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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 is alphabetical, 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 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.

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.

We acknowledge the generous financial support of Dorothy Hobbs Kroenlein.

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.

David Peart
Hanover NH, USA
18 August, 2010

SCHEDULE FOR DARTMOUTH TROPICAL BIOLOGY PGM - COSTA RICA, W 2010

			<u>Morning</u>	<u>Afternoon</u>	<u>Evening</u>
5 Jan	Tu	To San Jose	Travel	Travel	Arrive in evening
6 Jan		In San Jose	OTS, InBIO	free: shopping etc.	Group dinner in SJ
7 Jan		To Palo Verde	Travel	Orientation ^a	Lec: Intro CR ecology (DP)
8 Jan		At Palo Verde	Orientation	Lec: Avian Ecol (DP). Res. Qs.	Lec: Bioacoustics (LS)
9 Jan		At Palo Verde	FP ^b -1 (ant-acacia)	Stat lab (MC/LC)	Data analysis/synthesis
10 Jan	Su	At Palo Verde	FP-2	Arth lab Lec: Pl Rep Biol (DP)	FP-1 seminars. Writing.
11 Jan		At Palo Verde	FP-2	Vert lab Lec: Herp Ecol (MC)	Writing. FP1 ms due
12 Jan		At Palo Verde	SIFP ^c plan/proposals	Plant lab Data Anal/Writing	FP-2 seminars. Writing
13 Jan		At Palo Verde	SIFP-1	SIFP-1	Writing. FP-2 ms due.
14 Jan		At Palo Verde	SIFP-1	SIFP-1/analysis. Revisions.	DL crit. SIFP-1/anal. Revs.
15 Jan		At Palo Verde	River trip	SIFP seminars. Writing.	Writing: SIFP-1 ms due
16 Jan		To Santa Rosa	Travel/walk	Orientation. Lec: Turtles(DP)	Field: Sea turtle nesting
17 Jan	Su	At Santa Rosa	Lec: Mgrv(LS)	Exploration ^d	Field: Sea turtle nesting
18 Jan		To Monteverde	Walk/Trav	Orientation	Lec: DP
19 Jan		At Monteverde	Orientation	SIFP-2 planning	Lec: Amphibs (A Pounds)
20 Jan		At Monteverde	SIFP-2 pilot /props	SIFP-2	Lec: Lec: Div/biog(MC)
21 Jan		At Monteverde	SIFP-2	SIFP-2	Anal/writing
22 Jan		At Monteverde	SIFP-2	Analysis; SIFP-2 seminars	Writing
23 Jan		At Monteverde	Writing	Writing SIFP-2 ms due. Bat Jngl	Writing
24 Jan	Su	At Monteverde	Writing; mist nets	Writing; plant quiz	Writing
25 Jan		At MV Writing.	All fin. mss thru MV	due Exploration	Free
26 Jan		To Cuerici	Travel	Travel/Orientation	Lec: For. Dyn (DP).
27 Jan		At Cuerici	Trip to Paramo	Orientation	Lec: For. ConsMgmt (DP)
28 Jan		At Cuerici	Orient. SIFP-3plan	SIFP-3 planning/pilot data/anal.	SIFP-3 final proposals
29 Jan		At Cuerici	SIFP-3 (RC arriv)	SIFP-3 (DRP departs)	Lec: Coevolution (MA)
30 Jan		At Cuerici	SIFP-3	SIFP-3	Analysis. SIFP-3 seminars.
31 Feb	Su	At Cuerici	Writing	Writing/exploration	Writing SIFP-3 ms due
1 Feb		At Cuerici/travel	Explor.	Travel to La Palma	free
2 Feb		To Corcovado	Walk/orient.	Walk/orientation [dinner530]	Discussion
3 Feb		At Corcovado	Orientation	Orientation	Lec:
4 Feb		At Corcovado	SIFP plan	SIFP-4 plan/proposals	Lec:
5 Feb		At Corcovado	SIFP-4	SIFP-4	Writing/night walk
6 Feb		At Corcovado	SIFP-4	SIFP-4	Lec:
7 Feb	Su	At Corcovado	Exploration	Anal/writing: SIFP4 seminars	Writing: SIFP4 ms due
8 Feb		CV to Las Cruces	walk	travel	Guest lec Zak Zahawi
9 Feb		At Las Cruces	Plant lab.	Writing. SIFP4 rev due	Lec:
10 Feb		At Las Cruces	Bird lab/quiz	Plant lab&quiz. Writing	Writing.
11 Feb		Las Cruces/to LaS	To La Selva via Poas	Travel to La Selva/orientation	Lec:
12 Feb		At La Selva	Orientation	Orientation	Guest lec (Clarks) Writing
13 Feb		At La Selva	SIFP planning	SIFP planning/pilot	Writing
14 Feb	Su	At La Selva	SIFP-5	SIFP-5	Lec:
15 Feb		At La Selva	SIFP-5	SIFP-5/analysis	SIFP-5 seminars. Writing.
16 Feb		At La Selva	Agroecol. field trip	Writing: SIFP-5 ms due	Writing
17 Feb		At La Selva	Writing	Writing: <u>All final</u> CR mss due	CR mss proofing for public.
18 Feb		At La Selva, to SJ	Exploration	Travel to SJ	Group dinner in SJ
19 Feb	F	Depart for Little Cayman, leave LC	12 Mar		

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

^c SIFP = student initiated field problems

^d Explor. = Time to explore site

[Initials after lectures = student paper critiques]

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RESPONSE OF THE MUTUALIST ANTS *PSEUDOMYRMEX SPINICOLA* AND
CREMATOGASTER BREVISPINOSA TO SIMULATED HERBIVORY ON THEIR HOST,
ACACIA COLLINSII

NICHOLE J. BROWN, LAUREN E. DI BICCARI, JENNIFER R. FOWNES, F. CHARLES GOVERNALI, MOLLY
E. GREAR, DANIEL R. O'DONNELL

Project Design: Melissa S. Callahan; Faculty Editor: David R. Peart

Abstract: *Pseudomyrmex spinicola* and *Crematogaster brevispinosa* ants protect their host, *Acacia collinsii*, from herbivory. We hypothesized that chemical cues emitted by damaged leaves combined with physical disturbance would induce a greater response than physical disturbance alone because combined cues provide a stronger signal of herbivory. To test this hypothesis we measured ant activity on leaves with combined cues (leaf clipping and tapping base of leaf) compared to physically disturbed leaves (tapping base of leaf). We found no difference in ant response to combined cues compared to physical disturbance alone.

Key Words: Palo Verde, plant volatiles, tropical dry forest

INTRODUCTION

Acacia collinsii forms mutualisms with *Pseudomyrmex spinicola* and *Crematogaster brevispinosa* in which the tree provides shelter and extra-floral nectaries in exchange for protection from herbivory (Janzen 1983). Ants may react to herbivory through detection of physical disturbance or chemicals emitted by damaged leaves (Macintosh et al. 2000). We predicted that the simulated physical disturbance of a vertebrate herbivore in addition to chemical cues emitted by damaged leaves would induce a greater response than the simulated physical disturbance alone. We also predicted that ant response would be strongest directly following the physical disturbance and/ or release of chemicals (Macintosh et al. 2000).

METHODS

On the morning of 9 January 2010, in the tropical dry forest near Palo Verde Biological Station, Costa Rica, we haphazardly selected 42 single-stemmed *A. collinsii* trees, 21 occupied by *P. spinicola* and 21 occupied by *C. brevispinosa*.

We applied two treatments 0.5 m from opposite sides of the trunk simultaneously to two haphazardly selected branches. To simulate the physical presence of an herbivore (re-

ferred to as physical) we tapped the base of the leaf three times. To simulate a feeding herbivore that caused physical disturbance and the release of plant chemicals from damaged leaves (referred to as physical+chemical) we clipped once across each of three leaflets and then tapped the base of the leaf three times. For both treatments we recorded the number of ants that crossed the base of the disturbed leaf within the 0-1, 2-3, and 4-5 minute post-disturbance time intervals.

For *C. brevispinosa*, we normalized the distribution of ant responses with a $\ln(y + 1)$ transformation. For *P. spinicola*, no transformations were sufficient to normalize the skewed data, so we conducted a non-parametric Wilcoxon-Kruskal/ Wallis rank sums test comparing treatments and ignoring time of treatments.

RESULTS

Ants often failed to respond or responded weakly to disturbance in both treatments. We observed that ants en route to leaves in both treatments often stopped at the extra-floral nectaries and did not proceed onto the leaves. For *C. brevispinosa* there was no significant difference between treatments and no effect of time (two-way ANOVA $F_{5,120} = 1.36$, $P = 0.24$; for untransformed data see Fig. 1). For

P. spinicola, there was no significant difference between treatments ($X^2_1 < 0.01$, $P = 0.94$).

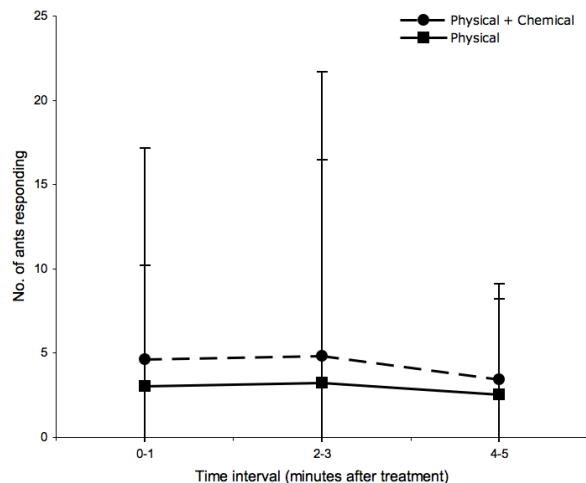


FIG 1. The number of *C. brevispinosa* ants responding to physical (tapping base of leaf) and physical + chemical (cutting leaves to release chemical cues) treatments on *A. collinsii* (N = 21) over three time intervals at Palo Verde, Costa Rica. Vertical bars are ± 1 S.E.

DISCUSSION

Aggressive ant species (e.g. *P. spinicola*) respond to both physical disturbance and plant chemical cues (Macintosh et al. 2000; Alexander et al. 2002), but our data did not show that *P. spinicola* response was greater when both cues were present. In our study, the overall mean response of both ant species to any cues was low (Macintosh et al. 2000 and Alexander et al. 2002 saw up to a five-fold greater response).

Our failure to observe a strong response in either ant species may have been due to our methodology. Potential flaws include an inaccurate representation of vertebrate herbivory: more ants may have responded if we had provided a stronger volatile chemical cue or a greater physical disturbance. For example, Barger et al. (2005) simulated the action of cattle tongues (which these browsers use to remove leaves) and elicited strong ant responses. The time scale of our experiment should not have been a factor since in previous studies ants responded strongly within

five minutes (Broughton et al. 1994, Macintosh et al. 2000, Alexander et al. 2002, Barger et al. 2005). To gain a clearer insight into ant response to herbivory signals, we suggest measuring ant response relative to a baseline activity and using a complete two-way design (treatments: no disturbance, physical disturbance, chemical signal, and both).

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EXPERIMENTAL TEST OF A BEHAVIORAL ASSAY TO DEFINE COLONY BOUNDARIES IN RED ACACIA ANTS, *PSEUDOMYRMEX SPINICOLA*

JANEL L. DiBICCARI, ALEXANDER R. DUCKLES, DAEWOONG LEE, CHASE R. RAINES, AMY H. STANESCO, EMILY V. A. UNGER, SARAH M. YU

Project Design: David R. Peart; Faculty Editor: David R. Peart

Abstract: Red acacia ants, *Pseudomyrmex spinicola* defend their home tree against intruders. We hypothesized that the ants would act more aggressively towards conspecifics from different colonies than towards ants from their home colonies. Though we did not find a significant relationship between host colony behavior and origin of introduced ants, there was a marginally significant trend of increased aggression towards foreign ants. It is possible that our methods were confounding, and methods could be improved in follow-up studies.

Keywords: acacia ants, aggressive response, colony identity, host colony, intruder, territoriality

INTRODUCTION

Queens of the mutualistic acacia ant species *Pseudomyrmex spinicola* fly away from their home trees, mate, and search for an unoccupied *Acacia collinsii* to establish a new colony. As a colony grows, it may spread to neighboring trees (Janzen 1984). Once a colony is established ants respond aggressively to intruders (Berry et al. 1994, Gilmartin et al. 1991).

Genetic testing of colony identity is impractical in the field, so a behavioral assay to determine if ants are from the same colony would be useful. We hypothesized that ants on a given tree would respond more aggressively to ants from another colony than to ants from their own colony. We tested this by observing the behavioral response of a colony to the introduction of both host colony ants and non-host colony (foreign) ants.

METHODS

On January 9, 2010 in Palo Verde National Park, Costa Rica, we observed the reaction of *P. spinicola* ants on nine “focal” acacia trees to the introduction of a host colony ant and a foreign ant. All focal trees had *P. spinicola* ants, and were 1) 2-5 m tall, 2) not in physical contact with other acacia trees, 3) at least 20 m from other focal trees, and 4) at least 20 m away from trees used to collect foreign ants.

We collected ants by cutting off the end of an inhabited acacia branch, putting it in a plastic bag, and storing it in the shade. Unlike some previous studies (e.g. Berry et al 1994) we marked ants to differentiate between host colony and introduced ants. To mark the ants we removed them one at a time from the plastic bag with soft forceps and used a whiteout wand to mark the dorsal side of the ant. We attempted to mark only the abdomen, but sometimes inadvertently applied whiteout to the thorax and head.

We alternated the order in which we introduced the host colony ant and foreign ant. We introduced ants to the end of a branch of the host colony tree that exhibited ant activity, and observed interactions between the introduced and the host colony ants for 90 seconds. We recorded time to first physical contact and first “grapple”, which we defined as physical contact between ants involving body parts other than antennae. We also recorded the total number of contacts involving the introduced ant occurring before 60 and 90 seconds, as well as introduced ant state (grappling, unmolested, ejected from the tree, or inside a thorn) at 60 and 90 seconds.

RESULTS

Instances of grappling were most relevant to our hypothesis, indicating an aggressive response. Ants reintroduced to their

home colony took longer to induce a grappling response than foreign ants on the same tree ($t_{4.48} = -2.52$, $P = 0.059$). Of all reintroduced home colony ants, 22.2% were grappled, compared to 55.6% for foreign colony ants ($X^2_1 = 2.16$, $P = 0.142$).

