with island biogeography theory (MacArthur and Wilson 1967), we predicted that larger and nearer artificial reefs would have the highest initial occupancy rates and would support a larger, more diverse population of juvenile diurnal fishes after four days.

Species may respond to size and distance of patch reefs differently, and species interactions may play a role in determining the rate at which the structures accumulate fish, as well as their eventual species composition (Almany 2004). Thus, we also examined species composition on the artificial reefs with the prediction that different fish species would show different patterns of use of the artificial reefs.
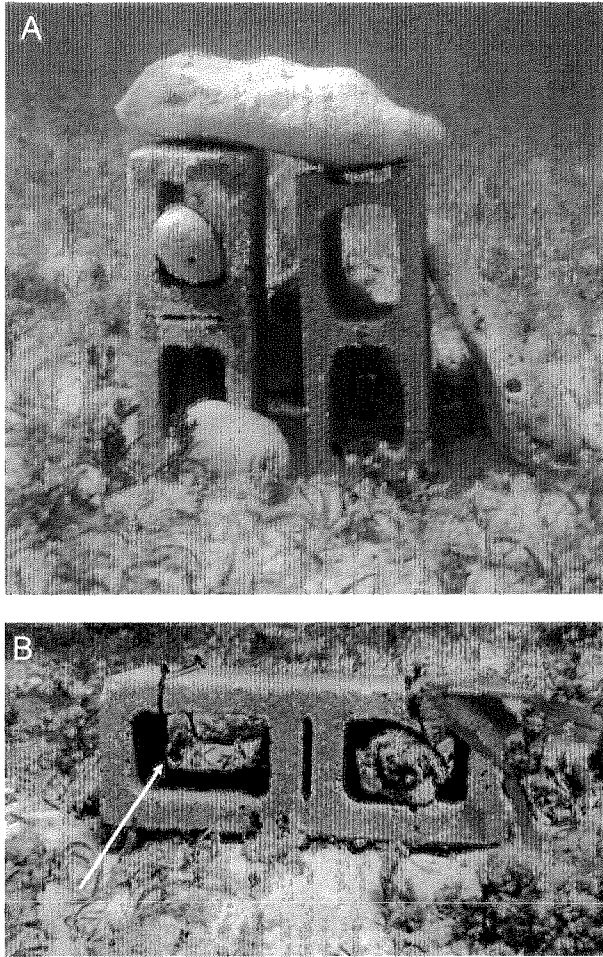
METHODS

We conducted our study in Grape

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FIG. 1. Representative photographs of artificial reef structures in Grape Tree Bay, Little Cayman Island. A, large structure (n = 8, four that were 5 m from back reef and four that were 15 m from back reef); B small structure, sample sizes and arrangement same as for large structures. Each structure consisted of cinderblocks, dried coral, and an algae-encrusted rock. Note the juvenile damselfish (indicated by arrow) defending the small structure.

Tree Bay, directly behind Little Cayman Research Center, on 25-28 February 2009.

First, we built 16 structures (Fig. 1). Each was either large or small and placed either near to (5 m) or far from (15 m) the back reef. We ensured that near and far structures were also placed least 5 m or 15 m, respectively, from any natural patch reef. The large structures consisted of two cinderblocks (40 cm x 20 cm x 15 cm), three "large" (ca. 30 cm diameter) and three "small" (ca. 10 cm diameter) pieces of dried coral, and two pieces of algae-covered dead coral (ca. 20 cm diameter). The small structures had one cinderblock, one medium piece of dried coral (ca. 20 cm diameter), and one piece of algae-covered dead coral. See the images in Fig. 1 for the relative sizes of small, medium and large pieces of coral used. Each structure was at least 15 m away from the next one and we assumed no movement of fish between structures. The sequence of structures along the back reef was, from east to west: small far, small near, large far, large near repeated four times.

Each time we sampled, two researchers spent two minutes observing each structure and identified and counted all fish within 1 m of the structure that were not moving away from the structure (to exclude fish passing by). We first observed the structure from a distance of about 1.5 m to note fish that might be affected by our presence, then inspected it more closely for concealed fish. We sampled fish presence 13 times, once immediately after constructing the structures and then three times daily, in the morning, afternoon, and evening, for four days.

RESULTS

We recorded 342 sightings of fish of 19 species in 11 families occupying the artificial reefs. Fish abundance increased with time since we placed the structures (Spearman's r = 0.21, $P = 0.02$). Consider-
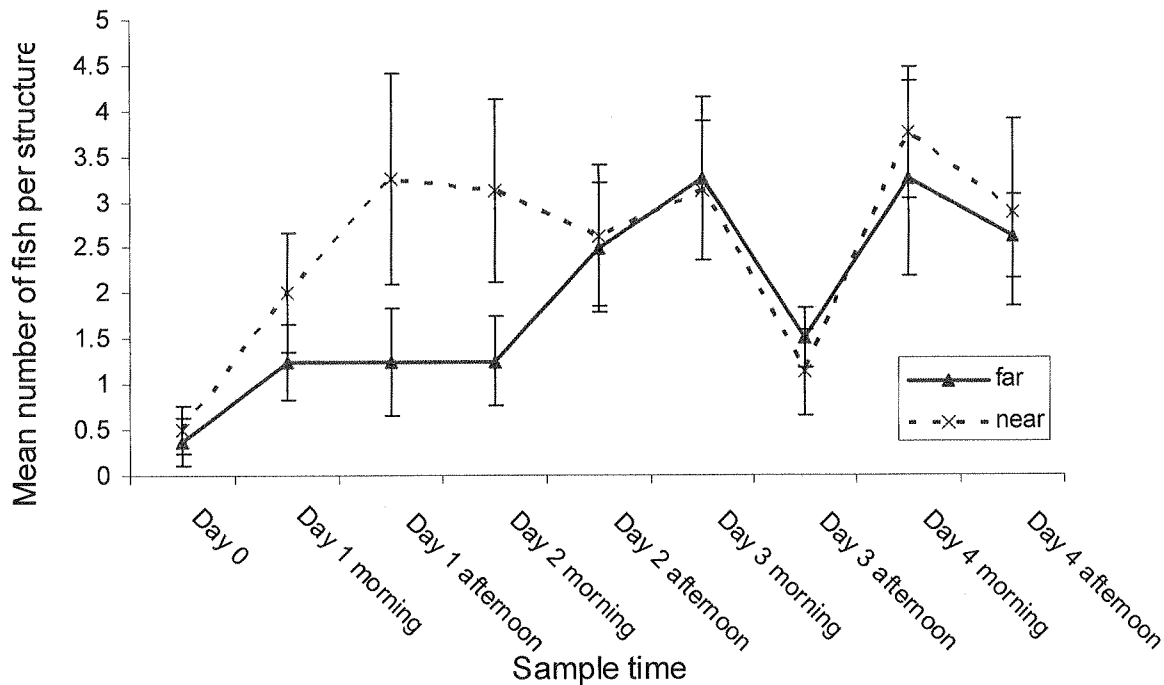
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FIG. 2. Abundance of fishes that occupied artificial reef structures on 25-28 February 2009 at Grape Tree Bay, Little Cayman Island increased rapidly on near structures in the first day and then changed little, while abundance of fishes on far structures increased steadily over the four-day study (n = 337 fish sightings at 8 near and 8 far structures per sample). Bars are mean ± 1 S.E.

ing each treatment separately, fish abundance increased with day for far (r = 0.30, P = 0.02) and small (r = 0.39, P < 0.01) structures (Fig. 2), but not near (r = 0.12, P = 0.36) or large ones (r = 0.02, P = 0.86).

During the first two days, fish abundance was greater on near structures than on far structures (χ^2_1 = 3.75, P = 0.05), but not different between small and large structures (χ^2_1 = 0.90, P = 0.34). However, over all four days, there was no difference in fish abundance based on distance from the back reef (χ^2_1 = 2.65, P = 0.10) or size (χ^2_1 = 0.00, P = 0.95).

Evenness was similar among all four treatments, ranging from 0.59 on large near structures to 0.73 on small far structures.

There were 23 damselfish on near structures and only 2 on far structures, a statistically significant difference (χ^2_1 = 17.68, P < 0.01; Fig. 3). Near structures also had slightly more wrasses (χ^2_1 = 4.06, P = 0.04) and fewer surgeonfish (χ^2_1 = 3.74, P = 0.05). Surgeonfish abundance was negatively correlated with damselfish abundance (Spearman's r = 0.20, P = 0.02; Fig. 4). Structure distance did not affect abundance of gobies and blennies (χ^2_1 = 0.27, P = 0.60). There was no difference between abundances on small and large structures for any group of fish (damselfish: χ^2_1 = 0.18, P = 0.67; wrasses: χ^2_1 = 0.02, P = 0.88; surgeonfish: χ^2_1 = 0.08, P = 0.77; gobies and blennies: χ^2_1 = 0.00, P = 1.00).
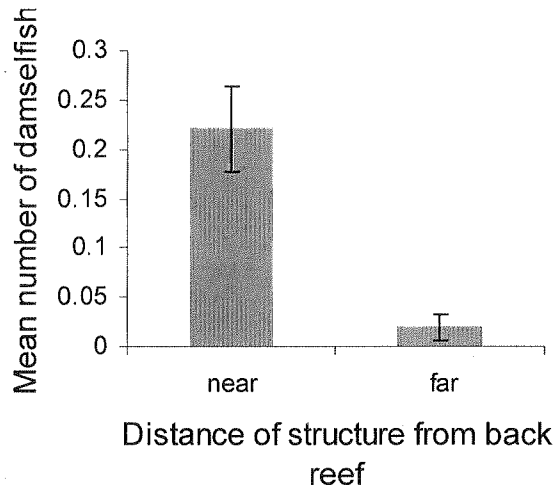
FIG. 3. Juvenile damselfish were more abundant on artificial reef structures nearer to the back reef in Grape Tree Bay, Little Cayman Island (n = 25 damselfish sightings over 128 pooled observations). Bars indicate mean ± 1 S.E.

DISCUSSION

The increase in fish abundance at the artificial reefs over time is consistent with past studies (Gorbatkin and Isbey 2007, Purdy and Spinoso 2008). However, there was no effect of structure size on fish abundance or diversity, contrary to the predictions of island biogeography theory (MacArthur and Wilson 1967). More consistent with our findings are the results of other artificial reef studies suggesting that presence or absence of structural relief is more important than quantity of relief (Gorbatkin and Isbey 2007) and that height of structure does not affect fish abundance (Gratwicke and Speight 2005).

Island biogeography theory predicts lower colonization rates on islands farther from the source (MacArthur and Wilson 1967), but distance from the back reef reduced fish abundance on our

structures only during the first two days. While some studies support the application of island biogeography to coral patch reefs (Molles 1978), others have shown an increase in fish abundance with distance (Walsh 1985; Lobben and Cheek 2008), perhaps because higher predation in patch reefs closer to the source reduces fish diversity (Schulman 1985; Belmaker et al. 2005). Similar species interactions may have influenced abundance of fishes on our artificial reefs.

Presence of juvenile damselfish on artificial structures was negatively correlated with abundance of juvenile surgeonfish, consistent with Risk's (1998) findings. Anecdotally, we observed territorial behavior by juvenile damselfish on our structures, which may drive away other herbivores to protect their territories (Deloach and Humann 2007). This suggests that the negative correlation between damselfish and surgeonfish abundance could be due to damselfish aggres-
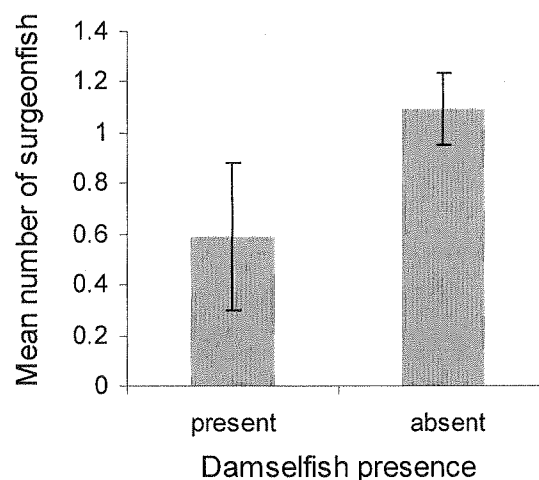

FIG. 4. In Grape Tree Bay, Little Cayman Island, juvenile surgeonfish were more abundant on artificial reef structures without damselfish (n = 128 structures observed). Bars indicate mean ± 1 S.E

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siveness towards the herbivorous surgeonfish. Other fish groups did not show negative correlations with damselfish or surgeonfish abundances, suggesting that this effect was not simply due to a limit on total number of fish that a structure could support. The high abundance of damselfish on near structures may have prevented use of these structures by surgeonfish. Such species interactions may cause fish abundance on far structures to eventually exceed that on near structures.

Increased risk of predation within the reef and the surrounding area may also drive fish to occupy more isolated structures. Almany (2004) found that excluding piscivores and damselfish may be more important than increased habitat structural complexity in affecting juvenile abundance on artificial reefs.