No other measures of ant reaction indicated differences in response between reintroduced home colony and foreign ants: time until first contact ($t_8 = -0.96$, $P = 0.352$), number of contacts before 1 min ($t_{16} = 1.04$, $P = 0.311$), and number of contacts before 1.5 min ($t_{16} = 1.11$, $P = 0.284$).

DISCUSSION

Our hypothesis that ants would respond more aggressively to conspecifics from different colonies was supported with marginally significant results, based on grappling frequency. However, our manipulations may have increased variability (by injuring ants with forceps) and potentially confounded our results (if whiteout on reintroduced host colony ants elicited an aggressive response from their nestmates).

A more benign marking method is needed because tagging with white out often impaired the antennae or legs. Declining ant activity during the one-hour sampling period may also have contributed to variability in our data.

We still consider the hypothesis to be viable, and if the methods could be altered to remove sources of variance and eliminate confounding factors, it may be possible to develop a powerful bioassay to determine the boundaries of a colony.

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FACTORS AFFECTING *CREMATOGASTER* SP. INHABITATION OF *ACACIA COLLINSII* THORNS

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Abstract: We investigated physical characteristics of *Acacia collinsii* thorns affecting *Crematogaster* sp. inhabitation. We hypothesized that ants prefer larger thorns, thorns near larger numbers of nectaries, and thorns with thicker walls. We compared these factors in pairs of adjacent inhabited and uninhabited thorns at Palo Verde National Park in Costa Rica. Contrary to our predictions, inhabited thorns had thinner walls than adjacent uninhabited thorns. Thinner walls may provide more internal space or require less energy to bore into, which are benefits that may outweigh the added protection of thicker walls. There was no relationship between thorn inhabitation and thorn size or nectary availability.

Key Words: acacia ants, mutualism, Palo Verde, tropical dry forest

INTRODUCTION

Crematogaster sp. are mutualists with *Acacia collinsii*. The ants provide protection against herbivores and nearby competing plants, and the tree provides food in the form of extrafloral nectaries and shelter in the form of hollow thorns (Janzen 1966). Most, but not all, thorns show evidence of inhabitation (holes bored by ants). We hypothesized that variation in physical characteristics of thorns explains habitation patterns. We predicted that thorns with greater nectary access, both in terms of proximity and number of nectaries, would be more likely to be inhabited. We also predicted that ants would prefer larger thorns with thicker walls, since these attributes might provide more habitable space and greater protection from mammalian and avian predators.

METHODS

We conducted our study on 9 January 2010 in a tropical dry forest stand of *A. collinsii* ca. 4 km SE of the OTS field station in Palo Verde National Park, Costa Rica. To compare physical characteristics of inhabited and uninhabited thorns, we sampled 11 trees inhabited by *Crematogaster* sp. For eight of those 11 trees, we sampled three randomly selected branches. For the other three trees, we were

only able to sample one to two branches due to time constraints but included available data in the analysis. “Inhabited thorns” were those with a hole made by *Crematogaster* sp., indicating that the thorn was previously or currently inhabited.

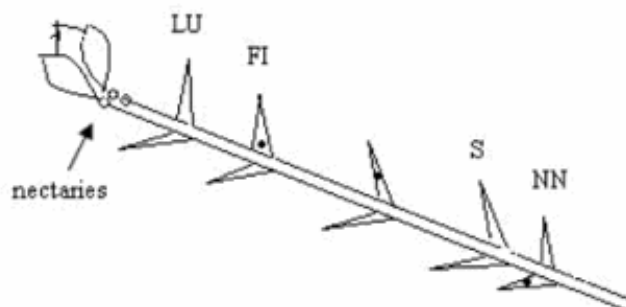


FIG. 1. Example of *A. collinsii* branch with thorn classification: distal uninhabited neighbor (LU), first inhabited thorn (FI), subsequent uninhabited thorn (S), nearest inhabited neighbor (NN). Black spots represent holes bored by mutualist ants.

On each branch we measured two classes of thorn pairs. Moving from the branch tip towards the trunk, we compared the first inhabited thorn (FI) to its distal uninhabited neighbor (LU) and any subsequent uninhabited thorn (S) to its nearest inhabited neighbor (NN) (Fig. 1).

Thorns of *A. collinsii* grow as sets of two fused cones with a hollow interior. If thorn halves were asymmetric, we measured the larger of the two halves. We measured the diameter of the thorn at its base, the height of

the thorn from the middle of the base to the tip, the thickness of the thorn wall at the thickest part of the base, the distance from the base of the thorn to the closest set of extrafloral nectaries, and the number of nectaries in that set. We measured the thickness of the thorn walls as the thickness of the appropriate number of pages in our lab notebooks. We used height and diameter measurements and assumed the thorns had a conical shape to calculate thorn volume.

We conducted an ANOVA to determine if physical characteristics differed between inhabited and uninhabited thorns at branch tips and mid-branch. We also performed paired t-tests comparing FI to LU and S to NN to analyze differences between individual thorn pairs.

RESULTS

Thorn thickness differed between inhabited and uninhabited thorns. Last uninhabited thorns differed significantly from first uninhabited and nearest neighbor thorns (Fig. 2). However, none of the other variables (thorn volume, height and diameter, or number of nectaries) varied by thorn type. We excluded nectary distance from analysis because it had a bimodal distribution.

We compared inhabited and uninhabited thorn pairs on the same branch (LU and FI, S and NN) to determine which variables differed between adjacent thorns. Thorn thickness was the only significantly different characteristic within thorn pairs. LU thorns were 1.58 notebook pages thicker than FI thorns (paired- $t_{18} = 2.46$, $P = 0.024$), and S thorns were 1.17 notebook pages thicker than NN thorns (paired- $t_{17} = 3.96$, $P = 0.002$).

DISCUSSION

Contrary to our prediction, inhabited thorns had thinner walls than uninhabited thorns. There is no evidence that thorn diameter, height, volume or number of nectaries drive *Crematogaster sp.* inhabitation. Bimodality of nectary distance may be a result of leaf

loss, given that nectaries are located at leaf bases. Thorns located on defoliated branches appeared to be farther from nectaries than thorns on foliated branches.

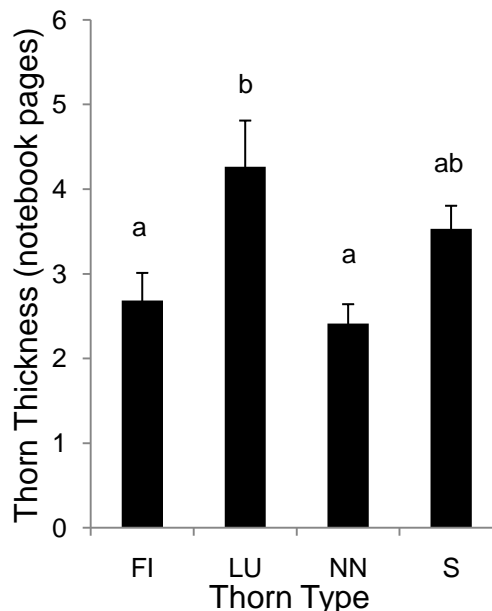


FIG. 2. Mean *A. collinsii* thorn wall thickness by thorn type in Palo Verde National Park, Costa Rica. Last uninhabited thorns (LU) were significantly thicker than all inhabited thorns (FI, NN) ($F_{3,68} = 5.11$, $P = 0.003$), but were not significantly different from subsequent uninhabited thorns (S). Different letters represent significantly different values. Error bars are ± 1 SE.

Crematogaster sp. chose to inhabit some thorns but not others, indicating that certain thorns provide more suitable habitats. Boring a hole through a thinner thorn wall may require less energy, and thorns with thinner walls may offer more internal living space for *Crematogaster sp.* The benefits of thinner thorn walls appear to outweigh the protection a thicker thorn wall may offer.

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COMPARISON OF HILLSIDE AND BASIN FOREST STANDS: BASAL AREA AND EARLY DRY SEASON LEAF PHENOLOGY

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Abstract: A majority of trees at Palo Verde, Costa Rica lose their leaves in the dry season. We hypothesized that trees in a basin site would drop their leaves later and have greater basal area than a hillside site because of the basin's moisture retaining topography. From plotless samples in ca. 2.1 ha study areas at each site, we examined a total of 223 trees, and found no difference in phenological leaf change or basal area between the two sites. Our assumption of greater soil moisture in the basin may not be correct. The hillside site may also be dominated by different tree species that are better adapted to dry conditions than those at the basin site.

Key Words: basal area, canopy coverage, leaf coloration, phenology, soil moisture, topography, tropical dry forest

INTRODUCTION

Trees in seasonally dry forests, such as those in Palo Verde National Park, Costa Rica, face stress as the dry season progresses and water becomes a limiting resource (Janzen 1983). If soil is shallow with little organic content and limited capacity to hold water, trees experience water stress earlier in the dry season than trees in soil that is deep, with high organic content. The combination of low water-holding capacity and poor soil would lead trees to experience water stress earlier in the dry season, and have lower overall levels of biomass and leaf area (Seandel et al. 1993). As basal area is strongly correlated with forest biomass and leaf area, forests in such soils would likely have a lower basal area as well.

The topography of basins, such as that formed by the Cerro Calizos limestone ridge and a similar ridge ca. 400m to the north, leads to little runoff, high water retention, and deep soils high in organic content. Hillsides with steep, rocky slopes, like the one directly west of the previously mentioned basin, typically have low water retention, high runoff, and shallow soils poor in organic content.

We hypothesized that trees on the hillside would have earlier leaf discoloration, lower canopy fullness, and lower basal area than trees in the basin. To test our hypothe-

sis, we compared the amount of leaf discoloration, level of canopy fullness, and basal area of the forest on the hillside with corresponding data in the basin.

METHODS

On the mornings of January 10 and 11, 2010, we sampled from two sites in Palo Verde National Park. Sites were selected north of the Cerros Calizos trail ca. 800 m north of the Estación Biológica and just below the Cerros Calizos ridge (our basin location), and ca. 1000 m further west on the same trail (our hillside location). Using these trails as baselines, we marked nine parallel transects at 90 deg to the approximate trail azimuth and ca. 45 m apart (using 50 calibrated paces). Data were recorded at sample points taken 30 m apart on each transect, with the first sample point located a random number of meters (0-9) from the trail. At the hillside, we recorded data at 2 sample points along each transect; at the basin, the number of samples varied between 1 and 3 depending on local topography.

At each sample point, we estimated basal area using a factor 10 metric basal area prism, ignoring trees < 5 cm in diameter at 1.22 m above ground. For each tree with a recorded basal area, we created a canopy fullness index classified as either full canopy (recorded as

“3”), moderate coverage (“2”), or few remaining leaves (“1”). We also created a leaf color index for entirely green (“3”), somewhat yellowed or discolored (“2”), or almost entirely discolored (“1”). Lastly, we recorded canopy height for each tree (as Tall, Medium, or Short), relative to the main canopy layer. Numbers recorded for level of foliage thickness and leaf coloration were then summed to create a leaf phenology index for each tree.

RESULTS

Based on a total of 223 trees, 120 in the basin and 103 on the hillside, we found no significant difference in the canopy fullness index ($\chi^2_2 = 0.32$, $P = 0.85$), basal area ($t_{35} = 1.16$, $P = 0.25$), or leaf color index ($\chi^2_2 = 0.16$, $P = 0.92$) between the hillside and basin forest sites. The leaf phenology index was marginally significantly higher in the basin site ($\chi^2_4 = 8.23$, $P = 0.08$; Fig. 1), indicating greater canopy fullness and more leaf color retention.

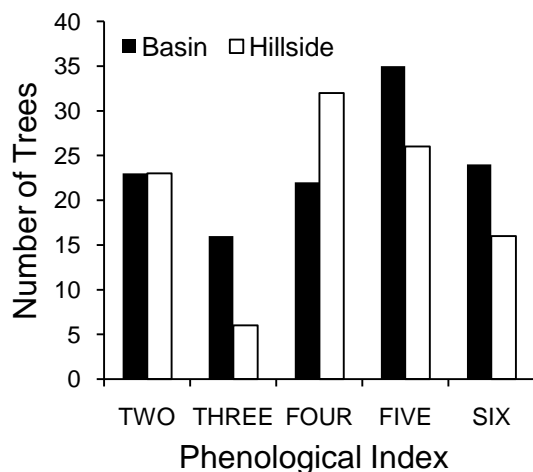


FIG. 1. Phenological index for trees in the basin ($n = 120$) vs. trees on the hillside ($n = 103$).

DISCUSSION

Basal area and phenological index (which indicated how far each tree had progressed in dropping its leaves) were similar in the basin and on the hillside. Our categories for assess-

ing phenological index were somewhat subjective, but given our sample sizes, we would expect to detect substantial differences between sites.

Our assumption that basins have greater water holding capacity and more fertile soils may not have been valid. However, we observed (but did not quantify) many more surface rocks and a much steeper slope in the hillside forest, consistent with our assumptions.

It is possible that the dominant species on the hillside differed from those in the basin and were adapted to less fertile and drier conditions. A different species composition may have allowed the hillside forest to attain a similar basal area and support a similar leaf phenology to that of the basin.

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GETTING STONED ONCE IS ENOUGH FOR *LEPIDACTYLUS MELANONOTUS*: FROG CALL RATE RESPONSE TO REPEATED DISTURBANCE

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Abstract: We examined the vocal response of the frog *Lepidactylus melanonotus* to single and repeated disturbance. Frogs must balance the benefits of mate attraction and territory defense against the cost of predation risk. We predicted that call rate would decrease following a single disturbance and would decrease further after repeated disturbances, due to perceived increased predation risk. We simulated disturbance by throwing rocks near calling frogs and recorded the call rate following each of five consecutive disturbances. Call rate decreased after the first disturbance but did not continue to decrease. Decreasing call rate further after repeated disturbances may be too great a cost to frogs' mating success and territory defense.

Key Words: Costa Rica, mate attraction, Palo Verde, predation risk, vocalization, wetland

INTRODUCTION

Male frogs use vocalizations to attract mates and defend territories, but in doing so risk attracting predators. Frogs (and other taxa) often respond to a perceived immediate predation risk by ceasing to call or fleeing (Ryan 1985). Many forms of anthropogenic disturbance, such as airplanes and traffic noise, cause frogs to alter the pitch of their calls and decrease overall calling activity (Lengagne 2008, Parris et al. 2009). Though these are unlike predator-related disturbances, the frogs' response may be an evolved general reaction to loud noise (Frid and Dill 2002). Reducing call rate could reduce frog reproductive success by reducing mate attraction and competitive success relative to other calling males. We predicted that a repeated disturbance would have a greater negative effect on frog call rates than a single disturbance, as repeated disturbances could represent an increasing threat. We tested this prediction on a Costa Rican frog (*Lepidactylus melanonotus*).