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Patterns of Juvenile Surgeonfish Distribution on Artificial Reef Structures

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Faculty Editor: David R. Peart

Abstract: We investigated factors affecting surgeonfish abundance on artificial reef structures. We manipulated algal abundance, censused fish, and counted nearby piscivores on 16 small artificial patch reefs. Neither algae nor predators influenced surgeonfish abundance, which was inversely related to damselfish abundance. Surgeonfish were significantly aggregated, due either to attraction of conspecifics or to unmeasured environmental factors.

Key words: Pomacentridae, Acanthurus

Introduction

Artificial reef structures provide habitat for fish, particularly habitat-limited juveniles (Schmitt and Holbrook 1999, Jones et al. 2004). Other studies have shown use of artificial reefs by juvenile fish in Grape Tree Bay behind Little Cayman Research Center (Gorbatkin and Isbey 2007, Purdy and Spinoso 2008, Stenquist et al. 2009). We build on those studies by investigating surgeonfish (Acanthuridae) distribution among artificial "patch" reefs, focusing on three factors suggested by Walsh (1985): food resources, predation, and competition. We considered damselfish separately from other herbivores because they are aggressive territory-holders that may drive away surgeonfish (Risk 1998, Deloach and Humann 2007), whereas the effects of other herbivores may be indirect, through competition for resources.

We looked at three species of surgeonfish, *Acanthurus coeruleus, A. bahianus,* and *A. chirurgus.* We hypothesized that surgeonfish abundance would be higher with greater algal availability and lower with higher presence of piscivores, damselfish, and other herbivores. Based on previous studies (Sweatman and Robertson 1994, Stenquist et al. 2009), we expected there would be more piscivores and more damselfish at the structures near to the back reef, causing the surgeonfish to inhabit the farther structures more often.

Methods

We conducted our study on 4-7 March 2009 in Grape Tree Bay behind the Little Cayman Research Center. We used 16 artificial reef structures that were constructed of cinderblocks and dried coral a week earlier (Stenquist et al. 2009). They were either small or large and either near (5 m) or far (15 m) from the back reef (see Stenquist et al. 2009 for details). Small and large structures originally included one and two algae-encrusted rocks respectively, but structure size did not af-
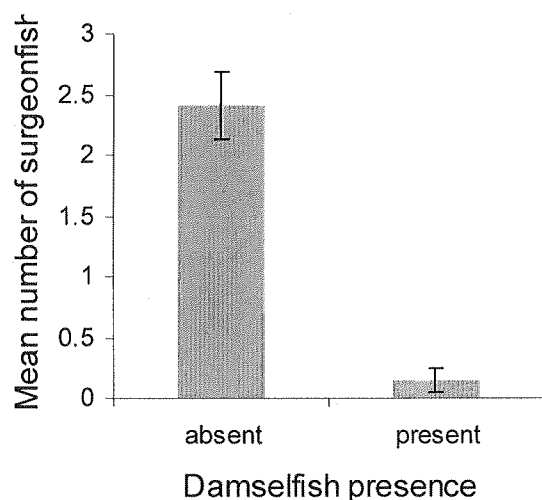
FIG. 1. Surgeonfish were significantly more abundant on artificial reef structures in Grape Tree Bay where damselfish were not present (n = 16 structures). Bars are means ± 1 S.E.

fect fish abundance (Stenquist et al. 2009), so we did not distinguish between small and large structures. On 4 March, to manipulate food abundance, we added five algae-encrusted rocks per structure to half the original structures. Although all 16 structures included at least one algal-covered rock, we will refer to those with one such rock as "without algae" and those with six algal-covered rocks as "with algae". In effect, our treatments were (1) near with six algal-covered rocks, (2) near with one algal-covered rock, (3) far with six algal-covered rocks, and (4) far with one algal-covered rock.

On 5-7 March we sampled each structure once a day. Each time we sampled, one researcher observed the structure for two minutes, identifying and counting all fish apparently using the structure. The other researcher counted for 5 min all piscivores visible from an observation point within 2 m of the structure, recording the approximate distance of piscivores from the structure as close (0-5 m) or medium (5-10 m). Consistently poor visibility due to high winds made it impossible to see piscivores in our far category (>10 m). Based on Randall (1967), we classed any species whose diet was more than 25% fish as a piscivore. In recording piscivores, we departed from the methods of Stenquist et al. (2009), who did not include passing piscivores in their counts.

Statistical analyses were done in JMP v. 7 (SAS Institute, Inc. 2007).

RESULTS

We sighted a total of 197 fish using our structures, including 84 surgeonfish, 14 damselfish, and eight other herbivores. In addition, we observed 118 predators, composed of 11 piscivorous fish species and one squid species, in the vicinity of the structures. Structures with more damselfish had fewer surgeonfish (Fig. 1; Spearman's r = -0.72, $P < 0.01$). Damselfish were more abundant on the near structures ($\chi^2_1 = 9.87$, $P < 0.01$) while surgeonfish were more abundant on far structures ($\chi^2_1 = 8.34$, $P < 0.01$). Damselfish abundance was greater on structures with algae (marginally significant, $\chi^2_1 = 3.55$, $P = 0.06$) while surgeonfish abundance was lower with algae ($\chi^2_1 = 6.42$, $P = 0.01$). Because damselfish may exhibit site fidelity (DeLoach and Humann 2007), we also tested whether damselfish abundance was already higher on ma-

nipulated structures before the additions of algae, and we found it was not ($\chi^2_1 = 0.86$, $P = 0.36$).

Even excluding plots with damselfish, surgeonfish were non-randomly distrib-

TABLE 1. Surgeonfish were distributed non-randomly on artificial reef structures in Grape Tree Bay, aggregating in groups of up to 7. Structures where damselfish occurred were excluded (n = 10).

Mean surgeonfish frequency	Number of structures
0	0
0-1	1
1-2	3
2-3	4
3-4	1
4-5	0
5-6	0
6-7	1

uted (Table 1), departing significantly from the random expectation of a Poisson distribution across structures ($\chi^2_7 = 63.19$, $P < 0.01$). Surgeonfish occurred in groups of up to 7 on the structures.

Surgeonfish abundance was not related to the abundance of other herbivores (i.e. other than damselfish and surgeonfish; Spearman's $r = 0.14$, $P = 0.35$) or piscivores (Spearman's $r = -0.23$, $P = 0.12$). Nor was there any effect of distance from the back reef on piscivore abundance ($\chi^2_1 = 0.69$, $P = 0.41$).

DISCUSSION

Damselfish presence appears to be the most important factor driving surgeonfish abundance on a structure. Damselfish aggressively defended structures,

chasing other fish and even biting us. The lower surgeonfish abundance on algae-added structures was probably due to the more frequent occurrence of damselfish on them. Similarly, the higher abundance of surgeonfish on far structures was probably due to damselfish abundance on near structures. Several other studies confirm that damselfish presence reduces the abundance of other fish (Almany 2004), particularly surgeonfish (Risk 1998). Sweatman and Robertson (1994) found that damselfish interacted aggressively with small fish more often near the reef (Sweatman and Robertson 1994), supporting our findings about distance.

The non-random distribution of surgeonfish among structures suggests that they may have a tendency to aggregate, as found by Risk (1998). This could be to reduce predation risk. The surgeonfish may have also responded to environmental differences that were not apparent to us. Contrary to the findings of Almany (2004) and Belmaker et al. (2005), presence of piscivores did not affect surgeonfish abundance. This may be because we made our observations in daylight, when fish predation is low (Deloach and Humann 2007); therefore,e the number of nearby piscivores in daylight may be a poor index of predation risk.

In summary, damselfish presence apparently affected surgeonfish use of artificial structures more than food availability, piscivores, or other competitors. If artificial structures are to be used to in-

crease habitat for juvenile reef fish, structures farther from the back reef appear to be better for small herbivores like surgeonfish because damselfish exclude them from closer structures.

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Niche differentiation in three species of Ophiocoma brittle stars (Echinodermata: Ophiuroides)

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Abstract: Brittle stars are an abundant group of suspension-feeders in shallow Caribbean coral reefs that often exhibit high local species diversity. We investigated spatial and temporal separation as possible modes of niche differentiation in three species of *Ophiocoma* (*O. echinata*, *O. paucigranulata*, and *O. wendtii*). We counted the number of individuals foraging and, as an index of foraging activity, the number of arms extended to feed, at three different times (afternoon, evening, and pre-dawn) and in two different habitats (live and dead coral). We also sampled under dead coral slabs ("rocks") on the sandy bottom to determine whether the community composition differed between live coral, dead coral, and under rocks. The number of individuals feeding within and across species did not change according to time of day. *Ophiocoma echinata* was relatively most abundant in live coral while *O. wendtii* was relatively most abundant under rocks. Our results suggest that these three species differentiate niches spatially (by habitat) rather than temporally.

Key words: coexistence, competitive exclusion

Introduction

Ophiocomidae is the most abundant and diverse family of brittle stars in shallow tropical waters (Sides and Woodley 1985). They filter large quantities of detritus out of the water column and are an important food source for predators (Rosenburg and Lundberg 2004). Several brittle star genera occupy the same habitat (crevices and under rocks), leading to high densities and local diversity (Lewis and Bray 1983; Paine and Platt 1999). Niche theory states that coexisting species must differentiate in habitat, foraging, or other characteristics to avoid competitive exclusion. We observed three species of suspension-feeding brittle stars from the same genus (*Ophiocoma pauci-* *granulata*, *O. echinata*, and *O. wendtii*) to investigate whether niche differentiation occurs between closely related brittle star species, and if so, whether they differentiate by habitat or time of feeding. One hypothesis is that co-occurring suspension feeders are more likely to specialize by habitat than by food type (Sides and Woodley 1985). We focused on time of feeding and on habitat preference among living coral, dead coral, and rocks. We predicted that the three *Ophiocoma* species would either feed at different times or occupy different habitat types.

Methods

Study Site and Organisms

We measured foraging activity of the three brittle star species on the back reef

of Preston Bay, Little Cayman Island. We identified species (Appendix 1) based on characteristic coloration of arms and tube feet (Sides and Woodley 1985; Hendler et al. 1995). *Ophiocoma echinata* have white tube feet, banded arms, and thickened dorsal arm spines, *O. wendtii* have red tube feet and banded arms, and *O. paucigranulata* have orange-to-white tube feet and a central white stripe along their arms (Appendix A, Hendler et al. 1995). This variation is more distinctive at night than during the day. All three species suspension feed by extending their arms, using tube feet and spines to trap debris, which they transport down the arm to their mouth (Sides and Woodley 1985).

Experimental Design

We sampled 60 plots during the afternoon (1630-1730), night (2130-2230), and pre-dawn (0530-0630) on 5-8 March 2009. We selected sampling times to span brittle stars' most active foraging time (Hendler 1984; Rosenburg and Lundberg 2004). We identified suitable brittle star habitat in patches of living and dead *Porites porites* based on the presence of large crevices (at least 5 cm deep) and low algae cover (Sides and Woodley 1985). Living coral had all live polyps; dead coral still had intact branching structure and in some cases up to 10% living polyp cover. Water depth was never greater than 2 m.

We haphazardly selected 60 sites that were at least 2 m apart, 30 on living *P. porities*, 30 on dead *P. porities*. Counting the number of limbs exposed has been used to measure brittle star feeding activity (Paine and Platt 1999). We considered individuals to be foraging when at least one arm tip was visible. Therefore, at each site, we identified brittle stars to species and counted both the number of individuals foraging and total arms exposed within two 900 cm² quadrats, combining them for one composite sample.

We positioned one quadrat near the top of the coral and the other on the lower, mid-section of coral head. We visually estimated percent open coral polyp cover in each quadrat to investigate whether there was a negative correlation in feeding behavior between coral polyps and brittle stars. To determine whether rock (dead coral on the sea floor) supported a different community composition of brittle stars than coral, we turned over 50 rocks along the back reef edge and identified and counted the brittle stars underneath. We then compared the relative abundances of each species among habitats.

Statistical Analyses

Species abundances across habitats and across time periods were non-normally distributed, so we analyzed each of these factors independently using nonparametric Kruskal-Wallis tests. We first tested whether abundances among species differed within each factor (habitat and time). We then separately tested whether the abundance of each species differed across time. To determine whether there was niche differentiation among habitats (in live coral, dead coral, and under rocks), we tested for a difference in relative abundance of spe-

TABLE 1. Brittle star abundance of three *Ophiocoma* species from 60 sites, each with two 900 cm² quadrats, across living and dead coral and different times (afternoon, 1630-1730, night, 2130-2230, and pre-dawn, 0530-0630) in Little Cayman Island, sampled from 5-8 March 2009.

Time	Live coral			Dead coral		
	Afternoon	Night	Pre-dawn	Afternoon	Night	Pre-dawn
Median abundance *O. echinata*	5.5	6	6.5	2.5	5	3.5
Median abundance *O. paucigranulata*	3	1.5	1	1.5	2	6
Median abundance *O. wendtii*	1.5	0	0	1	3.5	2
n	10	10	10	10	10	10
χ^2	6.21	9.98	11.79	0.32	1.93	6.32
df	2	2	2	2	2	2
p	0.04	0.007	0.003	0.85	0.38	0.04

cies among habitats. Finally, to determine whether there were interactions among species, we tested whether each species was distributed randomly with respect to others, within plots and across the entire sample. Note that because we had to run many separate tests due to the limited options available in non-parametric models, p values only slightly less than 0.05 should be considered marginal.