METHODS

We conducted our study in marsh habitat at Palo Verde National Park, Costa Rica, on 11 January 2010 from 1930 to 2200 hours. We collected all data along the edge of the

marsh, in ankle-deep mud and clumped 2 m tall vegetation. We haphazardly selected *L. melanonotus* individuals and measured baseline call rate for 60 sec prior to the first disturbance (D0-1). We created five repeated disturbances at 60 sec intervals by tossing a fist-sized rock near the focal frog and measuring call rate starting immediately after the disturbance, throughout each interval (D1-5). We used paired t-tests to compare individual

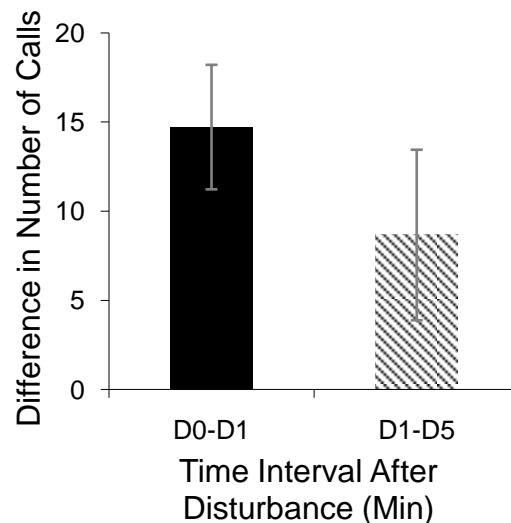


FIG. 1. *L. melanonotus* in the Palo Verde marsh, Costa Rica, decreased call rate after a single disturbance (D0-D1: $t_{33} = 3.98$, $P = 0.0002$), but further decrease in call rate after repeated disturbances was only marginally significant (D1-D5: $t_{33} = 1.52$, $P = 0.069$). Data ($N = 34$) exclude two unusually-behaving frogs. Error bars are \pm one S.E.

frogs' call rates between D0 and D1 and between D1 and D5. We applied a Bonferroni correction to both tests to adjust for non-independence.

RESULTS

While call rate decreased after a single disturbance (D0 to D1) ($t_{33} = 3.98$, $P = 0.0002$), it did not significantly decrease further after repeated disturbances ($t_{33} = 1.52$, $P = 0.069$). Two frogs behaved unusually by not calling for several minutes after the first disturbance. Excluding these, the mean difference in call rate between D0 and D1 remained statistically significant, equivalent to a 44% decrease in call rate (Fig. 1). Call rate decreased 30% between D1 and D5, which was marginally significant (Fig. 1).

DISCUSSION

L. melanonotus decreased call rate by nearly half following a single disturbance. This may be costly in mate attraction (Sullivan 2006) and territory defense (Lopez et al. 1987) but may reduce predation risk, as lowering call rate may reduce the flow of information to predators about frog location. Contrary to our prediction, repeated disturbance did not result in further decrease in call rate. In striking a balance between fitness costs and benefits, individuals may not further decrease call rate if the cost to mating success and territory defense is too great.

We suggest that other factors besides the repetition of disturbances may affect the response of *L. melanonotus*. Anecdotally, frogs calling alone had lower call rates and more strongly decreased their call rates when disturbed relative to individuals in areas of high conspecific caller density. In addition, frogs in taller and denser vegetation appeared to call at higher rates and respond less to repeated disturbance than more exposed individuals. Further studies should investigate the effects of conspecific caller density and vegetation on call rate.

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RANDOM SPATIAL DISTRIBUTION OF HUNTING SPIDERS (LYCOSIDAE) WITHIN AND AMONG SIZE CLASSES

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Abstract: We examined whether resource partitioning in different size classes was evident in hunting spiders (Lycosidae). Since body size and prey size are strongly correlated in hunting spiders, we hypothesized that Lycosids would reduce intraspecific competition by partitioning resources by size. We predicted that Lycosids within a size class would be distributed evenly, but that different size classes would not compete and thus be distributed randomly. We compared observed mean nearest neighbor distances (MNND) to simulated MNNDs and found that all hunting spiders were distributed randomly.

Key Words: nearest neighbor distance, Palo Verde, resource partitioning, spatial distribution

INTRODUCTION

Hunting spiders' body size is strongly correlated with prey size because the spiders actively select their prey, in contrast to passive prey capture by web weaving spiders. Therefore, hunting spiders' body size limits which prey they can capture. This can result in interspecific resource partitioning for co-occurring spider species of different sizes. Different sized spiders of the same species may also partition resources such that spiders of different size classes exert no intraspecific competition on conspecifics of other sizes (Werner & Gilliam 1984). We hypothesized that hunting spiders (Lycosidae), would reduce intraspecific competition by partitioning prey by size. We predicted that Lycosids would exhibit an even spatial distribution within each of three size classes. We expected a random distribution among different size classes on the assumption that they do not compete for the same prey items.

METHODS

We conducted our study on 11 January 2010 at the Palo Verde National Park Organization for Tropical Studies (OTS) field station—from 1900 to 2100. In a 4 m x 8 m grass plot demarcated by field tape, we located Lycosid spiders by eyeshine. For each spider, we recorded its location (coordinates) and cephalo-

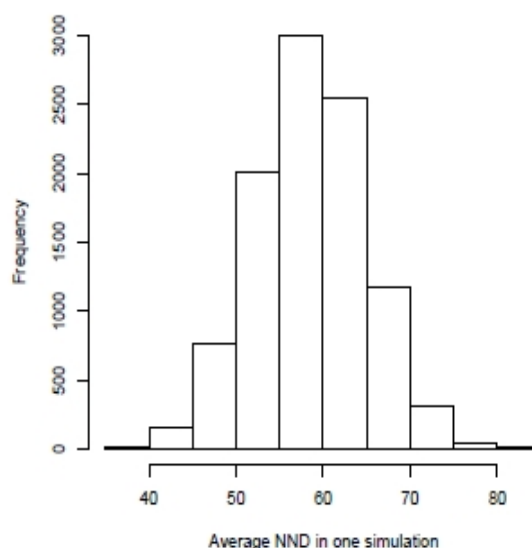


FIG. 1. Frequencies of mean nearest neighbor distance (MNND) for 10,000 simulations of 28 randomly distributed spiders in a 4 m x 8 m plot. Performed by R (v. 2.6.2).

thorax width using calipers, then removed it from the plot to prevent double sampling.

We divided spiders into three size classes using cephalothorax width—small (1.2 mm - 2.1 mm), medium (2.4 mm - 3.5 mm), and large (3.8 mm - 5.1 mm)—so that there were approximately equal numbers of spiders in each size class. We used R v. 2.6.2 to calculate mean nearest-neighbor distances (MNND) for 10,000 simulations of spiders in a 4 m x 8 m

plot, for each size class (Fig. 1). We then compared our observed MNND to the simulated MNND. We set $\alpha = 0.05$ and determined significant cut-off values for MNND for even and clumped distributions (Fig. 1).

RESULTS

Spiders within size classes and among size classes were randomly distributed. None of our observed MNND were above or below the cutoffs for even or clumped distributions (Table 1). Fig. 2 depicts observed distributions.

DISCUSSION

Contrary to our prediction that spiders would be evenly distributed within size classes, we observed a random distribution. Thus, there is no evidence of resource parti-

tioning based on body size within Lycosidae size classes. Among size classes, spiders were randomly distributed as predicted. Results may have been heavily influenced by our sampling methods. Walking around the perimeter of the plot may have caused spiders to flee the edges, and spiders often retreated into burrows when we attempted to collect them. Different distributions might emerge on a larger spatial scale.

The random distribution of spiders indicates that they do not interact as strongly as expected. Another possibility is that the combination of opposing mechanisms driving spatial distributions may have resulted in a random pattern. For example, habitat heterogeneity may influence suitable burrowing places that may push the population towards a clumped distribution.

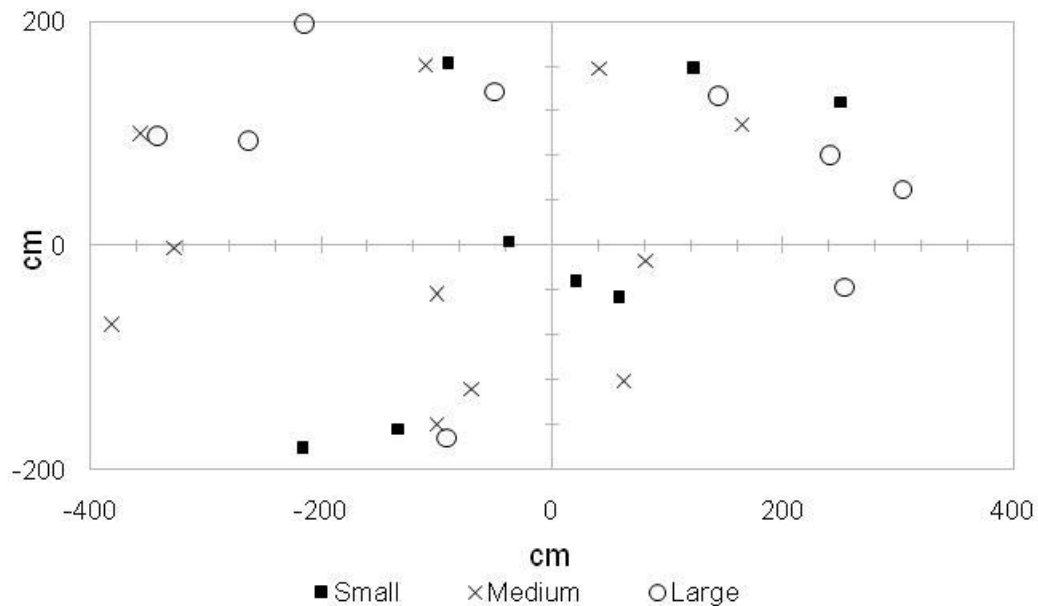


FIG. 2. Distribution of captured Lycosidae of small (1.2 mm - 2.1 mm), medium (2.4 mm - 3.4 mm), and large (3.8 mm - 5.1 mm) size classes at Palo Verde National Park in a 4 m x 8 m plot. Coordinate axes shown in cm.

TABLE 1. Observed and significant cut-off values ($\alpha = 0.05$) of mean nearest neighbor distance (MNND) within and among size classes of Lycosid spiders at Palo Verde National Park

Size Class	Observed MNND (cm)	Clumped Distribution MNND Cutoff (cm)	Even Distribution MNND Cutoff (cm)
Small 1.2 m m - 2.1 mm	93.9	< 77.9	> 162.3
Medium 2.4mm – 3.5 mm	99.4	< 70.2	> 127.7
Large 3.8 mm – 5.1 mm	123.7	< 75.0	> 148.3
All	52.2	< 48.0	> 69.0

ACKNOWLEDGEMENTS

We thank Laurel Symes for providing the R code.

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SCORPIONS DON'T CARE: PREY PREFERENCE IN *CENTRUROIDES MARGARITATUS*

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Abstract: We examined prey preference in the scorpion *Centruroides margaritatus*. Scorpions feed on many nocturnal prey species. We hypothesized that scorpions are opportunistic feeders, with no prey preference. We placed one of each of three prey types (nocturnal crickets, nocturnal moths, and diurnal grasshoppers) in shallow containers with a single scorpion, and recorded the first prey attacked and all prey eaten by each scorpion overnight to determine scorpion prey preference. The relative frequencies of first prey item attacked and overall prey items attacked were not statistically distinguishable from random, and scorpions exhibited no discernable prey preference.

Key Words: nocturnal, opportunistic feeders, Palo Verde, search image

INTRODUCTION

Scorpions consume a wide variety of nocturnal prey (Polis, 1987). We tested whether the scorpion *Centruroides margaritatus* displays a feeding preference for nocturnal species (crickets, moths) or diurnal species (grasshoppers), or if they feed on any accessible prey. We also tested whether scorpions demonstrated a preferential “search image” by presenting a familiar prey item (nocturnal cricket), an insect similar in morphology (grasshopper), and a morphologically distinct prey item (moth). We hypothesized that scorpions are opportunistic predators, capturing accessible prey at random. We predicted that there would be no evidence of preference for nocturnal versus diurnal insect species, and there would be no pattern to the order in which they capture prey.

METHODS

Since our hypothesis of random prey capture was null, the strength of our inference (if the null hypothesis was accepted) was the power of our test, which depends directly on sample size. We therefore collected as many scorpions as possible in the time available. We found 23 *C. margaritatus* on the nights of 12-14 January 2010 in Palo Verde National Park, Costa Rica. We divided them into three size classes of small (body length < 3cm), medium (body length 3cm to 4cm), and large

(body length > 4cm). We excluded scorpions smaller than 2cm, which may have been too small to consume the prey provided.

We collected approximately 20-30 each of diurnal grasshoppers, and nocturnal moths and crickets. We roughly matched prey size to scorpion size when selecting prey for each individual. Scorpions were housed individually in small, shallow round (ca. 18 cm diam., 8 cm depth) or square (12 x 12 x 4 cm) plastic containers that made all prey types equally accessible to the scorpions. We furnished the containers with leaf and rock matter and allowed the scorpions to acclimate to the containers for a minimum of 20 minutes before beginning each trial.

After nightfall, we placed one of each prey type simultaneously into each container. We used red lights to monitor the scorpions for preference (defined by first prey item consumed), and made a final tally of prey items eaten the next morning. When evaluating preference, we excluded the few replicates for which no prey were consumed or for which order of consumption could not be determined. Using a Pearson Chi-squared test, we compared the percentage of instances in which each prey item was preferred to the percentages we would expect if the scorpions selected their first prey item randomly. We also performed a Pearson Chi-squared test on the final tally of all predations to evaluate the

scorpions' willingness to consume each kind of prey.

RESULTS

Using the first consumed prey item as an indicator of prey preference, scorpions did not display a significant preference for any prey type. (Pearson Chi-Squared, $\chi^2_2 = 0.8235$, $P = 0.66$). As the scorpions continued to feed, all prey items were consumed with equal frequency (Pearson Chi-Squared, $\chi^2_2 = 0.18$, $P = 0.91$).

DISCUSSION

We found no evidence that scorpions have prey preferences. Our data on both first and total predations implied almost complete randomness in preference. This supports our hypothesis that scorpions are opportunistic hunters that will eat any accessible prey, and suggests that factors such as familiarity with nocturnal prey and similarity to common prey are unimportant. Although our results supported the null hypothesis, our sample size was too small to definitively conclude that scorpions have no prey preference.