RESULTS

To test whether the three species differed in their abundances, for each combination of habitats and times, we did six separate Kruskal-Wallis tests. Overall, species abundances were significantly different in the living coral plots at all times, while in dead coral, species abundances differed significantly only at our pre-dawn sample time (Table 1). *Ophiocoma echinata* was most abundant in all living coral plots, while *O. wendtii* was least abundant in living coral at all times. Abundance of each species did not vary over time ($\chi^2_2 = 0.22$, $P = 0.90$), but the proportional abundance of *O. wendtii* and *O. echinata* varied significantly across habitats (*O. wendtii*: $\chi^2_2 = 7.20$, $P = 0.03$; *O. echinata*: $\chi^2_2 = 12.18$, $P = 0.002$; Fig. 1). Compared to the other two species, *O. echinata* was most abundant in live coral and least abundant under rocks, while *O. wendtii* showed the opposite trend (Fig. 1). Finally, when examining each 1800 cm² composite plot separately across the entire sample, we found that the presence of one species was random with respect to the presence of other species within that same plot ($\chi^2_7 = 1.56$, $P = 0.96$); that is, we do not have evidence that a certain species is competitively dominant across all times and habitats at this scale. This does not contradict our result that the absolute abundances of species differed because this test took into account only presence or absence of a species and not absolute abundance. There was no evidence for competition between brittle stars and corals for food (percent active coral polyp cover did not correlate with

the number of brittle stars foraging; r = 0.15).

DISCUSSION

There was no temporal differentiation in feeding activity among species but there was evidence of niche differentiation by habitat (live coral, dead coral, and under rocks). *Ophiocoma echinata* had greatest abundance (both relative and absolute) in living coral, where *O. wendtii* was least abundant. *Ophiocoma wendtii* appeared to be most abundant under rocks, while *O. paucigranulata* appeared to occur at intermediate abundances across habitats.

This difference in abundance of *O.*

echinata and *O. wendtii* among habitats suggests that species are differentiating according to habitat, which is consistent with the "Kohn hypothesis" (Sides and Woodley 1985). From our visual observations, it appears that living coral offers more structural complexity and stability for brittle stars than dead coral or rocks. If so, *O. echinata* may be excluding other species from living coral habitat. Due either to competitive dominance by *O. echinata* or its own habitat preference, *O. wendtii* was more abundant under rocks. However, since the presence or absence of species was random with respect to one another, it is likely that exclusion is only occurring on the scale of microhabi-
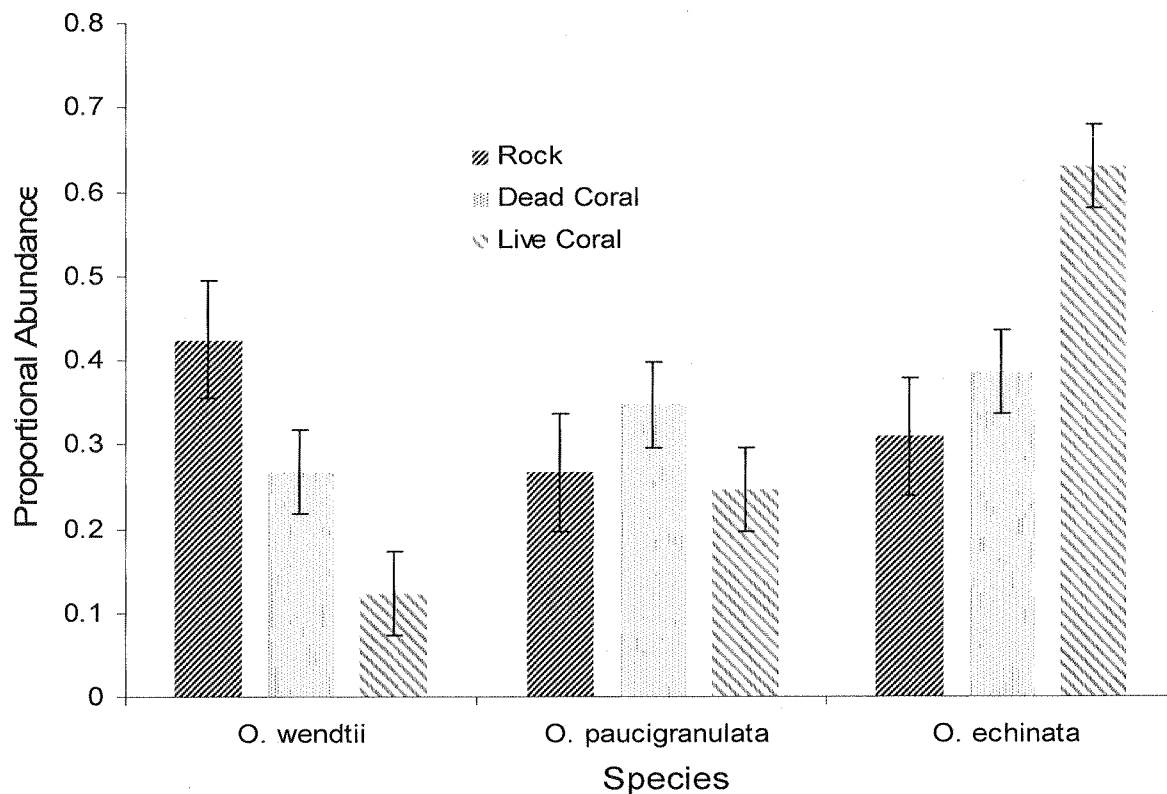

FIG. 1. Proportional abundance of brittle star species (*Ophiocoma wendtii, O. paucigranulata, O. echinata*) across different habitats (live coral, dead coral and rocks) in Little Cayman Island sampled from 5-8 March (N = 60 sites, each with two 900 cm^2 plots). Rocks were defined as lumps of dead coral on the sand. Bars indicate means ± 1 S.E.

tat, not on the larger scale.

Sides and Woodley (1985) found that microhabitat preference (crevice size) determined brittle star species distribution. Our results suggest that habitat differentiation is happening on a larger scale, more likely due to habitat preference than competitive dominance. A study focused on competition for space between species would help explain the detailed mechanisms driving these distributions.

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APPENDIX A:
BRITTLE STAR SPECIES IDENTIFICATION
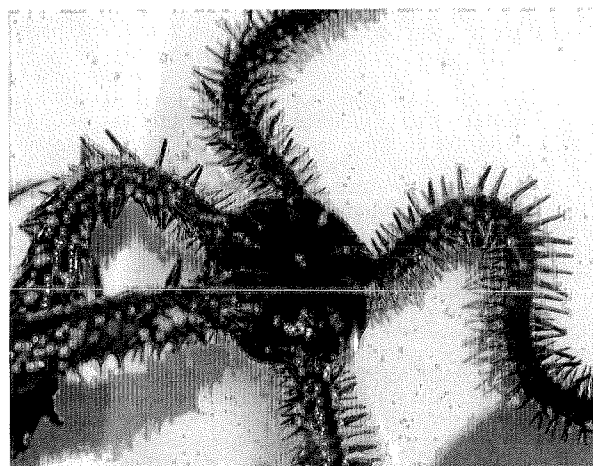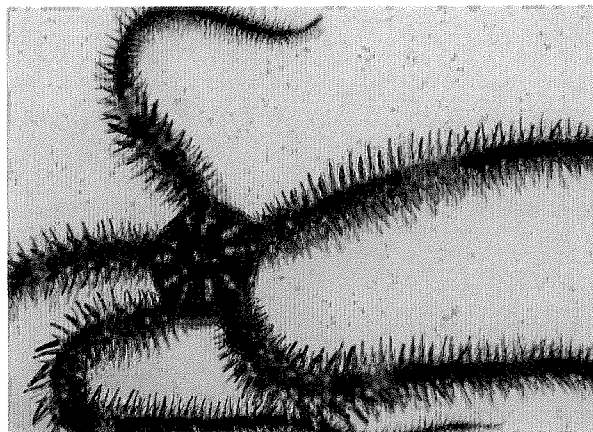
O. echinata
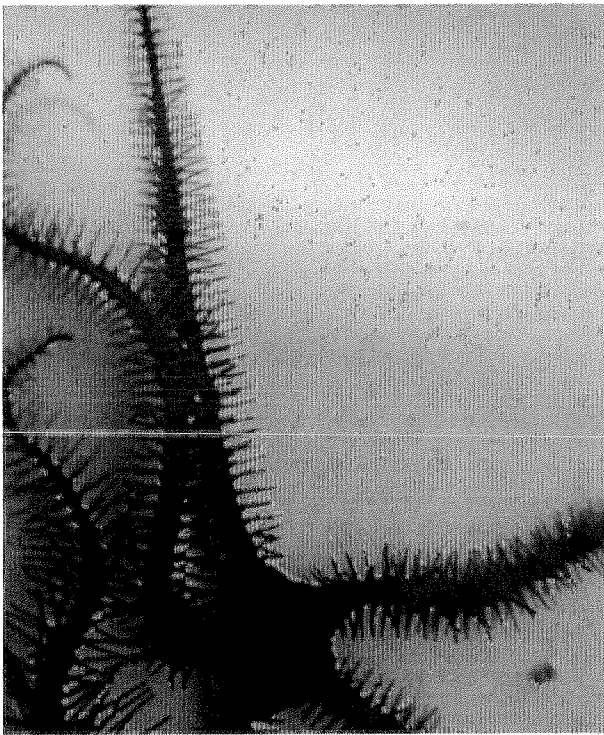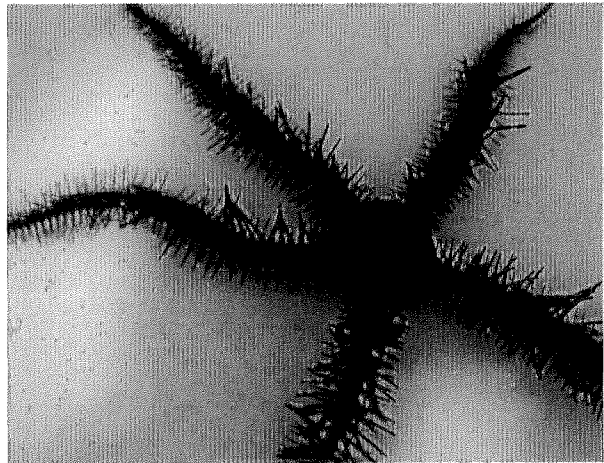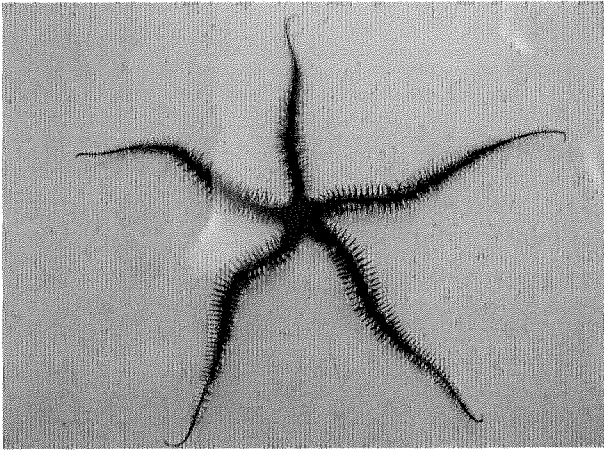
O. paucigranulata

O. wendtii

Sea urchins are boring
(in areas of highest percent cover of preferred algae)

Eben E.B. Bein, Cody P. Doolan, Karl Grunseich,
Emily L. Pizzichemi, Derek S. Stenquist

Faculty Editor: David R. Peart

Abstract: We sought to both establish and explain the distribution of the rock-boring sea urchin *Echinometra lucunter* at Preston Bay, Little Cayman Island. We tested whether local abundance of 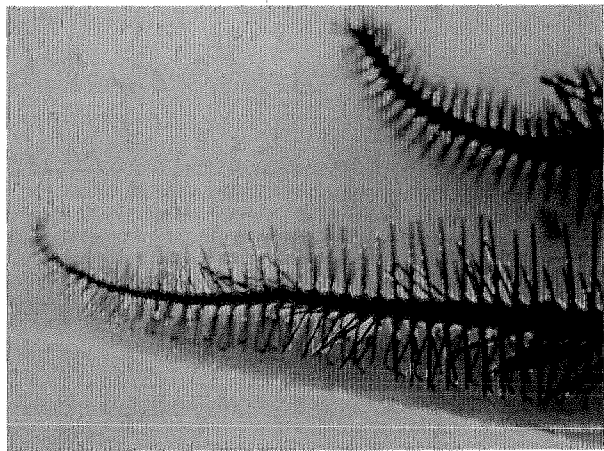urchins was related to food availability (attached algae), refuge hole preference, rock hardness, and/or water depth. Both urchin density and abundance of preferred macroalgae peaked at the same distance from shore, yet food abundance and urchin abundance were uncorrelated on the scale of 0.25 m² plots. We suggest that urchins are found where resources are most abundant and where productivity is probably highest but deplete algal food resources locally near their refuge holes.