A lack of preference, especially between nocturnal and diurnal prey, suggests that scorpions are not obligately nocturnal due to specificity of prey preference. Other factors, such as predation risk and temperature, may be more important in dictating scorpions' nocturnal activity. Scorpions' opportunistic behavior could enable them deal with changing habitats and species composition.

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HETEROSPECIFIC FLOCKS OFFER FORAGING ADVANTAGES FOR NORTHERN JACANAS (*JACANA SPINOSA*)

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Abstract: Heterospecific flocks in forest environments offer foraging and anti-predator benefits to the species involved, but the value of heterospecific flocking in wetland environments is less understood. We observed Northern Jacanas (*Jacana spinosa*) in Palo Verde National Park, Costa Rica, measuring the duration and frequency of foraging-related behaviors. In comparison to Jacanas foraging alone or in conspecific flocks, individuals in heterospecific flocks spent more time foraging, had a higher peck rate, spent less time scanning, and looked up to scan less frequently. These findings suggest that heterospecific flocking is beneficial in wetland environments, although the mechanisms need further study.

Key Words: anti-predator, competition, mixed flock theory, peck rate, time budget, wetland bird community

INTRODUCTION

Hypotheses to explain the formation of heterospecific flocks have focused on foraging and anti-predation benefits (Dolby and Grubb 1998). The costs and benefits of heterospecific flocks have not been as well documented in wetlands as in woodlands (Dolby and Grubb 1998, Grubb and Matthysen 2005). In the Palo Verde wetland in Costa Rica, the Northern Jacana (*Jacana spinosa*) forages individually as well as in heterospecific and conspecific flocks. We tested the hypothesis that, in comparison to jacanas foraging alone or in conspecific flocks, individuals in heterospecific flocks would experience foraging benefits. We predicted that jacanas in heterospecific flocks would spend more time foraging, have a higher peck rate, spend less time scanning, and look up to scan less frequently.

METHODS

We studied the foraging behavior of *Jacana spinosa* in different avian neighborhoods in wetlands at Palo Verde National Park, Costa Rica on January 13 and 14, 2010. From three locations at the edge of the wetlands in front of the Organization of Tropical Studies Palo Verde field station (directly underneath the radio tower 145 m SE of the field station, the observation tower 135 m W of the radio tower, and the boardwalk 220 m W of the ob-

servation tower), we took 193 observations of haphazardly selected individual adult jacanas ("focal birds") in two morning periods from 0730 to 1200 and one afternoon period from 1500 to 1730. The sex of focal birds was not determined because adult males and females are difficult to distinguish at a distance (see Stiles and Skutch 1989).

Each observation lasted 1 min or until the original neighborhood classification no longer applied, but we discarded observations less than 30 sec in length. We recorded the number and species of birds in a 3 m radius ("neighborhood") around the focal bird and categorized the neighborhood as heterospecific, conspecific, or isolated. In each observation period, we recorded the number of pecks by the focal bird, the number of aggressive interactions with other birds, and the amount of time that the bird was either foraging (head down, looking for food items), scanning (head up with clear pause from foraging), or preening.

We used Principal Components Analysis (PCA) to develop a behavioral index incorporating peck frequency, foraging time, scanning time, and scan frequency. We retained only the first principal component, which described 60% of the variation, with peck frequency and foraging time contributing positively and scanning time and scan frequency contributing negatively to index

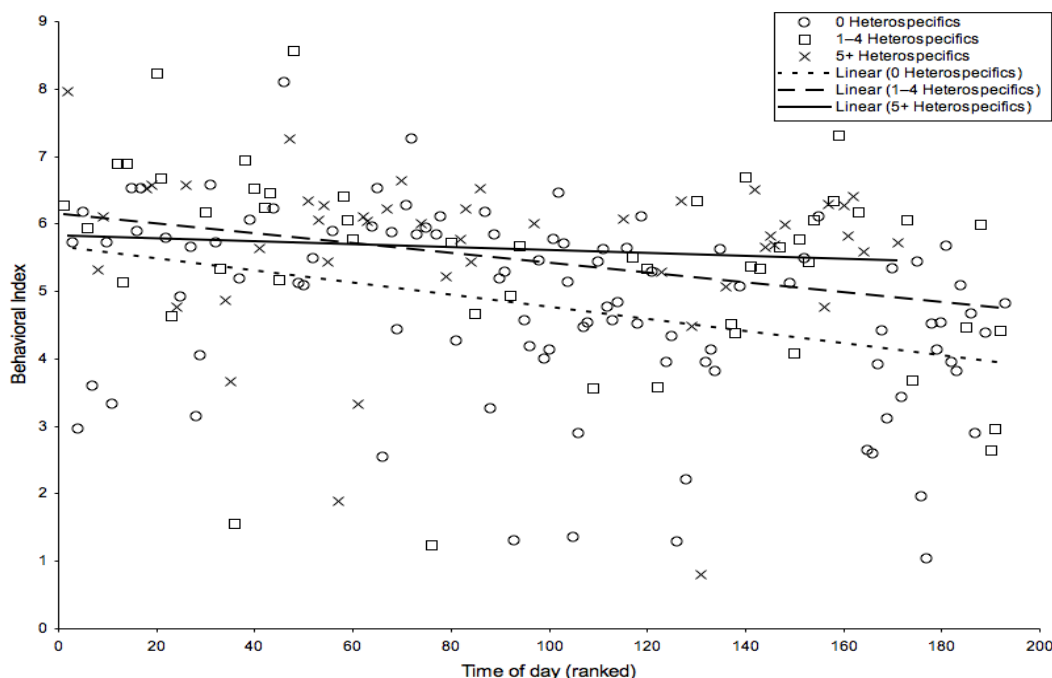


FIG. 1. Adult jacana behavior varied with the number of heterospecific birds within a 3-m radius ("neighborhood"). Jacanas in heterospecific neighborhoods (>0 heterospecifics) spent more time foraging, had a higher peck rate, spent less time scanning, and looked up to scan less frequently, relative to jacanas without neighbors or in conspecific neighborhoods (as indicated by higher values of the behavioral index, a PCA combination of these four behavioral measurements; ANCOVA, neighborhood heterospecificity: $F_{2,187}=7.58$, $P=0.0007$; time: $F_{1,187}=11.48$, $P=0.0009$). Jacana time budgets were constructed from 193 ca. 1 min observations of jacanas in wetlands at Palo Verde National Park, Costa Rica on January 13th and 14th, 2010.

values. We normalized the index values with a Box-Cox transformation and used an ANCOVA to assess the effects of neighborhood heterospecificity on this index with time as a covariate. We constructed linear contrasts (LC) to compare jacana behavioral indices in different heterospecific neighborhood categories (LC1: (0 heterospecifics) vs. (1-4 heterospecifics and 5+ heterospecifics). LC2: (1-4 heterospecifics) vs. (5+ heterospecifics)).

To assess jacanas' use of different flock environments, we categorized the neighborhood of every third individual within 60 m from each of the three observation points intermittently from 0630 to 0715 and 1330 to 1745 on January 15, for a total of 139 observations.

RESULTS

Relative to jacanas in conspecific neighborhoods and isolated jacanas, jacanas in heterospecific neighborhoods had higher (bene-

ficial) values of our behavioral index (LC1: $F_{1,187}=14.90$, $P=0.0002$). No difference in jacana behavioral index values was detected between neighborhoods with 1-4 and 5+ heterospecifics (LC2: $F_{1,187}=0.44$, $p=0.51$). Values of the behavioral index declined with time of day for jacanas in all neighborhood types (Fig. 1). Survey data showed that jacanas' neighborhoods were predominantly heterospecific in the morning and afternoon, and conspecific in the evening (Fig. 2).

DISCUSSION

Our data supported our hypothesis, showing benefits of heterospecific flocking for jacanas in a wetland environment, measured by an index combining foraging time, peck rate, scanning time, and scanning frequency. Previous studies have taken peck rate and foraging time to represent actual food intake (Owen 1972, Sedinger and Dennis 1988), while scanning precludes a jacana from

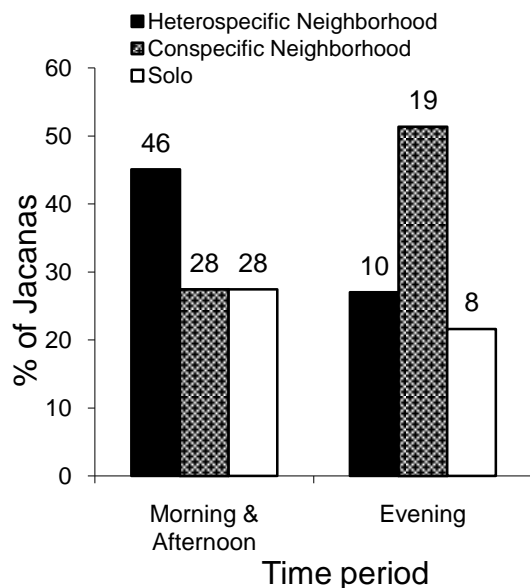


FIG. 2. The distribution of jacanas among neighborhood types changed throughout the day: nearly half of jacanas were in heterospecific neighborhoods during the most active foraging period (morning and afternoon), but most were in conspecific neighborhoods in the evening ($\chi^2=6.968$, $P=0.03$). Data are from a survey of every third jacana observed in sectors of 60 m radius around observation sites at Palo Verde National Park, Costa Rica on January 15, 2010. Values on top of bars indicate the number of jacanas.

foraging. Therefore, we believe that our index is a useful indicator of the integrated costs and benefits of jacana foraging behavior. The high proportion of jacanas observed using heterospecific neighborhoods during their most active foraging periods, contrasting with a majority in conspecific neighborhoods in the evening, would be expected if heterospecific flocking offers benefits. The observed decline in behavioral index values throughout the day may have been a product of both a Peregrine Falcon (*Falco peregrinus*) hunting in the vicinity during the late afternoon of the 13th and the reduction in jacana foraging activity as birds prepare to roost before dusk.

The benefits of heterospecific foraging that we found may result from reduced competition with conspecifics for food, vegetation disturbances by heterospecifics that increase access to jacana prey, enhanced predator de-

tection due to alarm signaling by heterospecifics, and the confusion effect reducing predator effectiveness (Gaddis 1980, Goodale and Kotagama 2005, and Morse 1977). Alternatively, heterospecific flocks may aggregate in areas that have high food availability for both heterospecifics and jacanas, so that our observed relationship resulted from higher food availability. Though future study is needed to understand the mechanisms driving heterospecific flocking in wetland environments, our study indicates distinct benefits to jacanas from associating with heterospecifics.

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MANAGEMENT OF THE PALO VERDE MARSH: IMMEDIATE EFFECTS ON PLANT COMMUNITY, WATER CHEMISTRY AND PHYSICAL PROPERTIES

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Abstract: In the marsh at Palo Verde National Park, Costa Rica, a *fanguedo* management strategy (cutting all plants using a tractor with cylindrical wheels with iron blades) is used to control the dominant cattail *Typha domingensis*. We compared two sites in the marsh, one that had been *fanguedoed* within 2 days (Recently Fanguedoed) and one that had been *fanguedoed* in 2008 or 2009 (Less Recently Fanguedoed). We hypothesized that the Recently Fanguedoed site would have lower plant species richness, percent cover, and proportion of the water column occupied by photosynthetic plant material. In addition we hypothesized that the Recently Fanguedoed site would have lower dissolved oxygen and pH and increased water temperature and salinity. We gathered data along two transects in each site. The Recently Fanguedoed site had a significantly different plant community, water chemistry, and physical properties from the Less Recently Fanguedoed site. Palo Verde National Park should consider the possible ecological consequences of changes in the chemical, physical, and plant sectors of the marsh community.

Key Words: Costa Rica, dissolved oxygen, *fanguedo*, pH, species richness, *Typha domingensis*, wetland

INTRODUCTION

The marsh at Palo Verde National Park (PVNP) is currently threatened by the dominance of the cattail *Typha domingensis*, which excludes other plant species and reduces the open water necessary to maintain resident and migratory bird populations (Trama 2005). To control *T. domingensis* PVNP implemented a management strategy in which a tractor with wheels in the form of cylinders with iron blades is driven through sections of the marsh, cutting all vegetation at water level (a process known as *fanguedo*).

We compared a site that had been *fanguedoed* within 2 days (Recently Fanguedoed, or RF) to a site that had been *fanguedoed* less recently, in 2008 or 2009 (Less Recently Fanguedoed, or LRF). In the RF site, plant cover has decreased and bird populations have increased (Trama 2005). In the LRF site, *T. domingensis* is not present above water (although its roots may be intact), and other marsh plant species have re-colonized (Nakarado et al. 2003).

We hypothesized that the RF site would have a different plant community, water chemistry and physical properties from the LRF site. We predicted that the RF site, as a result of physical disturbance by tractor

blades, would have decreased plant species richness, percent plant cover, and proportion of the water column occupied by photosynthetic plant matter. We also predicted that the changes in plant community and the physical disturbance of sediments would cause the RF site to have decreased dissolved oxygen and pH, and increased water temperature (due to decreased plant shade) and salinity (due to ions released from sediment). We focused on the plant community, water chemistry and physical structure because they are important for the overall ecosystem health of the marsh.

METHODS

We ran two 50 m transects parallel to shore, in each of two sites, in the marsh at Palo Verde National Park, Costa Rica (Table 1). One site was Recently Fanguedoed and the other Less Recently Fanguedoed. On 13 January 2010 from 1330 to 1730 we sampled one transect from the RF site followed by one transect from the LRF site. At the same time on 14 January 2010, we again sampled one transect from each site but in reverse order. In each site one transect was ca. 50 m from shore, and the second transect ca. 100 m from shore.

For each transect we walked east to west and took 10 samples at 5 m intervals. At each sample point we measured water depth, water temperature, pH, salinity, and dissolved oxygen (DO). In each site there were live, submerged aquatic plants. At each sample point, we measured the maximum depth of this photosynthetic plant material, from the water surface to the deepest plant leaf. We tossed a 0.5 m x 0.5 m quadrat within 1 m of each sample point (introducing a random element to the sampling), and estimated the percent cover of each plant species. We used JMP 7 and R to analyze data.

TABLE 1. GPS coordinates for transect locations in Recently Fanguoeed (RF) sites and Less Recently Fanguoeed (LRF) sites of the marsh at Palo Verde National Park.