Key words: algae, coral reef, herbivory

INTRODUCTION

Sea urchins tend to form single-species and mixed-species aggregations along Caribbean shores and reefs (Reese 1966). The reasons for these aggregations are not yet clear, but Reese (1966) suggests they result from individual responses to the physical environment. We noticed a distinct pattern in the distribution of the rock-boring urchin (*Echinometra lucunter*) in beachrock benches (Grunbaum 1978) at Preston Bay on the southern shore of Little Cayman Island. The benthic sample area consisted almost entirely of channels and depressions in the beachrock (refuge sites, which we will refer to simply as "holes") containing urchins at various densities. We established that the urchins reach peak abundance ca. 6 m from shore. We developed and tested several hypotheses for this pattern, including water depth,

rock substrate hardness, distribution of preferred algae, and hole size preference.

Food availability can positively affect urchin density, growth, survival, and reproduction (Vadas 1977; Shulman 1990). Thus, we predicted that urchins would be most dense in areas with highest cover of their preferred algal food sources.

METHODS

Study System
Echinometra lucunter inhabits beachrock benches in Preston Bay on the southern shore of Little Cayman Island. We observed that the urchins were concentrated along a ca. 30 m stretch of beach; urchins and their holes ranged from the shoreline to ca. 12 m into the bay. All measurements and experiments were conducted from 3-8 March 2009.

Field Methods
At 5m intervals along the shoreline,

we ran five 12 m transects perpendicular to shore, including the zone of urchin aggregation. The following data were collected along each transect, at 3 m intervals starting at 0 m: 1) number of urchins present within a 0.25 m² plot, 2) percent algae cover (by genus) within a 0.25 m² plot, 3) depth of water ca. 1 hr before low tide. We classified urchins by the size of their endoskeleton (test diameter): small (2-3.5 cm), medium (3.5-4 cm), and large (>4 cm). We classified each algal genus as "preferred" or "not preferred" based on the diet assessment of Lawrence (1975).

To determine individual movement over time, we established three additional plots of 1 m radius 5 m from shore on the afternoon of March 6. In each plot, we marked ten urchins by placing bands (telephone wire insulation) on one spine. Each band had a unique letter or number code (we used the characters already present on the insulation), and we recorded the position of each urchin at the time of marking (2 pm). At ca. 12 hours (2 am) and 48 hours (2 pm) after tagging, we searched the study area and recorded the position of each marked urchin we found.

We also tested the effect of depth on urchin distribution experimentally. In the lab, we simulated the range of depths over which we found urchins in the field, by filling a 120 cm x 50 cm x 33 cm tank with sand that was sloped to create a depth gradient from ca. 0.5 cm to 35 cm. In each trial, we placed 3 urchins of each size class at the shallow end, in middle of the tank, and at the deep end, for a total

of 9 urchins. After ca. 12 hr, we recorded the depth of each individual.

We designed a second lab experiment to determine whether urchins choose holes that fit them snugly. We placed urchins in one of 6 tanks, each containing three different sized holes made of PVC pipe. Small urchins were placed into tanks containing holes 2.1 cm, 3.1 cm, and 4.6 cm in diameter. Medium urchins were placed into tanks containing holes 3.3 cm, 6.1 cm, and 9.1 cm in diameter. Large urchins were placed into tanks containing holes 6.1 cm, 8.9 cm, and 11.5 cm in diameter. For each trial, one urchin was placed in the appropriate tank equidistant from all three holes. We ran 8 trials of each size class for a total of 24 trials. After 5 minutes, 10 minutes, and 4 hours, we recorded whether urchins were occupying one of the holes, and if so the hole size.

To determine whether the hardness of the rock correlated with urchin abundance, we twisted a screwdriver into the rock with uniform force for 3 minutes at 2 m, 5 m, 8 m, and 11 m on 4 of our 5 transects and measured how deeply the screwdriver penetrated the rock.

All statistical analyses were run using JMP 7.0 (SAS Institute, Inc. 2007).

RESULTS

Urchin density peaked at 40.5 m⁻², at 6.23 m from the shoreline. Their distribution was well fit by the quadratic equation $Y = -1.18x^2 + 14.71x - 5.26$ where Y is urchin density m⁻² and x is distance from shoreline in m (Fig. 1; quadratic; $r^2 = 0.48$,

$F_{2,22}$ = 10.12, $P < 0.001$, linear; r^2 = 0.01, $F_{1,23}$ = 0.18, P = 0.68). The percent cover of preferred algae reached its maximum of 14.7% at 6.23 m from the shoreline and the best fit quadratic was $Y = -0.4x^2 + 4.9867x - 0.84$ where Y is percent cover of preferred algae and X is distance from shoreline (Fig. 1; quadratic; r^2 = 0.26, $F_{2,22}$ = 3.87, P = 0.03, linear; r^2 = 0.00, $F_{1,23}$ = 0.10, P = 0.75). Clearly both distributions peaked at intermediate distances from shore. However, preferred algal cover was not related to urchin density on the scale of 0.25 m² plots (r^2 = 0.13, $F_{1,23}$ = 3.33, P = 0.0812.) The beachrock was more easily penetrated by a screwdriver further from shore on our transects (r^2 = 0.26, $F_{1,13}$ = 4.48, P = 0.05).

Of the 30 urchins tagged, 27 were re-covered in their original positions after 12 and 48 hours. One urchin remained in its original position after 12 hr but had moved 60 cm parallel to the beach after 48 hr, and two marked urchins could not be relocated, either because the tags were dislodged (which we consider most likely) or because the individuals moved too far away to be found. Urchins displayed no preference for depth in the lab; we found urchins distributed uniformly across the full range of depths (0.5 cm to 35 cm) in our tank. Urchins also showed no preference for hole size in the lab; 11 of 24 urchins were found in holes after 4 hr while the rest were found on the sand or walls of the tank. Of the 11 urchins that chose holes, the ratios of urchin test diameter to hole diameter ranged widely
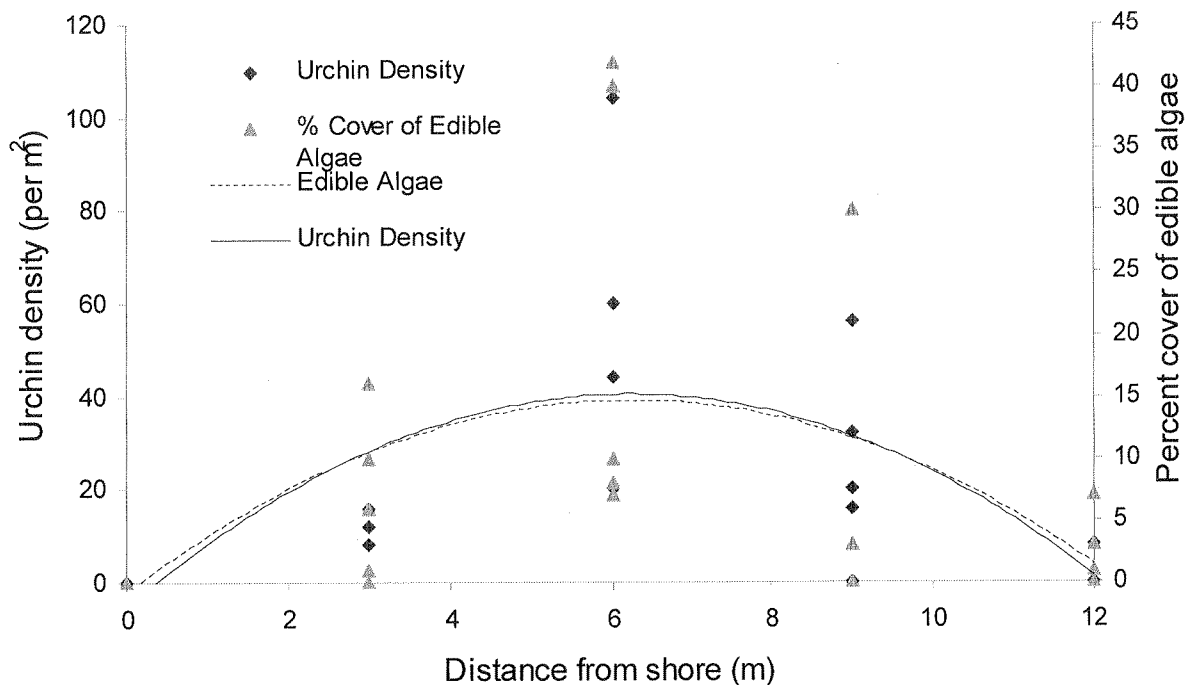

FIG. 1. Density of the rock boring sea urchin *Echinometra lucunter* and percent cover of preferred algae both peak at ca. 6 m from the low tide shoreline at Preston Bay, Little Cayman Island. (n = 25 plots, 0.25m²). Each point represents one plot. Algae classified based on echinoderm dietary information from Lawrence (1975). Lines are best fit by a quadratic model.

from 0.36 to 0.95.

DISCUSSION

Urchins did not demonstrate a preference for holes that fit them snugly in the lab. However, we are not confident that urchins do not prefer certain hole sizes because, during our experiment, the urchins did not explore all three available holes before settling in one. They appeared to avoid the sand and thus may have been less likely to explore all potential holes than they would in the field.

On a relatively large scale (over our 12-m transects), the distribution of sea urchins at Preston Bay closely matched the distribution of preferred algae, which suggests that individuals choose old or excavate new refuge holes in areas with the greatest access to food (Fig 1). Yet, on the very local scale of plots (0.25 m²) urchin density was unrelated to percent cover of preferred algal food. If the urchins are in fact eating the algae, we would expect algal cover to be locally reduced in areas of high urchin density. This may explain why urchin density and percent algal cover are unrelated locally, even while both peaked at 6 m from shore. The fact that urchins were surprisingly sedentary (only one of 27 tagged urchins had moved after 48 hours) further suggests that they are dependent on this local algae crop because they apparently forage in or very near their holes.

It is also possible that the standing crop of algae may not be the critical factor in urchin response to their food sources. The profitability of their food source depends more on the rate of supply than on the standing crop. Thus, the urchins may be aggregated in the zone of highest food productivity, and productivity would likely be correlated with the standing crop of algae, except where that standing crop has been locally depleted by urchin grazing. In some terrestrial systems, grazing has been shown to increase primary productivity (McNaughton 1976), so urchin grazing may also increase algal productivity. Future investigators might try excluding urchins from algal plots at different distances from the shore, to test if algae grow fastest in the areas where the percent cover is highest.

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Is zoop soup better where it's brighter?
Impact of night lights on amphipod predation of decapod larvae

Keng-Lou Hung, Charles W. Knape, Robin M. Meyers, and Brianna L. Wilkinson

Faculty Editor: David R. Peart

Abstract: We investigated the reaction of different zooplankton taxa to artificial light at night. Specifically, we predicted that primary predators that hunt visually would be attracted to light because they could forage more effectively. We also predicted that secondary predators, such as amphipods, would forage at a higher rate in the light where their prey may aggregate and are more visible. We tested prey attraction to light both in the lab and in the field, as well as amphipod attraction to light in the field, and amphipod foraging rate in the lab. We found that amphipods are attracted to artificial light at night, but found no evidence that this is due to increased foraging rate.

Key words: diel migration, foraging efficiency, Little Cayman

Introduction

Many species of zooplankton exhibit diel migration, hiding in the benthos by day and rising into the water column at night (Robertson and Howard 1978). The timing of this behavior has been attributed to avoidance of planktivorous fish, which are generally visual predators (Robertson and Howard 1978; Alldredge and King 1985). However, zooplankton taxa differ in their migratory patterns with respect to light levels at night: some respond to lunar phases while others (e.g. amphipods, Jacoby and Greenwood 1989) are unaffected. Variation in response to moonlight has been attributed to different predation pressures on different taxa (Jacoby and Greenwood 1989).

We observed that amphipods are attracted to artificial light sources at night, an unexpected behavior because it may increase their risk of predation by nighttime visual predators. We hypothesized that this phototaxis is beneficial for two reasons: 1) amphipods may see their prey better in the light than in the dark and thus hunt more efficiently, and 2) the prey species themselves may also aggregate around artificial lights at night due to increased foraging efficiency,

Methods

On 5-8 March 2009, we completed three experiments at Little Cayman Research Center: one in the field, near the back reef and two in the lab, using samples collected along the reef.

Our first experiment investigated the effect of light on local zooplankton abundance in the field. We took 20 samples from an area 5-15 m from the back reef. For 10 of these samples, we shined a flashlight into the water column and stood still for one minute, allowing sediment to settle and zooplankton to move in response to the light, then collected

zooplankton by spinning with a large net in the top half (ca. 1 m) of the water column for 20 seconds. For the other 10 samples, we waited in the dark for one minute, allowing sediment to settle before collecting by the same process. We treated our samples with a formalin solution immediately upon collecting them to minimize predation within our samples. We then counted all zooplankton present in each sample and classified them by taxon and size class. We used three size classes: small (<1 mm), medium (1-2 mm), and large (>2 mm).

Our second experiment investigated the effect of light on zooplankton movement within an artificial vertical structure. We placed ca. 70 decapod larvae in a 145 cm long vertical PVC tube of 4.5 cm diameter, filled with filtered seawater. We focused on decapods because they were abundant representatives of the small and medium size classes. For control trials, we covered the top of the tube, keeping the zooplankton in the dark for 40 minutes. For manipulated trials, we covered the tube for 20 minutes to allow habituation to the tube, and then shone a 20 watt, 300 mA energy-saving bulb above it for 20 more minutes. We then drained the zooplankton through a valve at the bottom of the tube in three equal increments, counted the zooplankton in each section, and classified them by taxon. We completed 13 trials: three with Brachyuran crab larvae in dark and three in light, and three with Caridean larvae in dark and four in light.

Our third experiment investigated the effect of light on amphipod predation in the lab. Amphipods are relatively large (>2 mm) predatory zooplankton that had a strong attraction to artificial light in our experiment on light attraction in the field. We placed 20 amphipods in a small plastic jar with 50 Brachyuran crab larvae, in both dark and light conditions. We counted the number of larvae remaining after one hour. We completed four dark and four light trials.

We used one-tailed t-tests to test for abundance differences in the field, because we predicted that zooplankton would be more abundant in the light than in the dark. We used two-tailed t-tests to test for effects of light on zooplankton movement within an artificial vertical structure. Finally, we used a one-tailed t-test to test the effect of light on amphipod predation in the lab, because we predicted that amphipods would have more predation success in the light than in the dark.

RESULTS

Large-bodied zooplankton were caught in higher abundances in the lighted samples than in the dark samples (one-tailed $t_{10} = 2.14$, $P = 0.029$). This trend was driven largely by amphipods, which showed a strong attraction toward light ($t_{10} = 1.89$, $P = 0.044$). Light treatment had no effect on decapod abundance ($t_{10} = 0.84$, $P = 0.21$) or on small and medium zooplankton (small, $t_{10} = -0.18$, $P = 0.57$; medium, $t_{10} = 1.10$, $P = 0.14$).

When we tested the effect of light on zooplankton movement within an artifi-
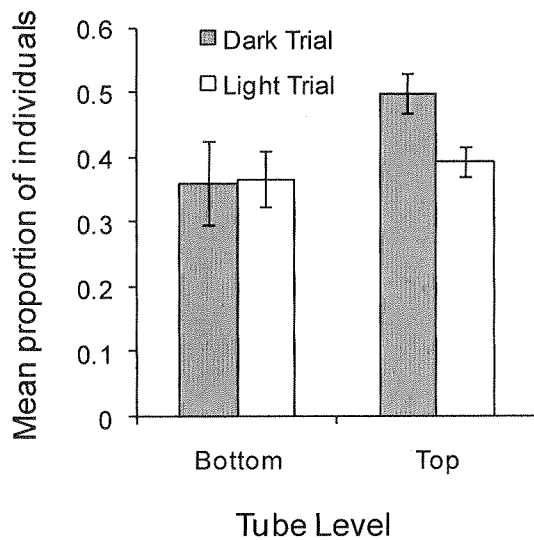
FIG. 1. Proportion of 70 decapod larvae (mean ± 1 S.E.) found in the top and bottom thirds (ca. 50 cm each) of a vertical PVC tube (after 40 minutes in the dark or 20 minutes in the dark followed by 20 minutes lit from above) at Little Cayman Research Center.

cial vertical structure, light had no effect on the proportion of decapods in the top or bottom third of the tube (top, two-tailed, $t_{11} = -1.48$, $P = 0.17$; bottom, $t_{11} = 0.08$, $P = 0.94$).

Amphipods did not consume significantly more decapods in the lighted trials of the predation experiment than in the dark trials (light mean = 28 decapods remaining, dark mean = 25 decapods remaining, one-tailed, $t_6 = -1.29$, $P = 0.012$).

DISCUSSION

Since decapod larvae showed no attraction to light and amphipod foraging rate did not increase in light, we concluded that prey availability and visibility does not explain amphipods' attraction to artificial light.

Decapod larvae were apparently unaffected by artificial light in both the field

and in an artificial vertical structure. This may be because their movements are largely dictated by circadian rhythms, or that the benefits of being in the light (e.g. higher foraging efficiency) at night are roughly balanced by the costs (e.g. higher risk of predation by nighttime visual planktivores).

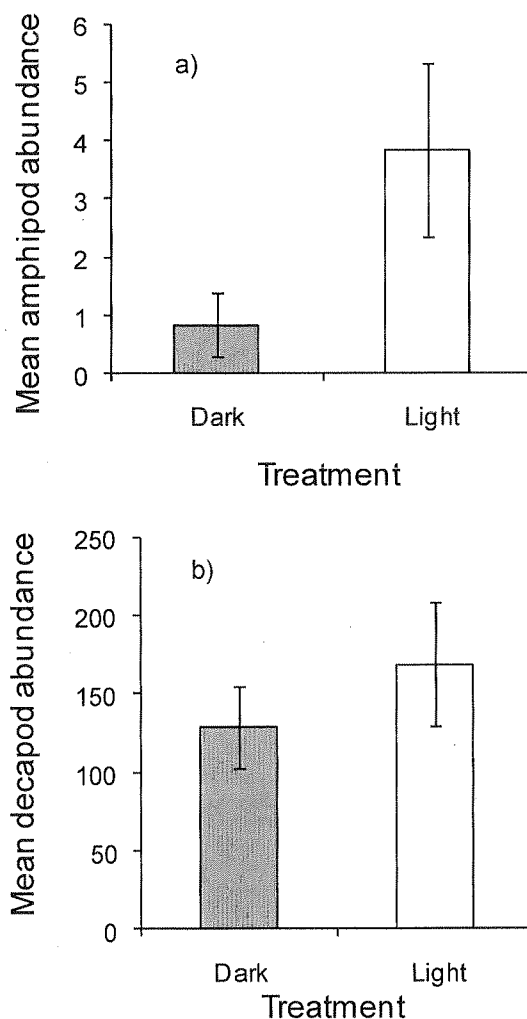Our field experiment on attraction to

FIG. 2. We found a greater number of amphipods in trials where an artificial light was shone for 20 seconds than in dark trials. However, we found no effect of light on decapod larvae abundance in field trials near the back reef adjacent to the Little Cayman Research Center (n = 12, 6 trials for both dark and light treatments).

light may have been confounded by the swimming speed of decapod larvae, which are much slower than amphipods. Decapod larvae may have had insufficient time to aggregate to or flee from our light source in the field. But even in the artificial vertical structure, where larvae had more time to migrate, decapods did not respond to artificial light. We noted that handling in the lab killed a number of decapod larvae, and we subjected them to unnaturally high densities, which may have stressed them. Thus, future experiments focusing on decapod migration and response to light may need to account for swimming speed and handling stress.

We suspect that the crowded conditions in the predation trials, with 20 amphipods and 50 decapod larvae in a small jar, could have led to an unnaturally high encounter rate between amphipods and decapod larvae, decreasing the importance of visibility in amphipod foraging. Because of limited sample size (n = 8), we lacked statistical power, which weakened our conclusion that prey visibility is not the mechanism for amphipod attraction to light. Future experiments may increase sample size and observe predation events at amphipod and prey densities closer to natural levels, to verify that increased light does not affect amphipod foraging success.

Many explanations other than effects on foraging have been put forth for migration of benthic zooplankton into the water column, including mate detection and attraction, and dispersal of juveniles (Robertson and Howard 1978). Phototaxis may thus specifically aid amphipods to gather at bright beacons at night to mate, or to ensure traveling in a consistent direction while dispersing.

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Diel Patterns of Zooplankton Density, Body-Length and Diversity in a Near-Shore Lagoon

Project Design: Thomas A. Morrison. Faculty Editor: David R. Peart

Brianna L. Wilkinson, Cody P. Doolan, and Keng-Lou Hung

Methods

On 2 March 2009 we collected zooplankton along four 50 m transects in Preston Bay on the South Side of Little Cayman during the afternoon (1600) and evening (2200) using a fine mesh drag net (30 cm diameter). We collected each sample by towing the net against the current within ca. 50 cm of the surface at a constant speed between two swimmers, at approximately 30 m from the shoreline and 30 m from the reef edge. After each transect, one of the swimmers came ashore and washed the sample into a plastic jar containing approximately 25 ml of 32% formalin solution.

In the lab, we strained and washed each 25 ml sample. We decanted the sand and washed organic contents into four Petri dishes. We divided each Petri dish into quarter sections and recorded abundance of all visible whole zooplankton by taxonomic group for one section. We did not record cnidarian larvae due to difficulty in identification. We measured and assigned each individual to one of three body length classes: <1mm, 1-2mm and >2mm.

We compared zooplankton densities and mean body length between day and night samples using two-tailed t-tests. We also calculated an overall diversity measure for day and night using the

TABLE 1. Mean densities and results of Student's t-test of near-reef zooplankton across all taxonomic groups in Preston Bay, Little Cayman Island, during day and night samples. We counted all individuals and placed them into 10 taxonomic groups. Each replicate represents a quarter section of a 50 m transect sampled using a fine-mesh tow net.

Taxonomic group	Mean density day (mean ± SE, n = 3)	Mean density night (mean ± SE, n = 3)	t-ratio	P
Amphipods	2.7 ± 2.1	13.3 ± 2.3	4.2	0.01
Annelids	3.0 ± 3.7	8.3 ± 2.5	1.5	0.13
Copepods	26.0 ± 4.6	35.3 ± 10.8	1.0	0.01
Cumaceans	1.0 ± 0.7	9.0 ± 1.2	6.9	0.39
Decapods	1.0 ± 0.7	49.7 ± 1.2	4.4	<0.01
Fish larvae	0.3 ± 0.4	2.7 ± 1.5	1.9	0.30
Isopods	2.3 ± 1.6	8.0 ± 1.2	3.4	0.01
Mollusks	6.3 ± 3.2	17.3 ± 10.8	1.2	0.02
Mysids	1.0 ± 1.2	108.7 ± 35.8	3.7	0.18
Ostracods	0.0 ± 0	2.3 ± 1.8	1.6	0.03
Total	44.0 ± 11.0	258.0 ± 27.8	8.8	0.21

TABLE 2. Summary of diversity and evenness for day and night samples. Initial number of individuals is a combined sum of all individuals found within either day or nighttime samples. To remove the effects of uneven sample sizes, we rarefied the nighttime sample down to 132 individuals and calculated H` and J.

	Initial no. individuals	Richness	H'	J
Day	132	10	1.43	0.62
Night	767	9.95	1.70	0.74

Shannon-Weiner Diversity index (H`). Finally, we compared evenness (J) between day and night samples after rarefying the data because of large differences in sample sizes between night and day.

RESULTS

We found the total density of zooplankton to be almost six times greater at night than during the day (Table 1). This trend was driven by greater densities of several groups (amphipods, cumaceans, decapods, isopods, and mysids) at night than during the day (Table 1). We found no day-night differences in the densities of copepods, ostracods, mollusks, fish larvae, or annelids (Table 1). The mean body length of zooplankton was significantly greater at night than during the day ($t_4 = 5.84$, P = 0.004). Diversity of taxonomic groups was higher at night than in the day (Table 2).

Diel patterns of fish diversity, abundance, and schooling frequency in turtle grass and back reef habitats on Little Cayman Island

Jeremy H. M. Chan, Karl Grunseich, and Emily L. Pizzichemi

Project Design: Ernesto Ruelas. Faculty Editor: David R. Peart

Introduction

We examined (1) fish species richness, abundance, and diversity in two distinct habitats (back reef and turtle grass) between day and night and (2) the influence of both habitat (back reef vs. turtle grass) and time (day vs. night) on the frequency of schooling.

Methods

On 4 March 2009, we set three plots in the lagoon shoreward of the back reef directly outside the Little Cayman Research Center (LCRC). Winds were moderately strong (ca. 16 knots) during the study. Plots were ca. 140 m long (parallel to shoreline, estimated by pacing along the shore) by ca. 70 m wide (visually estimated by observers in the water). Plots were contiguous, and the sample area extended both east and west of the LCRC. Each plot encompassed both turtle grass and back reef habitats. A team of 5 students surveyed fish for 40 minutes in each plot, covering both habitat types for 20 min. Plots were surveyed once each in "daytime" (ca. 1200-1240) and at "nighttime" (ca. 2100-2140).

Each team of five was divided into two groups. In each habitat, two students tallied the number of individuals of each species encountered, recording for each individual whether it was in a school.

The remaining three students in each team estimated the abundance of each fish species within each school encountered (where schools were defined as fish in groups of ≥2). Schools with two or more species of fish were designated as inter-specific regardless of the relative abundance of species. Intra-specific schools included just one species. We used only fish species found in ≥4 separate schools in our analysis comparing intra vs. inter-specific schooling tendency.