Transect	Starting Coordinate	Ending Coordinate
1LRF	N10.34406°, W085.34383°	N10.34387°, W085.34421°
2LRF	N10.34387°, W085.34349°	N10.34374°, W085.34393°
1RF	N10.34391°, W085.34361°	N10.34387°, W085.34349°
2RF	N10.34392°, W085.34422°	N10.34337°, W085.34258°

RESULTS

We found several differences in the physical and chemical characteristics of the water and in the plant community between the Less Recently Fanguoeed (LRF) and Recently Fanguoeed (RF) sites. Water depth and dissolved oxygen (DO) were significantly lower at the RF site, while pH was significantly higher at the RF site (Table 2). Because time of day could affect temperature, we used an ANOVA, blocked by time of day, to test if water temperature differed between the LRF and RF sites (using R to accommodate un-

equal sample sizes). Water temperature was lower in the RF site than in the LRF site (ANOVA, $F_{1,37} = 4.64$, 37, $P = 0.04$).

Because water depth differed significantly between RF and LRF sites and could have confounded our site comparisons by affecting water chemical properties, we used analysis of covariance (ANCOVA) to test whether the significant differences in water properties between sites could be due to differences in water depth. Water depth did not significantly affect any of the variables except salinity. Salinity decreased with increasing depth in the RF site, but was not affected by depth in the LRF site ($F_{3,35} = 31.22$, $P < 0.0001$). The average salinity in the RF site was 0.74 ± 0.04 ppt and 0.50 ± 0.00 ppt in the LRF site. Because the relationship between water depth and salinity differed between the LRF and RF sites, we could not statistically compare salinity between sites.

We identified seven types of aquatic vegetation; thalia (*Thalia geniculata*), water hyacinth (*Eichhornia crassipes*), water fern (*Salvinia auriculata*), sedge (*Oxycaryum cubense*), grass (*Poaceae sp.*), “Boro Dormilón” (*Neptunia sp.*), and bladderwort (*Utricularia gibba*). Thalia and water hyacinth occurred less frequently in the RF site than in the LRF site (Table 3). Total percent plant cover and percent of the water column occupied by photosynthetic plant material were significantly higher at the LRF site (Fig. 1). Species richness, measured as the average number of species found per quadrat at each site, was significantly lower at the RF site (2.95 ± 0.31 species) than at the LRF site (5.11 ± 0.27 species) ($t_{37} = 5.17$, $P < 0.0001$).

TABLE 2. Water properties in Less Recently Fanguoeed (LRF) and Recently Fanguoeed (RF) sites in the marsh at Palo Verde National Park, Costa Rica. Results of two-tailed t-tests comparing the means of the LRF site and the RF site are in the right-hand column. Mean values ± 1 S.E. are shown. LRF: n= 19 quadrats (0.5 m x 0.5 m); RF: n= 20 quadrats (0.5 m x 0.5 m). See text for definition of *fanguoeo*.

Water Properties	Less Recently Fanguoeed (LRF)	Recently Fanguoeed (RF)	Two-tailed t-test results
Water Depth (cm)	43.50 \pm 1.72	29.79 \pm 2.45	$t_{37} = 4.54$, $P < 0.0001$
pH	7.50 \pm 0.06	7.69 \pm 0.06	$t_{37} = -2.30$, $P = 0.03$
Temperature (°C)	26.72 \pm 0.31	25.71 \pm 0.47	Used ANOVA
Dissolved O ₂ (mg/L)	6.08 \pm 0.64	2.99 \pm 0.38	$t_{37} = 4.21$, $P = 0.0002$

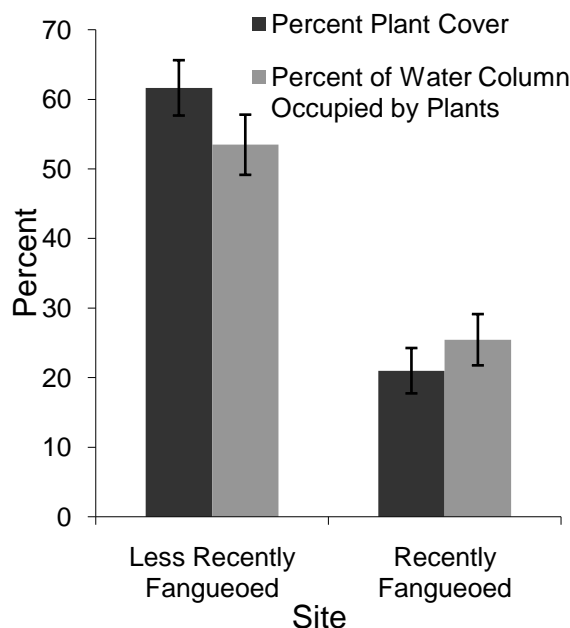


FIG. 1. Percent total plant cover and percent of water column occupied by photosynthetic plant material in the Less Recently Fungueoed site (LRF, fungueoed 2008 or 2009) and Recently Fungueoed site (RF, within 2 days of sampling), in the marsh at Palo Verde National Park, Costa Rica. For LRF, $n=19$ quadrats ($0.5 \text{ m} \times 0.5 \text{ m}$); for RF, $n=20$ quadrats ($0.5 \text{ m} \times 0.5 \text{ m}$). Both percent total plant cover ($t_{37} = 8.57$, $P < 0.0001$) and percent water column occupied by photosynthetic plant material ($t_{37} = -5.60$, $P < 0.0001$) were higher in the LRF site. See text for definition of *fungueo*.

TABLE 3. Percentage of $0.5 \text{ m} \times 0.5 \text{ m}$ quadrats containing the four most common plant species in a Less Recently Fungueoed (LRF) site and a Recently Fungueoed (RF) site in the marsh at Palo Verde National Park, Costa Rica, January 2010. RF: $n=20$ quadrats; LRF: $n=19$ quadrats. See text for the definition of *fungueo* and details of LRF and RF sites.

Plant Type	Less Recently Fungueoed (LRF)	Recently Fungueoed (RF)
Water Hyacinth	100%	50.0%
Water Fern	78.9%	90.0%
Thalia	84.2%	15.0%
Bladderwort	94.7%	85.0%

DISCUSSION

When compared to the Less Recently Fungueoed site, the Recently Fungueoed site had lower plant species richness, percent cover, and proportion of the water column occupied by photosynthetic plant material, indicating that the *fungueo* had an immediate effect on the plant community. The RF site

also had significantly altered chemical and physical water properties. Decreased dissolved oxygen in the RF site may lead to reduced primary productivity and ability to support aquatic organisms. Increased pH and decreased temperature and water depth in the RF site may harm organisms with a low tolerance for extreme conditions. The natural salinity-water depth gradient in the LRF areas may be altered by the *fungueo*. These alterations may affect the overall community composition of the marsh. Changes in the food web may have important conservation implications for the marsh birds that the Palo Verde National Park seeks to preserve.

Our findings are limited because we studied only one RF site and one LRF site, a small sample of the marsh. The implications of our study apply only to immediate effects of the *fungueo*, and future studies could investigate the long-term effects of the *fungueo*, and sections of the marsh that have not been *fungueoed*. Although the *fungueo* appears to control *T. domingensis*, Palo Verde National Park should consider the possible ecological costs of this management strategy.

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RESPONSE OF *PSEUDOMYRMEX SPINICOLA* TO CHEMICAL CUES SIMULATING HERBIVORY

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Faculty Editor: David R. Peart

Abstract: We examined the mutualistic relationship between *Pseudomyrmex spinicola* ants and their host plant, *Acacia collinsii*. We hypothesized that damaged *A. collinsii* would release chemical cues that induce a defensive response by *P. spinicola*. We predicted the ants would respond more aggressively to chemical cues released by damaged *A. collinsii* leaves than to those released by other tree species. We presented suspensions of ground leaves from *A. collinsii* and two other tree species to ants on *A. collinsii* and measured their response to each treatment. Ant response did not differ among treatments ($F_{3,51} = 0.08$, $P = 0.97$). Response decreased over time regardless of treatment ($F_{12,36} = 3.36$, $P = 0.002$), which may have reduced our power to detect differences among treatments.

Key Words: *acacia*, *ants*, *herbivore defense*, *mutualism*, *Palo Verde*

INTRODUCTION

Acacia collinsii has a mutualistic interaction with *Pseudomyrmex spinicola* in which the acacia provides food and shelter for the ants, and the ants defend the tree against herbivory and remove surrounding vegetation, thus reducing competition (Zuchowski 2005). The ants react aggressively when they detect volatile chemical cues released by damaged acacia leaves (Alexander et al. 2002). We tested the hypothesis that damaged acacia leaves release a specific chemical cue that elicits a response in *P. spinicola* and predicted that *P. spinicola* would respond more aggressively to cues released by damaged acacia leaves than to cues released by those of other plants.

METHODS

We compared ants' responses to chemical cues of damaged leaves from three tree species on 14 January 2010 from 0800 to 1400 at Palo Verde National Park, Costa Rica, 6 km southeast of Palo Verde Biological Station off La Carreta Road (location details in Wilson et al. 2004).

To simulate chemical cues released by leaves damaged by herbivory, we used a mortar and pestle to crush leaves of three species: *A. collinsii*, *Pithecellobium saman* and *Guazuma ulmifolia*. We mixed one gram of each sample of crushed leaves with 40 ml of water. We re-

frigerated these samples overnight and kept them on ice while we were in the field. We used water as a control, for a total of four solutions.

We haphazardly selected 52 well-foliated *A. collinsii* trees 2-5 m tall, at least 5 m apart, and inhabited by *P. spinicola*. We divided the trees into groups of four, and within each group we applied the four treatments in a random order. We applied each treatment to three equally spaced branches on one tree. Three people worked simultaneously to apply the treatment on each of the three branches. Each investigator selected a leaf approximately 0.5 m from the trunk that had at least 3 pairs of leaflets and pipetted 0.5 ml of the appropriate treatment onto the 3rd leaflet of the selected leaf. During a 4 min period, we counted the number of ants that crawled onto the leaf and passed the base of the second pair of leaflets.

RESULTS

Ants exhibited the same response to crushed acacia leaves, crushed leaves of other species, and water (one-way ANOVA blocked by time $F_{3,51} = 0.08$, $P = 0.97$). To assess changes in activity level, we conducted an ANOVA on $\ln(Y+1)$ transformed data. Ant activity declined through the day ($F_{12,36} = 3.36$, $P = 0.002$; Fig. 1).

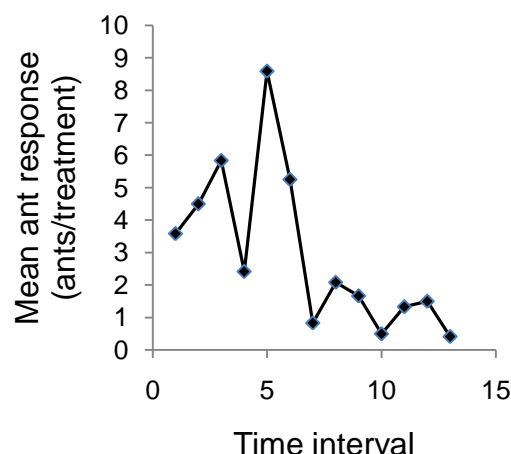


FIG. 1. Time trend of mean *P. spenicola* response (number crossing a designated point on an *A. collinsii* leaf) to plant chemical cues from damaged leaves recorded over six hours (0803 to 1400 hours) in Palo Verde National Park, Costa Rica. Each time interval represents one roughly 30 minute period.

DISCUSSION

Contrary to our prediction, *P. spenicola* did not respond more aggressively to chemical cues from *A. collinsii* leaf damage than to cues from damaged leaves of other species. This may indicate that the ants do not recognize a leaf-damage cue specific to *A. collinsii*, but rather respond to a cue common to all or many plant species. However, we draw this conclusion cautiously because ants have been shown to respond to acacia leaf damage chemical cues (Alexander et al. 2002), and in our study no more ants responded to the crushed acacia leaves treatment than to water. If we did not accurately simulate leaf damage due to herbivory, comparing ants' response to crushed acacia leaves to crushed leaves of other species may not be valid. Additionally, our treatments were kept overnight prior to use, and the chemical cues may not have been as strong as cues from freshly crushed leaves. Finally, ant activity decreased significantly over time (Fig. 1). As a result we may have had insufficient power to detect a difference between treatments.

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MALE AND FEMALE SCANNING IN HOWLER MONKEYS (*ALLOUATTA PALLIATA*)

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Abstract: *Allouatta palliata* live in male-dominated hierarchical troops. We conducted an observational study in Palo Verde National Park on two *A. palliata* troops. We hypothesized that *A. palliata* would scan and forage more in the morning and rest more midday, and that males would scan more than females. We found that males scanned more than females, possibly due to the fitness benefits of guarding their females against rival males.

Keywords: hierarchical social structure, howler monkeys, Palo Verde

INTRODUCTION

Allouatta palliata (mantled howler monkeys) live in troops of 2-25 with a hierarchical structure (Wainwright 2002). We hypothesized that *A. palliata* would alter allocation of time spent resting, scanning, and foraging throughout the day. We predicted that *A. palliata* behavior would change as temperature rises, with more scanning and foraging in the morning, more resting midday. In *A. palliata* troops all males are dominant to all females, and the dominant male mates with all females in the troop (Wainwright 2002). We predicted males would scan more than females, as males could potentially experience a severe fitness loss if a rival male were to become more dominant.

METHODS

On 13 January 2010 from 0600 to 1100, we observed a troop of *A. palliata* (Troop 1; 4 individuals) for ten 30 min sessions ca. 2 km NW of the OTS field station at Palo Verde National Park. The next day from 0630 to 1100, we observed Troop 2 (6 individuals) ca. 3 km E of the station and collected nine 30 min observation sessions. Each researcher observed a single *A. palliata* in each session and recorded the length of time foraging, resting, scanning, or traveling. We defined foraging as the active search for or consumption of food; scanning as the visual assessment of surroundings, including calling; resting as sleeping or sitting without scanning; and traveling as movement from one place to another, not

directly associated with feeding. At the start of a new session, each researcher observed an *A. palliata* individual different from the previous session. We recorded if the target individual was male, female, or female with infant. We defined infant as an individual that depended on its mother to travel.