There were some limitations in our methods. First, the replicate plots may have been of somewhat different sizes. Second, it was impossible (for some groups) to sample the entire plot, depending on the number of fish encountered. Thus, the samples were more actually more based on time searching for fish (20 minutes) than on area sampled. Third, we could not sample all the individuals simultaneously, so fish moving into or out of the plot area over the 20-minute period would have affected our estimates. Fourth, we may have re-sampled individuals due to fish movement within a plot. Fifth, our estimates of the numbers of fish of each species in a school may not be 100% accurate, though
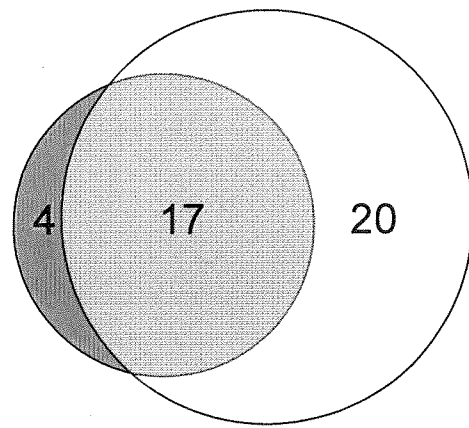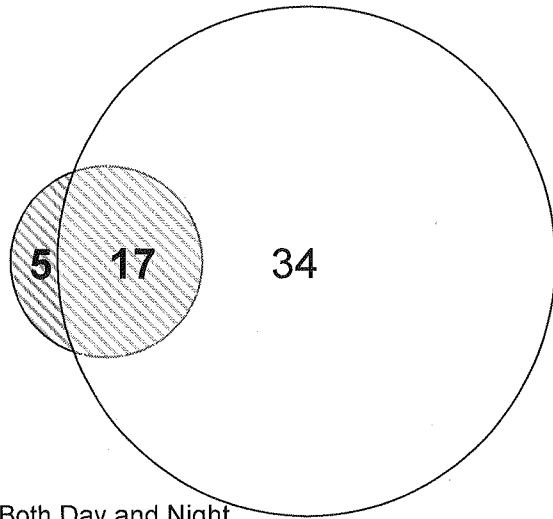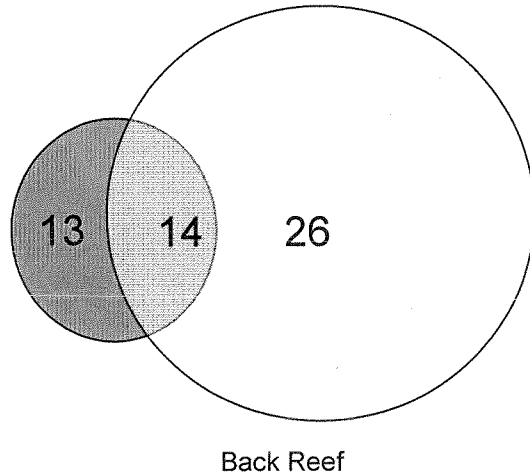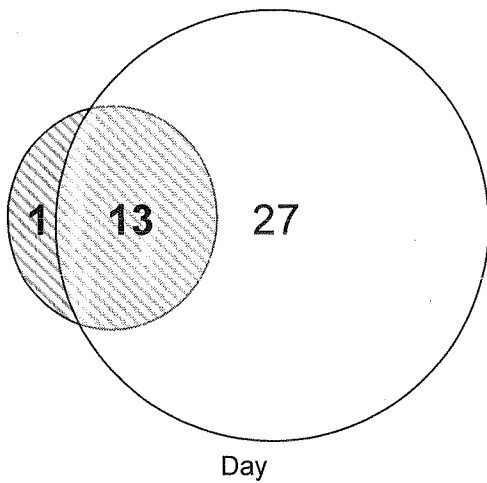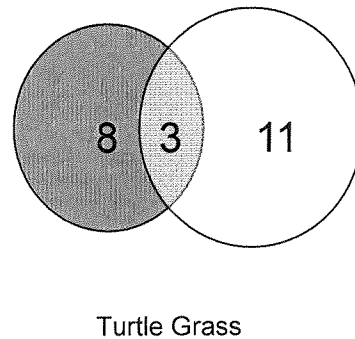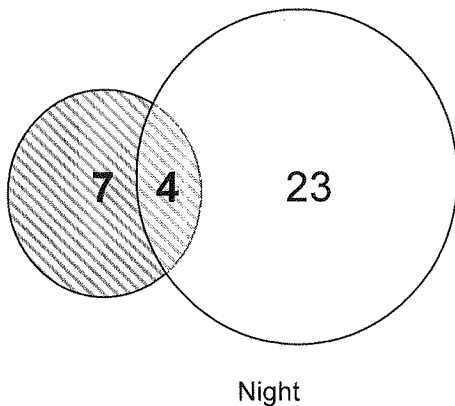
FIG. 1. Venn diagrams of number of fish species observed during day and night surveys in both turtle grass and back reef habitats near the Little Cayman Research Center, Little Cayman Island, on 4 March 2009. A team of five searched for 40 min in each of three ca. 140 m x 70 m plots, once during the morning (1200-1240) and once at night (2100-2140). Sizes of circles are proportional to the total number of species observed in each case.

in most cases observers had confidence in their counts (no very large schools were encountered). Finally, we could not identify all individuals to species, especially small juveniles. But in most cases observers had high confidence in their identification of adults.

We assumed observations in different plots were independent and random for the purposes of analysis (though neither is strictly true). We did not test all patterns statistically, so some results referring to "greater than," "less than," etc. are based on totals or mean values only. Such differences would not necessarily be confirmed by statistical analysis on rigorously replicated independent random samples. However, some differences were so large that underlying differences are likely.

RESULTS

We recorded a total of 818 individuals of 27 species in schooling observations. In our observations of individuals, we recorded a total of 619 individuals of 39 species. These total numbers included all plots across day and night, including both habitats.

Species richness was higher in daytime in both habitat types, and higher (both day and night) on the back reef than in turtle grass (Fig. 1). The mean species-level abundance (i.e. treating each fish species as a replicate) was not significantly different between habitats in the AM survey (Student $t_{23} = -0.645$, $P = 0.2626$), but in the PM survey was higher on the back reef (Student $t_{33} = -2.453$, $P = 0.0098$).

On the back reef, fish species diversity, estimated by the Shannon-Wiener (S-W) diversity index, was higher in the

TABLE 1. Schooling patterns in fish sampled in back reef and turtle grass habitats near the Little Cayman Research Center, Little Cayman Island, on 4 March 2009. A team of five searched for 40 min in each of three ca. 140 m x 70 m plots, once during the morning (1200-1240) and once at night (2100-2140). Only species found in more than more than 4 schools are tabulated.

Fish Species	Total number of schools	Number intraspecific schools	Number interspecific schools	Proportion intraspecific schools	Proportion interspecific schools
Banded Butterflyfish	4	2	2	0.50	0.50
Horse-eye Jack	4	1	3	0.25	0.75
Bermuda Chub	5	1	4	0.20	0.80
Mahogany Snapper	5	2	3	0.40	0.60
Doctorfish	7	1	6	0.14	0.86
Schoolmaster	8	3	5	0.38	0.63
Seargent Major	8	3	5	0.38	0.63
Stoplight Parrotfish	9	8	1	0.89	0.11
Bluestriped Grunt	11	2	9	0.18	0.82
French Grunt	14	6	8	0.43	0.57
Caesar Grunt	15	4	11	0.27	0.73
Bluehead	23	7	16	0.30	0.70
Ocean Surgeonfish	26	10	16	0.38	0.62
Blue Tang	27	8	19	0.30	0.70
Slippery Dick	27	20	7	0.74	0.26

AM than in the PM survey (Hutcheson t_{282}=4.34, $P < 0.001$). In contrast, in the turtle grass, S-W diversity did not differ between day and night (Hutcheson t_{18}= -0.69, $P > 0.5$). (The procedure to estimate differences in diversity indices is described by Hutcheson (1970) and cited in Zar (1999), pp. 156-158.) When data were pooled across day and night, S-W diversity was higher in the back reef than in turtle grass (Hutcheson t_{147}= -21.01, $P < 0.001$).

There was much variability among fish species in their schooling tendencies. For fish that were found in more than four schools, there was no significant difference between the number of inter- and intra-specific schools in which they were found ($t_{28} = 1.27$, $P = 0.21$; Table 1).

<div align="center">LITERATURE CITED</div>

Hutcheson, K. 1970. A test for comparing diversities based on the Shannon formula. Journal of Theoretical Biology 29:151-154

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APPENDIX A: NUMBERS OF FISH FOUND

Numbers of each species of fish found in two habitats near the Little Cayman Research Center, Little Cayman Island, on 4 March 2009. A team of five students searched for 20 min in each of three ca. 140 m x 70 m plots, once during the morning (1200-1240) and once at night (2100-2140).

Species	Turtle Grass		Back Reef	
	am	pm	am	pm
Balloonfish	0	0	0	1
Banded Butterflyfish	1	0	9	9
Bar Jack	11	0	1	0
Beaugregory	10	0	11	0
Blue Tang	0	0	108	10
Bluehead	19	0	66	1
Bluestriped Grunt	25	0	12	5
Caesar Grunt	2	0	80	1
Cocoa Damselfish	0	0	1	0
Doctorfish	3	0	10	4
Dusky Damselfish	1	0	7	0
Foureye Butterflyfish	0	0	2	1
French Grunt	25	0	64	25
Great Barracuda	0	0	8	0
Lane Snapper	1	0	1	7
Longjaw Squirrelfish	0	1	5	5
Longspine Squirrelfish	0	4	7	4
Mahogany Snapper	25	1	29	2
Nassau Grouper	0	0	2	0
Ocean Surgeonfish	28	0	48	6
Porcupinefish	0	0	0	1
Princess Parrotfish	0	0	23	0
Puddingwife	0	0	1	0
Reef Squirrelfish	0	0	0	13
Rosey Blenny	3	0	0	0
Schoolmaster	0	0	77	3
Sergeant Major	0	0	17	3
Slippery Dick	60	0	93	0
Smooth Trunkfish	1	2	1	0
Spanish Hogfish	0	0	1	0
Spotted Goatfish	0	0	10	0
Spotted Trunkfish	1	1	2	0
Stoplight Parrotfish	0	0	53	6
Striped Parrotfish	0	0	4	0
Threespot Damselfish	0	0	2	0
Twospot Cardinalfish	0	0	0	2
Yellowfin Mojarra	4	0	1	0
Yellowtail Damselfish	0	1	11	1
Yellowtail Parrotfish	0	0	9	0
Yellowtail Snapper	0	0	4	0

Coral Identification Guide for the Back reef at the Little Cayman Research Center

Sarah E. Wengert

This is a non-comprehensive list of the corals present on the back reef behind the Little Cayman Research Center (the "Center") on Little Cayman Island. In combination with a photo database in an appendix on the online version of this paper, this guide can be used to identify many of the corals present in the shallow waters near the Center. This guide is meant to supplement, not replace, Humann and DeLoach's Caribbean reef coral identification guide (2002). It should make local identifications easier by only including locally occurring species and by providing photographs of local specimens and notes on their local distribution and abundance. This preliminary version of the guide can be improved and expanded in the future.

Methods

All observations and photographs were taken between 1-9 March 2009 on the back reef behind the Center. I covered ca. 200-300m along the back reef, and on some patch reefs, starting at the Center and heading east. Descriptions, distribution, and abundance are entirely my personal observations and identifications, and accuracy is not guaranteed. My descriptions do not include detailed morphology. Humann and DeLoach

(2002) was my reference for identification and descriptions. Jonathan Clamp, the manager of the Center, also confirmed many of my species identifications from photographs I provided. For abundance I used descriptors as in Humann and DeLoach (2002): abundant (at least several sightings can be expected on nearly every dive/snorkel), common (sightings are frequent, but not necessarily on every dive/snorkel), occasional (sightings are not unusual but not on a regular basis), uncommon (sightings are unusual), and rare (sightings exceptional). Distribution refers to where the species is found with respect to the main back reef structure. For distribution across the Caribbean, see Humann and DeLoach (2002). I did not attempt to systematically sample the reef, so my estimations of abundance are based on many haphazard observations. Many of the species that are occasional or uncommon are more prevalent 100 m or more to the east of the Center.

Photo Archival

I also assembled folder of photographs documenting each species, to be made available as an appendix when this book is published online and also to be put on the computers at the Center and on the Dartmouth FSP computer in a

folder labeled "Coral Guide Identification Photographs 2009." Within this database the photographs are organized in the same way the guide is organized — first by class (Hydrocorals, Octocorals, Stony Corals), then by genus, and finally by species. Each species has its own folder of photos. Where possible there are photos of the whole colony and close-ups of parts of colonies, the latter with and without polyps extended. Photos of any variations found are also included. Photos of any coral diseases that were found are included in their own folder.

HYDROCORALS

Millepora complanata – Blade Fire Coral
> Shape and pattern: vertical, thin blades from an encrusting base. Appears smooth, no obvious pores.
> Color: yellow-brown to brown; top edge whiter
> Size: blades ca. 1-5 inches wide, up to 1.5 ft tall
> Distribution and abundance: common on the reef crest, occasional on patch reefs
> Notes: Can also encrust other corals, particularly sea fans, although this appears rare in this area.

OCTOCORALS

Plexaura homomalla – Black Sea Rod
> Shape and pattern: branching coral, stalks are usually relatively smooth. Tends to branch laterally.
> Color: light colored polyps with dark stalks (brown to black)
> Size: individual branches <0.5 inch

wide. Colonies range from single, small stalks of 1-4 inches high up to large branching colonies of ca. 1-2 ft high and ca. 1 ft wide.
> Distribution and abundance: occasional on the back reef and patch reefs

Eunicea spp. – Knobby Sea Rods
Species within *Eunicea* are hard to differentiate without microscopic analysis (Humann and DeLoach 2002).
> Shape and pattern: branching coral, stalks have many protrusions ("prominently extended calyces" (Humann and DeLoach 2002)) along their length. Branching not obviously lateral or dichotomous.
> Color: light to dark brown stalk with paler protrusions
> Size: all colonies seen here were small 4-8 inches high and only 3-4 inches wide.
> Distribution and abundance: occasional on the back reef and patch reefs

Briareum asbestinum – Corky Sea Fingers
> Shape and pattern: encrusting base (not always apparent and sometimes only see encrusting section) with cylindrical, unbranched rods. Polyps are very long and wispy, often fully or partially extended during the day.
> Color: stalks and surface purple, polyps dark brown to black
> Size: rods are 1-2 inches wide and 1-

15 inches tall. Colonies vary widely in overall size

Distribution and abundance: abundant on the back reef and patch reefs

Gorgonia spp. – Sea Fans

I was not able to identify the sea fans beyond family due to a lack of information available. It appears that both *G. ventalina* and *G. flabellum* are common in this area.

Shape and pattern: single plane fans that grow from one base. Differentiation of *G. ventalina* and *G. flabellum* based on the flattening of individual pieces of the fan, which is difficult to see in the water (see Humann and DeLoach 2002).

Color: green/yellow or purple

Size: 0.5-2 ft tall and 0.5-2 ft wide

Distribution and abundance: common near the back reef, often not attached to the reef itself but near the reef base

STONY CORALS

Agaricia agaricites – Lettuce Coral

Shape and pattern: encrusting with vertical plates. Long, steep ridges with long valleys.

Color: yellow-brown

Size: colonies range in size, but individual plates are ca. 1-12 inches diameter

Distribution and abundance: abundant on the back reef and patch reefs

Notes: Similar to the encrusting *A.*

humilis, differentiated by the length of the valleys and the presence of vertical plates.

Agaricia humilis – Low relief lettuce coral

Shape and pattern: encrusting and colonies usually small. Has steep ridges that section it off into small, deep pockets (<0.5 inches across). Never has long valleys.

Color: yellow-brown

Size: colonies 1-5 inches

Distribution and abundance: occasional on the back reef and patch reefs

Notes: Similar in appearance to *A. agaricites* but does not have any plates and never has long valleys.

Diploria strigosa – Symmetrical brain coral

Shape and pattern: most obvious brain coral on the back reef. Massive, most commonly forms domes in this area. Has a faint groove along the top of the ridges.

Color: dark yellow-brown

Size: ranges from small colonies of <1 ft to large colonies of >5 ft wide

Distribution and abundance: abundant on the back reef and patch reefs, makes up a lot of the structure of the reef

Notes: Can also have a plated form, but that form is not apparent on this back reef.

Diploria clivosa – Knobby Brain Coral

Shape and pattern: "Brain coral," forming uneven, encrusting

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structures with several protrusions per colony.

Color: brown to yellow-brown

Size: colonies ca. 1-2 ft

Distribution and abundance: uncommon on sand near the back reef and patch reefs, apparently not a part of the greater reef structure

Notes: Similar in appearance to *D. strigosa* but does not form massive hemispheres and does not have a groove on the ridges.

Eusmilia fastigiata – Smooth Flower Coral

Shape and pattern: polyps all on individual stalks located close to one another with no coral surface intervening.

Color: yellow-brown variation seen here but can also have blue-green tinting

Size: individual polyps <1 inch, the one colony seen here was 4 inches wide but can be up to 2 ft

Distribution and abundance: rare on the back reef and patch reefs

Notes: Possibly related to some of the Unidentified Stony Corals.

Favia fragum – Golfball Coral

Shape and pattern: small round colonies with oval, unevenly spaced and shaped corralites. Flat surface with the rims of corralites slightly protruding.

Color: cream colored with darker yellow polyps

Size: colonies 1-3 inches

Distribution and abundance: common on the back reef and patch reefs, generally on top of dead coral, also sometimes on the ground

Notes: Similar in appearance to *Dichocoenia stokesi* but with less protruding corralites and smaller size overall.

Isophyllastrea rigida – Rough Star Coral

Shape and pattern: small hemispherical dome with wide, fleshy, bumpy ridges that have an obvious groove. Ridges form valleys that are short and sectioned off. Each valley has one or two polyps which are extended at night.

Color: ridges brown to green, valleys pale, polyps light with blue tints

Size: colonies 2-6 inches

Distribution and abundance: uncommon on the back reef and patch reefs, generally on the lower half of the sloping/vertical sides of the main reef structure

Notes: Similar to *Isophyllia sinuosa*, differentiated by the bumpy ridges and the sectioned valleys that are smooth and interconnected in *I. sinuosa*.

Isophyllia sinuosa – Sinuous cactus coral

Shape and pattern: small hemispherical dome with wide, fleshy ridges without noticeable bumps that form deep, narrow valleys that are long and interconnecting.

Color: gray or brown-yellow seen

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here, can also be green, yellow, or brown or have some iridescent orange or blue. Ridges and valleys often contrasting colors

Size: colonies 1-6 inches

Distribution and abundance: uncommon on the back reef and patch reefs, generally on the lower half of the side of reef structure

Notes: Similar to *Isophyllastrea rigida*, differentiated by the smooth ridges that create interconnected valleys.

Montastraea annularis – Boulder star coral

Shape and pattern: encrusting or massive in irregular shapes. When polyps are closed there is an obvious star shape to each corallite and they protrude slightly from the surface.

Color: gray and red variations most common, can also be yellow to brown

Size: colonies variable in size, sometimes small 4-8 inches and often quite large, encrusting 3-7 ft wide

Distribution and abundance: abundant on the back reef and patch reefs, usually found on the sides of reef structures

Notes: Similar in appearance to *M. cavernosa*, but differentiated since the polyps and surface of *M. annularis* are usually similar in coloration while they are contrasting colors in *M. cavernosa*. The closed polyps of *M. cavernosa* are also full hemispheres while those of *M. annularis* protrude less

from the surface.

Also, star shape of corallites differentiated from that of *Siderastrea* spp. because the corallites protrude from the surface, while they are pushed into the surface in *Siderastrea* spp.

Montastrea cavernosa – Great Star Coral

Shape and pattern: encrusting or massive in irregular shapes. When polyps are closed there is an obvious star shape to each corallite and they form small hemisphere protrusions on the surface.

Color: surface gray to brown, polyps green to yellow

Size: colonies variable in size, sometimes small 4-8 inches and often quite large, 3-7 ft wide

Distribution and abundance: common on the back reef and patch reefs, usually found on the sides of reef structures

Notes: Similar in appearance to M. annularis, differentiated by the contrasting colors of polyps and surface and also by the hemispherical shape of corallites.

Also, star shape of corallites differentiated from that of Siderastrea spp. because the corallites protrude from the surface while they are pushed into the surface in Siderastrea spp.

Porites astreoides – Mustard Hill Coral

Shape and pattern: can be encrusting but in this area usually form rounded heads with many lumps.

Corallites are close together and appear porous. No star shape to the corallites. Polyps are often out during the day and appear fuzzy.

Color: two varieties: yellow or gray

Size: colonies are variable in size, can be small 1-5 inches or up to 2 ft wide

Distribution and abundance: common on the back reef and patch reefs, usually on top of dead coral, can also be along the ground

Porites porites – Finger Coral

Shape and pattern: short, stout, smooth branches with blunt tips. Many branches clustered together, but not all obviously connected. Corallites are close together and appear porous. No star shape to the corallites. Polyps are often out during the day and appear fuzzy.

Color: usually purple but I also found a yellow-gray form

Size: branches are ca. 1-2 inches wide and 1-7 inches tall. Whole colonies range from one branch to > 2 ft of branches

Distribution and abundance: common on the back reef and patch reefs, usually on top of dead coral, can also be on the sand

Siderastrea radians – Lesser Starlet Coral

Shape and pattern: usually small, flat, encrusting colonies with star pattern of corallites when polyps are not extended. Colonies can also sometimes be small domes.

Corallites are indented into the surface.

Color: whitish to gray, often with some pink or red

Size: colonies 1-3 inches

Distribution and abundance: abundant in the area up to the back reef and around the patch reefs, usually found on the sand or in turtle grass.

Notes: Differentiated from *Montastrea* spp. by the indentation of the star shaped corallites.

Siderastrea siderea – Massive Starlet Coral

Shape and pattern: large, massive coral that forms domes or hemispheres, with a star pattern of corallites when polyps are not extended. Corallites are indented into the surface.

Color: each colony has a uniform color, usually red-brown in this location, but can be light gray to brown

Size: colonies are large, 1-6 ft wide

Distribution and abundance: abundant on the back reef and patch reefs, usually making up part of the reef structure

Notes: Differentiated from *Montastrea* spp. by the indentation of the star shaped corallites.

UNIDENTIFIED STONY CORALS

There are four stony corals that I was unable to identify at the time of this project because I could not match my photos

to any photos or descriptions in Humann and DeLoach (2002). Detailed photographs are included for all species in the Appendix for future identification. I have given each a provisional name so that if necessary they can be referred to in future studies as morphospecies without species identification.

Type 1 – "Large red golfball" coral
> Shape and pattern: round domes with large corallites that protrude slightly from the surface. Corallites irregularly spaced and shaped.
> Color: red-brown with slightly paler polyps
> Size: colonies 4-8 inches
> Distribution and abundance: rare directly behind the Center, to uncommon on the eastern portion of the area observed. Occur low to the sand on or near the back reef or patch reefs.
> Notes: Possibly *Dichocoenia stokesii* but the coloration appears different. Similar to *Favia fragum* but a different color with more pronounced projection of the corallites.

Type 2 – "Mouthy" coral
> Shape and pattern: long, lumpy coral that sits on top of dead coral. When corallites are closed, the surface is almost flat with pinched in corallites. Surface appears pliable. During the day, polyps are in various stages of openness with some corallites closed but

protruding from the surface while others are completely flat and pulled in and still others are extended.
> Color: whitish with pale yellow polyps
> Size: colonies 5-12 inches long, individual polyps large, ca. 0.5 inch
> Distribution and abundance: rare on the back reef
> Notes: similar in appearance to Unidentified "White stalky flowers" coral, possibly the same species

Type 3 – "Large encrusting polyps" coral
> Shape and pattern – encrusting or massive coral with large polyps that extend from the surface when open. Some polyps open fully during the day while others are closed. Closed corallites protrude from the surface but do not have a star pattern and do not fully close.
> Color – brown with lighter colored polyps
> Size – colonies 2-4 ft wide
> Distribution and abundance – rare on the back reef and patch reefs, the two examples seen were freestanding next to the larger reef structure

Type 4 – "White stalky flowers" coral
> Shape and pattern: small coral sphere with large polyps extending far from the surface
> Color: whitish to pale yellow

Size: colonies small ca. 3-4 inches

Distribution and abundance: rare on the back reef, found on top of dead coral

Notes: Similar in appearance to Unidentified "Mouthy" coral. Only one example found which had all polyps extended, so it was difficult to compare.

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Little Cayman Research Center: Marine Plants Identification Guide

Jonathan M. Wachter and Sarah E. Wengert

Introduction

This paper presents a non-comprehensive list of the algae genera common on and around the back reef behind the Little Cayman Research Center, Little Cayman Island. We hope to help standardize algae identifications across years for any long-term studies and to offer a stepping stone into more technical literature. This guide is designed to be used in combination with the photo database included in the online appendix of this paper and to supplement the use of more complete algae identification literature. It is by no means complete, and should be expanded in the future to include more taxa and more complete genus descriptions.

The identifications, descriptions, and information in this guide are based on the opinions and observations of the author Jonathan Wachter. Identifications were made using *Caribbean Reef Plants* by Littler and Littler, *Marine Algae of the Eastern Tropical and Subtropical Coasts of the Americas* by Taylor, and *Marine Plants of the Caribbean* by Littler et al. Informal descriptions of the major differentiating characteristics of each genus are given, with a strong bias toward species and trends in this locality. Where there are genera that could be easily confused, we

offer the simplest way to differentiate them, when available. Abundance is given in three categories: very common (seen frequently throughout every dive/ snorkel), common (seen on most dives/ snorkels), and occasional (seen every few dives/snorkels). Descriptions are of the large defining characteristics of the genus; for more positive identification and identification to species we recommend *Caribbean Reef Plants* by Littler and Littler, which is the most recent and comprehensive guide.

All photographs for identification were taken by Sarah Wengert. We assembled a folder of photographs documenting each species, to be made available as an appendix when this book is published online and also to be put on the computers at the Center and on the Dartmouth FSP computer in a folder labeled "Algal Guide Identification Photographs 2009." Some taxa listed in this guide were not documented with photos due to time constraints. Within this database the photographs are first organized by phylum (green, red, brown, and flowering plant) and then by genera. Most genera have several pictures to aid in identifications.