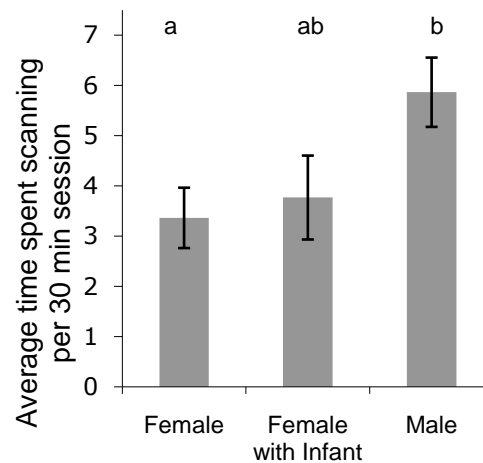


FIG. 1: The average time spent foraging during 30 min sessions ($n = 66$) for two troops of *A. palliata* in Palo Verde ($F_{2,63} = 3.99$, $P = 0.02$). Error bars are ± 1 S.E. Different letters above bars indicate significant differences.

RESULTS

Males spent significantly more time scanning than females but not significantly more time scanning than females with infants (Fig. 1). Males, females, and females with infants did not differ in time spent foraging ($F_{2,63} = 0.04$, $P = 0.97$), resting ($F_{2,63} = 0.17$, $P = 0.84$) or traveling ($F_{2,63} = 0.68$, $P = 0.51$). Data points from time session eight on the first day were outliers by the 1.5*IQR Rule and were

excluded from the analysis. During this time we observed a dominance interaction between the focal troop and a neighboring troop, and we believe that the activities recorded did not represent frequently observed *A. palliata* behavior.

As the day progressed, *A. palliata* devoted significantly less time to resting ($r^2_{65} = 0.07$, $P = 0.04$) and more time to scanning ($r^2_{65} = 0.10$, $P = 0.01$). The time spent foraging or traveling did not change over time (Foraging: $r^2_{65} = 0.01$, $P = 0.45$; Traveling: $r^2_{65} = 0.03$, $P = 0.15$).

DISCUSSION

Males may invest more time scanning than females to reduce the chance of a rival male taking over the troop. On day 1 we observed a dominance interaction between Troop 1 and a rival troop where the dominant males exchanged aggressive calls. Following the interaction, the dominant male from the rival troop mated with an adult female from Troop 1. All females and infants from Troop 1 joined the neighboring troop, rejecting the dominant male from Troop 1. This interaction shows the potential repercussions of losing a dominance interaction, indicating the importance of male scanning behavior. Females with infants also invest time in scanning for cats, weasels, snakes, and eagles that prey on young (Wainwright 2002).

Throughout the day, resting decreased, and scanning increased, suggesting that there may be a greater chance of encountering predators or rival troops as the day progresses. Future studies would benefit from observing *A. palliata* for a longer time period to document how behaviors change over the course of the day.

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WINGBEAT FREQUENCY IS RELATED TO FORAGING STRATEGIES OF HUMMINGBIRDS AT MONTEVERDE, COSTA RICA

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Abstract: Hummingbirds practice different foraging strategies that may influence natural selection on traits related to flight mechanics. We predicted that territorial hummingbirds that rely on high speed and maneuverability would have the highest wingbeat frequencies (relative to body mass). Trapline-feeding hummingbirds that fly longer distances may have lower wingbeat frequencies than territorial species. We recorded wingbeat frequencies of eight species of hummingbirds at the Hummingbird Gallery at Monteverde, Costa Rica. As predicted, territorial species had higher wingbeat frequency to mass ratios than trapline feeders.

Key Words: flight energetics, territorialism, traplining

INTRODUCTION

The diverse foraging strategies and energetically costly nature of hummingbird flight places a premium on flight mechanics. Territorial species defend and feed on a clump of flowers. This energetically expensive behavior requires high speed and maneuverability but is rewarded with a rich, consistent source of nectar (Feinsinger and Colwell, 1978). Traplining species forage on a circuit of multiple undefended flowers, which requires flight over longer distances (Feinsinger and Colwell, 1978). Generalists exhibit a mixture of territorialism and traplining (Feinsinger and Colwell, 1978). Because territorial and trapliners have different flight needs, we expected them to have different flight mechanics. Wing-disc loading (WDL), the ratio of body weight to area swept out by the wings during one wing beat cycle, does not differ between territorial and traplining hummingbirds (Feinsinger and Chaplin, 1975; Altshuler et al., 2004). Wingbeat frequency (WBF), the number of wingbeats per second, decreases with increasing body size, but little is known about whether WBF differs according to foraging strategy. We predicted that territorialists would have a higher WBF to body mass ratio than trapliners because higher WBF may increase flight maneuverability (Feinsinger and Chaplin, 1975) and lower WBF may allow

birds to conserve energy during long distance flight.

METHODS

We observed hummingbirds at the Hummingbird Gallery near the entrance of the Monteverde Cloud Forest Reserve at Monteverde, Costa Rica on January 21 and 22, 2010. The Gallery is a patio ca. 8 x 30 m, with a dozen hummingbird feeders, surrounded by forest trees. We recorded the stationary hovering flight of eight species of hummingbird (Appendix 1). All recordings were made with a 22" Telinga parabola with a Sennheiser ME62 microphone running on a K6 power module and a Marantz 661 solid state digital recorder sampling at 24 bits and 96kHz. Because of its consistency and ease of recording, we used hovering flight as a proxy for the WBF of general flight. Male and female Purple-throated Mountain-gems (*Lampornis calolaema*) were considered separate "species" for this study because they have different foraging strategies (Appendix 1). We extracted wing beat frequency (WBF = no. of beats/ sec) using Raven Lite 1.0 acoustic analysis software (Cornell University). We excluded observations that were statistical (box plot) outliers within groups, as defined by JMP 8, and observations for which the bird's mass was unavailable. Given the acoustic interference in some samples, we removed outliers because

of the chance of missed wing beats and misleading noise. This left 155 usable observations. We could not ensure independence because birds were not individually marked. Average bird mass and foraging strategy were assigned to species based on the consensus of at least three sources in the literature (from Feinsinger et al. 1979, Feinsinger and

Colwell 1978, Stiles and Skutch 1989, Fogden 2005). We designated species as trapliners or territorialists if three sources agreed (Appendix 1). We designated species as generalists if sources conflicted or stated that the birds employed mixed strategies. We calculated WBF-to-mass ratios by dividing the WBF of each individual by the literature value for its mass.

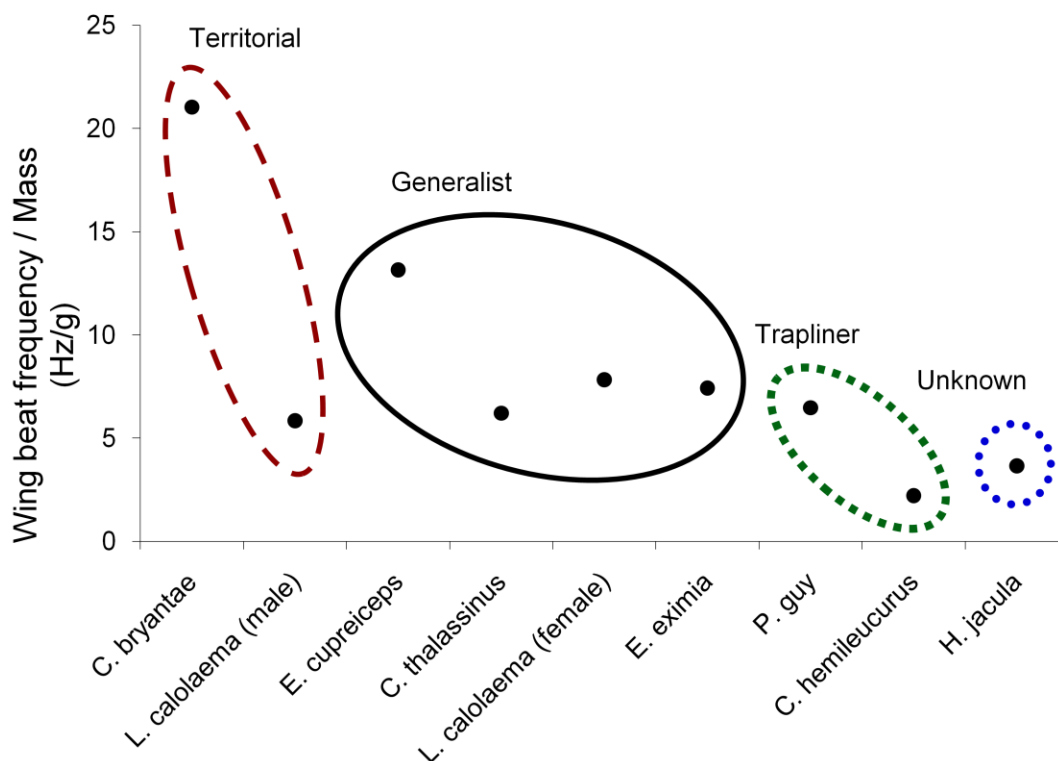


FIG. 1. Wing beat frequency to mass ratios (mean \pm 1 S.E.; bars barely visible) for eight species of tropical cloud forest hummingbirds, grouped by foraging strategy, using information from the literature (Appendix 1). Wing beat frequencies based on 155 recordings at 12 outdoor feeders at the Hummingbird Gallery at Monteverde, Costa Rica. Hz = Hertz (cycles per second).

RESULTS

Based on the 155 recordings of the eight species of hummingbirds, species differed in WBF to mass ratio (ANOVA $F_{8,146} = 2186.84$, $P < 0.0001$). Territorial birds had a higher WBF/ mass ratio than trapliners (Linear Contrast 1: Territorial vs. Trapliner, $F_{1,146} = 5440.75$, $P < 0.0001$; Fig. 1). The species with an unknown foraging strategy (*H. jacula*) had a lower WBF/ mass ratio than the generalists

(Linear Contrast 2: Generalist vs. Unknown, $F_{1,146} = 1121.67$, $P < 0.0001$; Fig. 1).

DISCUSSION

As expected, territorialists' hovering WBF/ mass ratios were 4X higher than those of trapliners (Fig. 1), suggesting that selective pressures on trapliners to conserve energy while flying may have resulted in lower WBF/ mass and that pressures on territorial for high maneuverability may have resulted in higher WBF/ mass.

When little is known about a species' life history, a simple measure of WBF may offer insights into their foraging strategy. To our knowledge, the Green-crowned Brilliant's (*Heliodoxa jacula*) foraging strategy is uncharacterized. Based on our findings, *H. jacula*'s WBF/ mass ratio suggests that they are trapliners. However, this was contrary to our anecdotal observations that they tended to dominate heterospecific interactions at feeders.

Species diverging from the relationship we found between WBF/ mass and foraging strategy may have different selective pressures shaping their flight energetics. For example, annual migratory distance (including elevational migration) may represent a stronger selective pressure on flight energetics than daily foraging patterns. Also, some birds use other foraging strategies than the three we considered, and some use more than

one strategy in different environments, (e.g. the Green Violetear (*Colibri thalassinus*) is a trapliner at 1400 m elevation but territorial at 3100 m; Feinsinger, et al. 1979). It may be difficult to resolve differences in WBF/ mass ratio based on foraging strategy for these birds, as their wing morphology must allow for these various strategies.

Previous studies have focused on whether WDL can predict foraging strategy (Feinsinger and Chaplin 1975, Altshuler 2004); yet, little is published about the relationship between foraging strategy and WBF/ mass ratio, which is another index of energy expenditure during flight. Our findings suggest that WBF/ mass ratio may be a valuable predictor of hummingbird foraging strategy. We speculate that evolved differences in WBF may confer advantages to hummingbirds of a given body size utilizing different foraging strategies.

APPENDIX 1

TABLE 1. Hummingbird species observed at the Hummingbird Gallery at Monteverde, Costa Rica. N refers to number of audio recordings of each species and sex included in analysis. Sources are 1 = Feinsinger et al. 1979; 2 = Feinsinger and Colwell 1978; 3 = Stiles and Skutch 1989; 4 = Fogden 2005.

Species	Sex	N	Mass (g)	Source	Foraging Strategy	Source
Green Hermit (<i>Phaethornis guy</i>)	M/F	14	5.16	1	trapliner	4
Violet Sabrewing (<i>Campylopterus hemileucurus</i>)	M	19	11.22	2	trapliner	4
Green Violetear (<i>Colibri thalassinus</i>)	M/F	11	5.24	2	generalist	2
Coppery-headed Emerald (<i>Elvira cupreiceps</i>)	F	2	3.02	2	generalist	2
Coppery-headed Emerald (<i>Elvira cupreiceps</i>)	M	24	3.22	2	generalist	2
Stripe-tailed Hummingbird (<i>Eupherusa eximia</i>)	M	9	4.48	2	generalist	2
Purple-throated Mountain-gem (<i>Lampornis calolaema</i>)	F	7	4.23	2	generalist	2
Purple-throated Mountain-gem (<i>Lampornis calolaema</i>)	M	31	5.6	2	territorialist	2
Magenta-throated Woodstar (<i>Calliphod byrantae</i>)	M	19	3.31	2	territorialist	2
Green-crowned Brilliant (<i>Heliodoxa jacula</i>)	F	11	8	3	unknown	
Green-crowned Brilliant (<i>Heliodoxa jacula</i>)	M	8	9.5	3	unknown	

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HERBIVORE DAMAGE INCREASES SURFACE WATER RETENTION ON CLOUD FOREST LEAVES

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Faculty Editor: David R. Peart

Abstract: Many plants in wet climates have adapted to shed water efficiently from leaves with a long narrow “drip tip.” We hypothesized that herbivory would reduce the ability of leaves to shed water, which can decrease photosynthesis and transpiration and create a hospitable environment for epiphylls. To test this hypothesis we collected paired leaves from the Begoniaceae and Piperaceae families and simulated herbivory on half of the leaves, using a hole punch. On some of the Piperaceae leaves, we cut off the drip tip to mimic leaves without drip tips. Herbivory increased surface water retention on all leaves, whether intact or with drip tips removed, probably by disrupting water flow to the drip tip. In wet environments, the decreased water-shedding capacity of herbivore-damaged leaves may result in costs of herbivory beyond simple tissue loss.

Key Words: *drip tips, Monteverde, plant morphology, water shedding*

INTRODUCTION

Water accumulation on leaf surfaces has negative effects on plant growth by reducing transpiration via lowering temperature, reducing photosynthesis by reflecting sunlight, and improving conditions for epiphyll and fungal colonization (Dean and Smith 1978). Plants in wet environments have morphologically adapted to high precipitation by developing long, narrow tips (“driptips”) for rapid water shedding (Bein et al. 2009). We hypothesized that herbivore damage would increase surface water retention by increasing ratio of leaf edge area to surface area. Water may accumulate around the edges created by herbivore damage, due to water’s cohesive and adhesive properties, reducing the effectiveness of drip tips in drawing water downwards. We also predicted that herbivory would have a greater impact on water shedding by plants with drip tips, compared to plants without drip tips, because drip tip plants might rely more heavily on their structure to shed water efficiently.