Above all, this guide aims to make the study of algae more easily approachable. Marine reef plants are a very di-

verse and complex group, and relatively little is known about them and their interactions (Littler and Littler 2000). Studying them both casually and scientifically can be great thrill and an important contribution to our understanding of coral reefs.

FLOWERING PLANTS (MAGNOLIOPHYTA)

Thalassia testudinum — Turtle Grass
> not photographed
>> Hydrocheritaceae
> Grass-like, with flat leaves that reach up to 1 m high. Mostly <30 cm in the shallow water in front of the Center. The predominant plant growing abundantly along the shore. Its density appears to decrease as you approach the reef. Very common.

Syringodium filiforme — Manatee Grass
> not photographed
>> Cymodoceaceae
> Grass-like, with stiff cylindrical leaves that can reach up to 45 cm high. Mostly < 30 cm in the shallow water in front of the Center. Often grows among *T. testudium*. Very common.

GREEN ALGAE (CLOROPHYTA)

Acetabularia spp. — Mermaid's Wine Glass
>> Polyphsaceae
> Solitary or in clusters, these resemble cups with parasol-like ridges on thin stalks. Usually pale green or whitish. Grow on hard surfaces, such as rocks and shells, mostly along the sandy bottom. Never

higher than 10 cm. Very common.

Avrainvillea spp.
>> Udoteaceae
> Solitary or in clusters. Erect fan-like thallus on a pronounced stalk. Concentric bands on the fan blade. Dark green to black-green. Usually growing on sand or sand-covered rocks. Stiff but not calcified. Often has a dense bulb-like mass of rhizoid imbedded in the substrate. Common.
> Closely resembles species of *Udotea* in shape, but these species are highly calcified, lighter in color (light green to yellow-green) and has visible filaments radiating from the center of the fan blade. *Udotea* is uncommon around the Center.

Caulerpa spp.
>> Caulerpaceae
> Distinguished by a running root-like rhizoid with erect branching shoots coming up from it, growing up to 20 cm in height but usually between 5-10 cm. The erect shoots are made up of a central stalk with many opposite-branching branchlets.
> *C. racemosa* (not pictured) is a slight variation, with small bead-like thalli instead of erect branches. The smooth green root-like rhizoid is usually very obvious in this species, which grows on rock surfaces more than in

sand substrate. Very common.

Dictyosphaeria spp.
Siphonocladaceae

Clusters irregular green bubbles, sacs or lobes that can reach up to 10 cm in diameter. Surface is most often bumpy or angular in appearance. Sacs are sometimes broken when old, but continue to grow. Lightly attached to rocks or dead coral. Common.

Halimeda spp.
Udoteaceae

Thalli are branching and divided into distinct segments with flexible joints between segments. Segments are often flat and disc-like, rounded for a few species. Dark to light green. Diverse habitat, from sandy bottoms to dead coral. Common.

Penicillus spp.
Udoteaceae

Resembles a brush-like ball on a stiff calcified stalk. The brush cap is most often very round, sometimes flaring out from the stalk, occasionally with a flat top, made up of small calcified filaments. Stalk never branching, usually <10 cm tall. Solitary or in small clusters of independent stalks, mostly on sandy substrate. Stalk attached to a dense round rhizoid mass at its base. Common.

BROWN ALGAE (PHAEOPHYTA)

Dictyota spp.
Dictyotaceae

Bushy growth, thallus most often flat, branching dichotomously. The margins are sometimes toothed and the face of the thallus sometimes has superficial hairs. Brown in color and sometimes iridescent. Loosely attached to firm substrate such as dead coral or rock. Very common.
Structure closely resembles that of Dictyopteris species (not pictured), but the two are very easily distinguishable by the lack of a central vein in Dictyota.

Padina spp.
Dictyotaceae

Clusters of curled blade-like or foliose thalli, usually with visible concentric bands and a distinct lip on the outermost edge. Blades can be split into thinner spatula-like segments. The margins of the segments are always in-rolled toward the center. Lightly to heavily calcified, brown to white. Grows on hard surfaces. Common.
Can resemble Stypopodium, but is easy to distinguish because of the in-rolled margins in Padina that is never present in Stypopodium.

Stypopodium spp.
Dictyotaceae

Clusters of leaf- or blade-like thalli. Thallus starts as a plane at

the base and splits into irregular narrower segments, becoming bushy at the top. Yellow-green to iridescent, often with concentric bands; not calcified. Common. Can resemble *Padina*, but is easy to distinguish because of the in-rolled margins in *Padina* that is never present in *Stypopodium*.

Turbinaria spp.
>   Sargassaceae
Usually composed of many air-filled 1-2 cm pyramids clustered around a central stalk, that is standing erect up to 40 cm high. Pyramids are oriented with their tips attached to the stalk and their flat bases facing outward. These outer faces is often speckled and sometimes has toothed edges. Brown to yellow-brown. Always attached to hard surfaces. Occasional.

RED ALGAE (RHODOPHYTA)

Acanthophora spp.
>   Rhodomelaceae
Cylindrical stalks up to 25 cm in length, alternately and irregularly branching, with short spine-like branchlets covering main branches. Color variable, but often pale brown with reddish hues. Usually growing on dead coral. Occasional.

Ceramium spp.
>   not photographed
>   Ceramiaceae
Tufts of very fine dichotomously branching filaments, rarely more than 15 cm high. Filaments are usually obviously banded and <0.5 cm in diameter. Tips of filaments usually tapering, sometimes curved like a hook. Varied habitat, usually on rock or dead coral. Yellow-brown to red. Very common.

Galaxaura spp.
>   Galaxauraceae
Bushy growth of stiff and compact dichotomously branching tubes, up to 12 cm high. Heavily to lightly calcified. Tubes are cyclindrical, up to 1.5 cm in diameter, blunt and non-tapered at the tips. Sometimes lightly banded or with very fine superficial hairs around the tubes. Occasionally, thallus is flattened instead of tube-like. Grows on hard surfaces throughout the reef. Common.

Liagora spp.
>   Liagoraceae
Bushy growth of soft, fleshy, radially-branching thallus. Base sometimes calcified, while the top is usually soft, almost gooey. Tips tapering to a blunt end. Creamy white, often with red fringes. Growing to 15 cm high on hard substrate.

Can sometimes resemble *Ceramium*, but *Liagora* is never banded and is usually much different to the touch. Occasional.

OTHER

Chrysocystis lewisii

Chrysophyta (diatom)
Very common and abundant throughout the back reef, on the sandy bottom as well as on dead coral and rocks. Individual cells form chains, giving the appearance extremely fine filaments that form soft clumps up to 10 cm long. Usually with the same yellow color. Very common.

Red Crustose

A group of red algae forming hard red to orange crust on rock and dead coral, responsible for cementing together coral blocks and contributing to reef structure. There are likely several species of Red Crustose algae that are common around the reef, but they are very difficult to differentiate in the field. Very common.

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Primate behavior: A study of our studies

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Abstract: By collating studies we chose to conduct during our time in Costa Rica and Little Cayman, I succeeded in eliminating some of that annoying free time. Some results were predictable, some surprising, a few somewhat embarrassing, but all amusing. Enjoy!

Key words: fun!

Introduction

Homo sapiens, a ubiquitous primate, exhibits complex and puzzling behaviors. One of the least explicable is "science." There are several aspects of this behavior, including lectures, where a senior member of the troupe leads junior members in discussions of abstruse topics, but most bewildering is one known as "conducting studies," in which small social groups spend long periods examining some feature of the world in excruciating detail and with painful precision. They appear to become bored during the process and often exhibit signs of despair if they fail to find anything of interest, yet some individuals and groups repeatedly engage in this behavior. To explore this apparent anomaly, I examine what may drive these primates to carry out "studies" by documenting the types of studies carried out by fifteen different individuals who engaged in "science" for a period of nine weeks in Costa Rica and Little Cayman. Based on the apparent absurdity of the behavior, I predicted the total absence of any pattern whatsoever.

Lest the reader suspect that my study is yet another example of this ridiculous activity, I emphasize that my study does not conform to the scientific method and is completely devoid of rigor.

Methods

This non-study took place in Costa Rica and Little Cayman Island between 6 January and 12 March 2009. I observed fifteen primates, each of whom I gave a 2-4 letter code for identification (Table 1). Their "studies" lasted between two and four days each. I classified "studies" based on focal subject, the excruciating aspect of it being studied, and other unique features. I compared number of studies falling in each category among the fifteen primates to see whether they had preferences. I excluded from all analyses six studies (three on ant-acacias, one comparing birds between sites, one on day-night zooplankton abundance, and one on day-night fish abundance) that were controlled by the alpha male (known to these primates as a "professor"), to focus on the choices primates make of their own volition. I also

TABLE 1. A key to primate identification codes and how they correspond with names used among primates for themselves.

Primate ID	Name used by other primates
BLW	Brianna Wilkinson
CWK	Charlie Knape
CPD	Cody Doolan
DLS	Dan Susman
DSS	Derek "Sven" Stenquist
EEBB	Eben Bein
ELP	Emily Pizzichemi
JKLH	James Hung
JHMC	Jeremy Chan
JMW	Jon Wachter
KG	Karl Grunseich
MND	Margi Dashevsky
RDDW	Rebecca Davidson Wolf
RMM	Robinho Meyers
SEW	Sarah Wengert

evaluated group composition and the tendency for certain individuals to associate with each other. All statistical analyses were done using Grandmother Test v. 1 (SAS Institute, Inc. 2007).

RESULTS

Individuals showed consistent preferences for certain types of study (Table 2). Group-wide, the primates conducted 34 studies. Of these, the subjects were distributed as follows (categories not exclusive): seven on birds, four on fish, nine on arthropods, five on other animals, and twelve on plants and coral. Their focus was on foraging 11 times, distribution 16 times, and plant features 4 times. Not all studies had unique features, and these features were not exclusive. Thirteen studies were experimental, four dangerous, three long-term, and five conservational. Of Costa Rican projects, six were aquatic; all Little Cayman studies were aquatic, due again to control by the alpha male.

Group membership was also different for different primates (Table 3). The average group size was 3.5 primates, with a range of 1 to 5 individuals. On average, each primate worked with 10.7 other individuals out of the 14 possible.

One of the fifteen primates, KG, appeared to be a generalist, not occupying any extremes for any of the analyzed categories.

DISCUSSION

Surprisingly, there were patterns in what appeared to be random behaviour. Given the broad scope of this study, I can only highlight a few of the most obvious reasons for the patterns I observed. CPD's penchant for dangerous situations was commonly acknowledged among the other primates, as was JKLH's obsession with arthropods. Anecdotally, I observed him frequently halting to point out a bug no one else noticed, typically identifying it and giving a brief explanation of its life history traits. EEBB's focus on experimental studies was also well-acknowledged, while MND was known for her commitment to the environment and conservation. KG, the generalist, was probably best recognized for his photo-taking ability, but also widely acclaimed as a master of "statistics," a bizarre

TABLE 2. Primates exhibited clear preferences for certain kinds of study.

Person of interest	Study category	Studies of that kind carried out	Mean studies of that kind others carried out
RMM, SEW	Birds	3	1.0
CWK, RDDW	Fish	2	0.62
KLH	Arthropods	4	1.5
DLS	Other animals	3	1.21
JMW, RDDW	Plants	4	2.08
BLW, ELP	Foraging	4	2.08
KLH	Distribution	1	1.57
EEBB, JHMC	Plant features	2	0.54
ELP	Aquatic	3[1]	1.29[1]
EEBB	Experimental	6	1.0
CPD	Dangerous	4	0.5
JMW	Long-term	2	0.29
MDD	Conservation-related	3	0.5

[1] Only Costa Rica studies were included in this, due to the intrinsic aquatic nature of Little Cayman projects.

method characteristic of the "scientific subculture" that uses complex calculations, obscure terminology and Greek symbols to make it impossible for non-members of the subculture to participate in or understand "science". However, statistical methods sometimes were successful in demonstrating that their hard work was often in vain. There is speculation that the predilection for birds shown by RMM and SEW is connected to their full names: "Robin" and "Wing it" (from Wengert). ELP's love of the water—she swims frequently, sometimes competing

TABLE 3. Primates exhibited clear preferences for associating with certain other individuals during "studies".

Person of interest	Distinction	Person's stats	Group average stats
DLS	Lowest evenness	0.603	0.720
RDDW	Highest evenness	0.840	0.720
RDDW	Fewest people per project	2.857	3.533
DSS, JHMC	Most people per project	4	3.533
DLS	Fewest different people worked with	8	10.667
CPD	Fewest times working with girls	3	6.2[1]
DLS, JMW	Most times working with same person	4 (with each other)	2.867[2]

1. This average is for males only. A male primate had five potential female group members, whereas each female had only four. The female average was 5.6.
2. For each primate, I determined the most times that that primate worked with any single other primate. This is the average of those numbers.

with other primates from different troupes—makes her preference for aquatic studies straightforward.

Altogether, all primates appeared to enjoy themselves immensely, despite the intense workload. Future studies could look at correlations between Lizano or galletas and primate happiness (which could be evaluated by looking at smile frequency) to further elucidate some of the more mysterious workings of the mind of *Homo sapiens*.