METHODS

We gathered pairs of leaves from Begoniaceae and Piperaceae families and manipulated one from each pair to mimic herbivory and test the water retention of leaf surfaces.

We conducted this study from January 20-22, 2010 in the cloud forest near the Estación Biológica de Monteverde, Costa Rica along the Sendero Principal trail. We collected leaves by taking a random number of steps (1-9) and then skipping a random number of suitable Begoniaceae or Piperaceae plants (1-9). For each selected plant, we collected two leaves of similar size and shape, with minimal herbivory present. If no such pair of leaves was present, we selected the next plant. We collected 34 Begoniaceae and 63 Piperaceae leaf pairs.

We simulated herbivore damage with eight randomly located punched holes on one leaf of each pair. For 25 of the Piperaceae pairs, we cut off the drip tips to make a smooth rounded edge. We took the dry mass of each leaf and placed it on two straightened paper clips extending from a windowsill at a 20° angle below horizontal. We sprayed each leaf ten times with a spray bottle. The wet leaf was then weighed 5 sec after spraying. We measured the upper surface area of each leaf by tracing the leaf onto graph paper and counting the graph paper squares. We calculated surface water retention by subtracting dry mass from wet mass. We normalized the data by log_e transforming surface water retention per unit leaf area.

RESULTS

We conducted a paired t-test to test the effect of herbivory on leaf surface water retention. Leaves with herbivore damage retained significantly more water per unit leaf area than undamaged leaves (pooled sample of

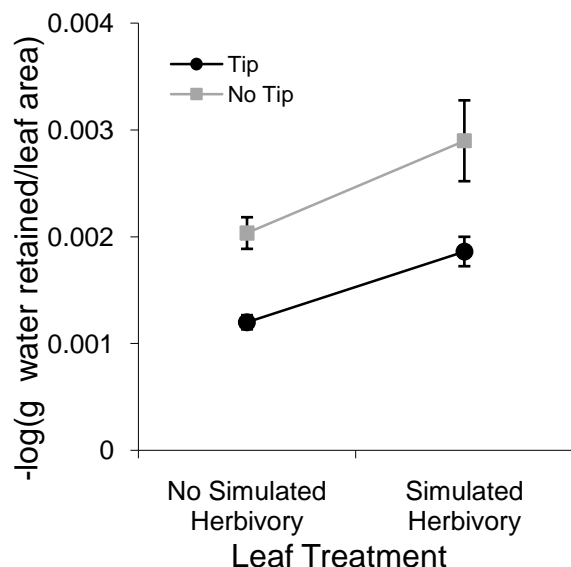


FIG. 1. Paired-sample comparison of surface water retention of Begoniaceae and Piperaceae leaves with and without simulated herbivory. Water retention measured as wet mass (5 sec after saturation) - dry mass. 72 leaf pairs were collected from cloud forest near Monteverde, Costa Rica on January 20-22, 2010. Error bars represent ± 1 S. E.

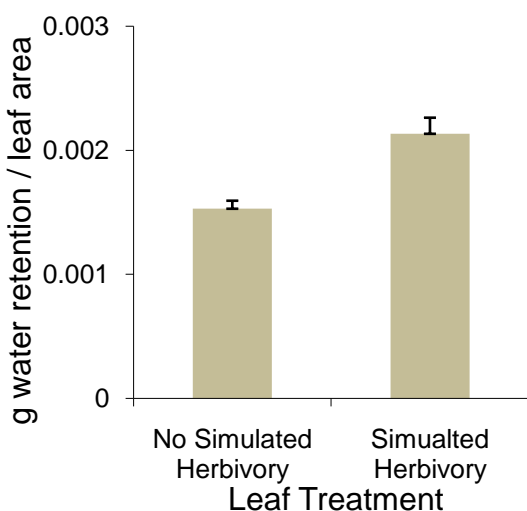


FIG. 2. Effect of simulated herbivory on surface water retention on Piperaceae leaves with and without drip tips removed. Water retention measured as wet mass (5 sec after saturation) - dry mass. 63 leaf pairs were collected from cloud forest near Monteverde, Costa Rica on January 20-22, 2010. Error bars represent ± 1 S.E.

Piperaceae and Begoniaceae with drip tips intact; paired $t_{71} = 6.57$, $P < 0.0001$; Fig. 1). This effect was significant when tested separately for Begoniaceae (paired- $t_{33} = 2.98$, $P = 0.0054$), Piperaceae (paired- $t_{37} = 6.46$, $P < 0.0001$), and Piperaceae with drip tips removed (paired- $t_{24} = 3.81$, $P = 0.0008$). We also conducted a 2-way ANOVA to test the effects of herbivory and drip tip removal. We found a significant main effect of herbivory ($F_{1,122} = 18.86$, $P < 0.0001$) and drip tip removal ($F_{1,122} = 37.56$, $P < 0.0001$), but no interaction ($F_{1,122} = 0.66$, $P = 0.42$; Fig. 2). For all leaf types, surface water retention decreased with leaf size (linear regression; $r^2_{192} = 0.17$, $P < 0.0001$).

DISCUSSION

As hypothesized, herbivory increased surface leaf water retention. The effect of herbivory on water retention was not dependent on drip tips and apparently depended only on the ratio of plant edge area to total surface area.

This was consistent with our results showing that smaller leaves with inherently larger edge area to surface area ratios had greater surface water retention per unit area. Thus, in addition to the direct loss of biomass, herbivory in wet environments increases surface water retention, with negative consequences to plants (Dean and Smith 1978). Herbivory in specific locations, along veins or in the center of the leaf, may have a larger impact on water-shedding capability. We suggest that plants in wet environments may need to invest more in herbivore defense because of this added cost of herbivory.

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BEHAVIORAL THERMOREGULATION IN AN UNIDENTIFIED SPECIES OF BUTTERFLY (NYMPHALIDAE) IN A CAPTIVE ENVIRONMENT

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Faculty Editor: David R. Peart

Abstract: Butterflies thermoregulate with a variety of behaviors to maintain thoracic temperature. We studied an aggregation of an unidentified species of Nymphalidae in the cloud forest at Monteverde, Costa Rica. We investigated whether nymphalid butterflies practice behavioral thermoregulation. The incidence of several behaviors changed with temperature, including shivering, basking and flying.

Key Words: butterflies, flight, Monteverde National Park, temperature variation

INTRODUCTION

Butterflies must maintain high thoracic temperature to sustain flight, since flying decreases thoracic temperature by expending heat. However, too high a thoracic temperature is lethal (Heinrich 76). Butterflies regulate thoracic temperature through behaviors such as basking or shivering to generate heat, and flying or wing flapping to expend energy and lower thoracic temperature (Clench 1966). We hypothesized that an unknown species of butterfly, in the Nymphalidae family, would exhibit similar thermoregulatory behaviors. We predicted that individuals would fly and flap wings in warm temperatures and bask and shiver in cool temperatures.

METHODS

On the afternoon of 21 January 2010, we collected 26 individuals from an aggregation of Nymphalidae butterflies on the side of a bank 100 m from the Estación Biológica in Monteverde, Costa Rica. We housed the butterflies in a 38 cm x 85 cm cylindrical soft mesh butterfly cage, kept in forest shade to reduce temperature fluctuations.

To test the behavioral response of the butterflies to temperature, we observed them in the driveway outside the Estación Biológica at four times (1500 and 1900 on 21 January 2010 and 0755 and 1110 on 22 January 2010). We allowed them to acclimate for 5 min before observation. Using a BAT 12 thermistor,

we measured the temperature at the bottom and top of the cage and used the average of the two in our analysis.

We counted the number of butterflies engaged in each of four different behaviors (basking, shivering, flapping, and flying) every minute for 10 min. Additionally, we counted the number of butterflies not engaged in active thermoregulation, which we classified as resting. Butterflies were considered to be resting if they were perched on the mesh with wings folded perpendicular to the mesh, basking if wing surfaces were orientated toward sunlight, shivering if their bodies were shaking, flapping if they were slowly opening and closing their wings, and flying if they fluttered from perch to perch in the cage.

RESULTS

The proportions of behaviors changed with temperature ($\chi^2_{12} = 22.52$, $P = 0.03$).

We conducted a logistic regression to test for behavioral changes at different temperatures. Because these proportions were not independent of one another, and we analyzed the same data set multiple times, we applied a Bonferroni correction to our alpha value. We observed significant decreases in shivering ($r^2_{42} = 0.28$, $P = 0.0001$) and basking ($r^2_{42} = 0.32$, $P = 0.0001$), and a significant increase in flying ($r^2_{42} = 0.34$, $P = 0.0002$), with increasing temperature. We observed no significant relationships between resting ($r^2_{42} = 0.003$, $P = 0.71$) or flapping ($r^2_{42} = 0.029$, $P = 0.27$) and

temperature.

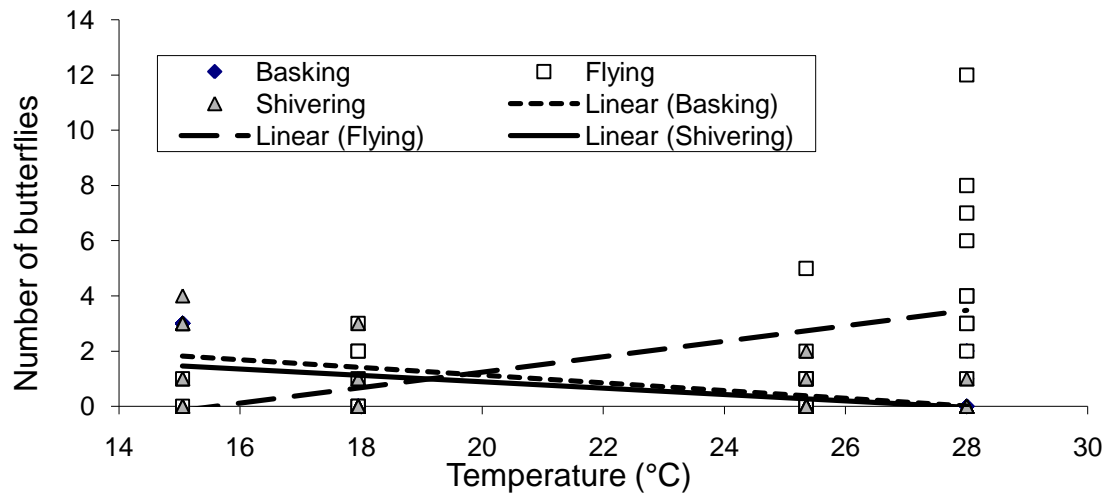


FIG. 1. Number of butterflies performing thermoregulatory behaviors at given temperatures. We observed 26 butterflies in a 38 cm x 85 cm butterfly cage. We counted the numbers of butterflies performing each behavior every minute for 10 minutes at four different temperatures.

DISCUSSION

Our results support the hypothesis that butterflies display thermoregulatory behaviors at different temperatures, and we observed the predicted patterns in basking, shivering and flying (Fig. 1). This may demonstrate that Nymphalidae butterflies exhibit classic behavioral thermoregulation.

We did not find a relationship between flapping wings and temperature change. This may be because it was difficult to distinguish between flapping and preparing for flight.

Although our results were significant, our small sample size and the unnatural cage setting may have affected our results. Furthermore, we could not identify the butterfly species, and thus were unable to compare our results to other studies on this species.

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EPIPHYTE COVER AND PHYSIOGNOMY INCREASES WITH ELEVATION IN THE MONTEVERDE CLOUD FOREST

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Faculty Editor: David R. Peart

Abstract: Epiphytic plants are limited by water availability. Moisture in the Monteverde cloud forest in Costa Rica increases with elevation and we hypothesized that epiphyte communities at higher elevations would have higher abundance and greater diversity of growth forms. We recorded the species present and measured their abundance along an elevation gradient from 1520 m to 1785 m, just below the Continental Divide. Epiphyte percent cover, species richness, and diversity increased with elevation, independent of tree size.

Key Words: altitude, bryophyte, Costa Rica, moss

INTRODUCTION

Epiphytes are polyphyletic growth forms that rely on other plants for support but not for water or nutrients. They play a central role in cloud forest nutrient dynamics (Nadkarni 1984). Because epiphytes often grow on vertical surfaces, water availability is the most important factor limiting growth (Zotz and Heitz 2001).

Trade winds hit the Atlantic side of the Monteverde ranges and cool as they rise, condensing into clouds and dropping moisture (Clark et al. 2000). Some clouds pour over the divide and lose cloudwater on impact with vegetation as they descend on the drier Pacific side, generating a moisture gradient with gradually drier conditions down the Pacific slope.

Thus, we predicted that epiphyte communities would have greater percent cover, number of species, and diversity on trees at progressively higher elevations on the Pacific side.

METHODS

On 21 and 22 January, 2010, we sampled trees in the neotropical cloud forest around the Monteverde Biological Station along the Sendero Principal from 1520 m (150 m NE of the station) to 1785 m elevation (just below the Continental Divide). Along the trail, we sampled two trees (the first eligible tree on

each side of the trail) for every 10 m increase in elevation ($n = 51$). Eligible trees were 10–75 cm in circumference, accessible from the trail, and with trunks angled $< 45^\circ$ from vertical.

For each tree, we collected data along circumferential transects at 1 m and 1.5 m above ground. On each transect, we measured tree size (circumference) and epiphyte coverage (percent of transect covered by plant morphotype: bryophytes, ferns, orchids, bromeliads, fungus or other). We also counted the number of epiphyte morphotypes in the area between the two transects.

We calculated Simpson's index of diversity for each transect, using the percent cover of each plant morphotype, and calculated the average Simpson's Index and average circumference for each tree.

RESULTS

Epiphyte diversity (Fig. 1), percent cover, and species richness all increased with elevation (percent cover: $r^2_{49} = 0.18$, $P = 0.002$; species richness: $r^2_{49} = 0.18$, $P = 0.002$).

All three variables also increased with tree size (diversity: $r^2_{49} = 0.13$, $P = 0.008$; percent cover: $r^2_{49} = 0.18$, $P = 0.002$; species richness: $r^2_{49} = 0.22$, $P = 0.0004$). However, tree size was not correlated with elevation ($F_{49} = 0.87$, $P = 0.35$), and there was no interaction between tree size and elevation (diversity: $F_{37} = 0.42$, $P = 0.90$; percent cover: $F_{47} = 7.20$, $P = 0.84$; species richness: $F_{37} = 8.74$, $P = 0.70$). Be-

cause our response variables did not co-vary with tree size and elevation, we can discuss the epiphyte relationship with elevation.

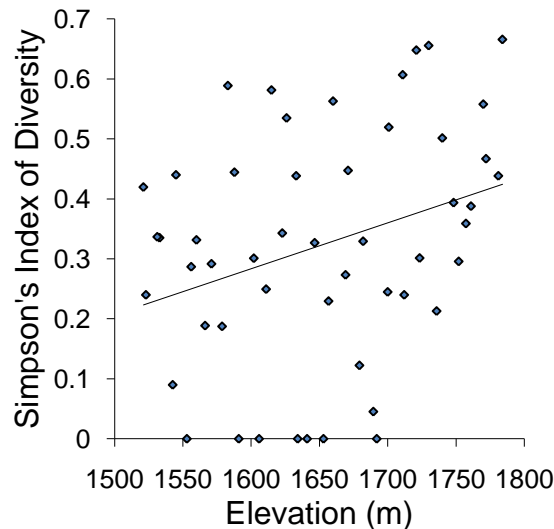


FIG. 1. Relation between epiphyte Simpson's Index of Diversity on tree stems and elevation on the Pacific slope 1520-1785 m in the Monteverde cloud forest, Costa Rica (linear regression, $r^2_{49} = 0.10$, $P = 0.03$, $n = 51$ trees).

DISCUSSION

On the Pacific slope of the Monteverde cloud forest, epiphyte communities became more diverse and abundant with increasing elevation, linked to increasing moisture. Our results cannot be applied to other forest ecosystems, where elevation may have a different relationship with water availability. In addition, moisture in the Monteverde cloud forest may vary seasonally (Clark et al. 2000) and future studies would benefit from measuring moisture directly instead of assuming a relationship with elevation.

Changes in moisture gradients, a potential result of climate change, may alter both the geographic distribution and overall health of epiphyte communities.

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ABUNDANCE OF MACROINVERTEBRATES IN DEBRIS DAMS AND ROCK RIFFLES IN A FIRST-ORDER TROPICAL STREAM

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Faculty Editor: David R. Peart

Abstract: We investigated the importance of debris dams and rock riffles as macroinvertebrate habitats. Using a kick net, we collected macroinvertebrates from above and below debris dams and rock riffles in a tropical stream. We found more macroinvertebrates and higher dissolved oxygen in rock riffles than in debris dams. Our results suggest that debris dams may be less important as macroinvertebrate habitats in the Quebrada Máquina stream, Monteverde, than in most temperate streams.

Keywords: detritus-based food webs, Monteverde cloud forest, Quebrada Máquina

INTRODUCTION

Debris dams (sources of detritus) are productive habitats for macroinvertebrates in temperate streams (Malone 2008), but this relationship is less clear in the tropics (Mathuriau 2008). We sampled stream macroinvertebrates in two habitats, debris dams and rock riffles, both of which provide shelter for invertebrates and interrupt the flow of water, but which vary in structure, stream flow, and detritus buildup. We hypothesized that the average number of macroinvertebrates would differ between debris dams and rock riffles in a tropical stream. Testing for differences between these habitats may clarify the role of debris dams as habitats for macroinvertebrates in tropical streams.

METHODS

We collected stream macroinvertebrates from above and below five debris dams and five rock riffles in Quebrada Máquina, a first-order stream at Monteverde Biological Station, Costa Rica on 21–22 January 2010. We started sampling at the site farthest downstream by collecting below and above a debris dam or rock riffle. Sample sites were ≥ 10 m apart. We collected debris and macroinvertebrates in a 20 cm wide kick net by disturbing the substrate with our feet for 5 sec 0.5 m upstream from the net. We measured dissolved oxygen using a YSI ProODO meter 0.5 m up-

stream of the kick net.

For analysis we pooled invertebrate abundances from above and below the habitat (rock riffles or debris dams) at each site. We compared the mean invertebrate abundances and mean dissolved oxygen between debris dams and rock riffles using JMP 5 statistical analysis software to compute 95 % confidence intervals, which were used to assess difference between debris dams and rock riffles.

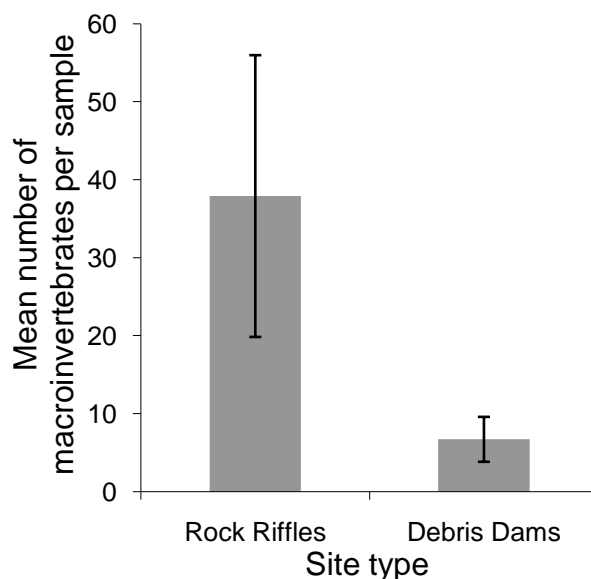


FIG. 1. Mean number of macroinvertebrates caught in kick nets after 5 sec of substrate disturbance above and below rock riffles and debris dams in Quebrada Máquina, a first-order stream in Monteverde, Costa Rica (N = 10). Samples above and below were pooled for each habitat. Bars are means with 95% confidence intervals.

RESULTS

We found significantly more macroinvertebrates (Fig. 1) and higher dissolved oxygen (Fig. 2) in rock riffles compared to debris dams.

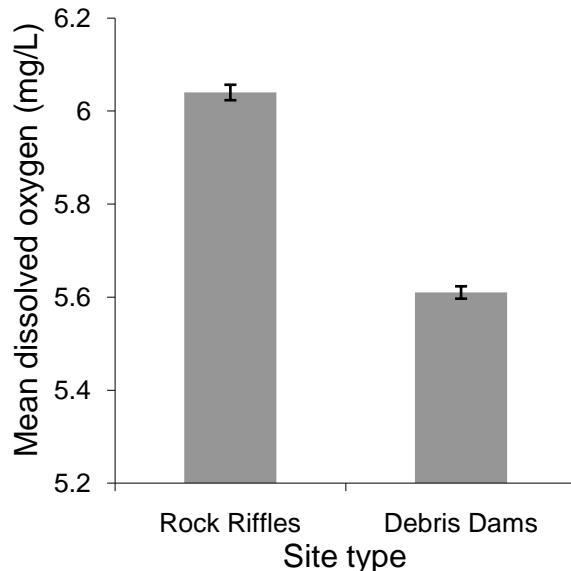


FIG. 2 Dissolved oxygen (mg/L) measured above and below in rock riffles and debris dams in Quebrada Máquina, a first-order stream in Monteverde, Costa Rica (N = 10). Samples above and below were pooled for each habitat. Bars are means with 95% confidence intervals.

DISCUSSION

Contrary to studies on temperate streams (Malone 2008), our results suggest that debris dams in tropical streams are not productive habitats for macroinvertebrates. Because of higher allochthonous inputs in the tropics, detritus may not be a limiting resource in tropical streams (Mathuriau 2008); habitat quality (in terms of dissolved oxygen or substrate structure) may dominate in determining macroinvertebrate abundance in tropical streams. Dissolved oxygen was lower near debris dams than rock riffles, possibly due to the slower flow rate or the consumption of oxygen by decomposing organic matter in debris dams. We sampled debris dams in the

afternoon and rock riffles in the morning, so the difference in dissolved oxygen could have been temperature driven.

A major limitation of our study was the lack of precision in kicknet sampling. Stream flow rate and looseness of substrate likely affected the number of organisms caught in the kick net. We observed that kick netting near debris dams trapped more substrate, so any sampling bias may have increased abundances in our debris dam samples; however, this bias was not reflected in the data. Our conclusion of greater abundances in rock riffles is therefore robust to potential sampling bias. Taylor et al. (2001) suggest electroshocking invertebrates for more precise, quantitative samples. Based on our results in Quebrada Máquina, debris dams were not favorable habitats for macroinvertebrates and may be lowering the overall abundance of macroinvertebrates in streams.

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HOT POLLINATORS: THE THERMAL REWARD SYSTEM OF *ZANTEDESCHIA AETHIOPICA*

JANEL L. DiBICCARI, ALEXANDER R. DUCKLES, MOLLY E. GREAR, ERIN I. LARSON, SARAH M. YU

Faculty Editor: Matthew P. Ayres

Abstract: Flowers can increase their internal temperature by focusing and retaining solar energy, which may increase pollination because arthropods are more active at higher temperatures. Alternatively, arthropods may remain on warm flowers longer (to the detriment of pollination services) because of the thermal rewards. We observed arthropod visitation on 16 *Zantedeschia aethiopica*, eight with artificial shade treatments, and classified each floral structure as warm or cool, based on whether it was higher or lower than ambient temperature. More arthropods visited warm floral structures, and arthropods stayed longer on cool floral structures. The increased visitation rate of insects is likely beneficial to *Z. aethiopica* pollination; however it is still unclear whether this is a result of an evolved thermal reward or a coincidental result of increased insect activity at increased temperatures.

Key Words: calla lily, Cerro de la Muerte, Crysomelidae, Cuericí, pollination

INTRODUCTION

All flowers heat up in the sun because of their thermal mass, but internal temperature can be increased further through structural components (Cooley 1995). *Zantedeschia aethiopica* (calla lilies), in particular, have a parabolic shape, which appears to focus heat in the center of the bract. This internal increase in temperature could be non-beneficial, or could aid in pollen development, seed development, or attracting pollinators (Gallen and Stanton 2003). In cold habitats, arthropod pollinators are limited in their activity by low environmental temperatures (Block 1990). Flowers could thus attract pollinators by providing a thermal reward. In that case, arthropods might remain on warmer flowers longer because it is a favorable microhabitat (which is not necessarily in the interests of the plant) or they might leave the flower more readily because the warmth permits them to fly away. We tested these possibilities through a combination of observations and experiments.

METHODS

On 29 January 2010 we conducted a pilot study to see which flowers surrounding the Cuericí Biological Station in Cerro de la Muerte, Costa Rica exhibited high internal temperatures relative to ambient. We measured

the internal flower temperature and shaded ambient temperature for five individuals each of five common species. We selected *Z. aethiopica* as our focal flower species because its internal floral temperature was the greatest compared to the ambient temperature.

We observed 16 randomly selected *Z. aethiopica* floral structures in a patch located approximately 0.5 km east of the Cuericí Biological Station during the day on 30 January 2010. Cuericí is a high altitude site located on the continental divide, with ambient temperature dependent on sunlight availability. We randomly selected eight of the floral structures for our shade treatment, which consisted of magnolia and calla lily leaves configured to shade the floral structure throughout the day and create an artificial temperature gradient. The remaining eight floral structures received direct sunlight. For our analysis, we classified floral structures depending on whether their internal floral structure temperature was higher (“warm”) or lower (“cool”) than shaded ambient temperature.

We conducted 30 minute observations every hour from 0630 to 1530, observed the arthropods (“visitors”) that landed on the floral structure, and recorded the duration of their stays. We also recorded the internal floral temperature of each floral structure with a Raytek™ infrared temperature sensor, which measures temperature at a distance of ~0.5 m,

and its external ambient temperature with a Sensortech Bat-12 Type T thermocouple twice during each 30 minute time period. We used survival analysis to determine whether the duration of visits on the floral structures differed between the cool and warm categories and used a Wilcoxon/ Kruskal-Wallis rank sums test to determine if the number of visitors differed between the cool and warm floral structures.

We conducted a census of the distribution of the Chrysomelidae population on 31 January 2010 to determine whether the beetles were moving away from *Z. aethiopica* plants throughout the day. Chrysomelidae are leaf-beetles, between 0.5 and 1 cm in length and feed on plant tissue (Borror and DeLong 1964). We assigned each of the 144 floral structures in the patch a number and counted the number of Chrysomelidae present on each floral structure every two hours from 0730 to 1330. We calculated turnover rate as the difference in beetle concentration on each floral structure between time periods.

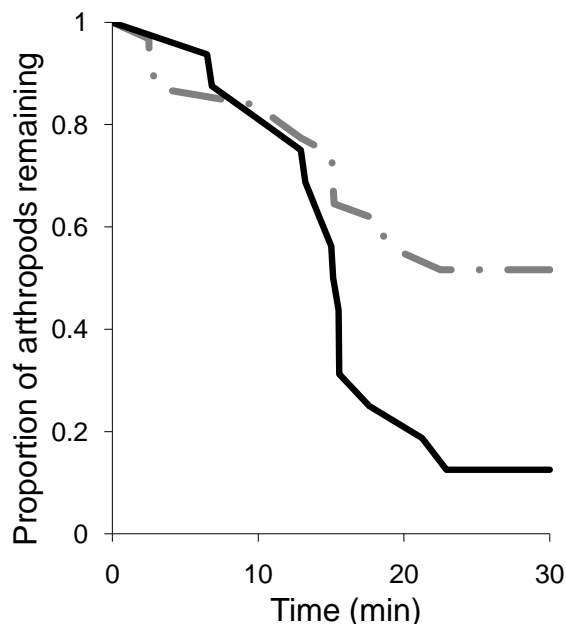


FIG. 1. Proportion of arthropods remaining on cool (colder than ambient, grey dashed line) and warm (warmer than ambient, black solid line) *Z. aethiopica* ($\chi^2_1 = 5.83$, $P = 0.02$) using a survival analysis at Cuerici Biological Station, Costa Rica on 30 January 2010.

RESULTS

Arthropods visited warm *Z. aethiopica* more often than cool *Z. aethiopica* (median = 2 vs. 1 individuals, $\chi^2_1 = 12.45$, $P < 0.01$). Arthropods stayed longer on cool *Z. aethiopica* than on warm *Z. aethiopica* (Fig. 1), often entering the floral structures and remaining on the bract for the rest of the observation period. Some arthropods stayed only on the edge of the floral structure, while Chrysomelidae, which represented 49.8% of all arthropods, were found to be more concentrated towards the base of the floral structure, occasionally crawling up and down the spadex.

Chrysomelidae relocated between floral structures consistently throughout the day (average turnover per 2 hr sampling period = 119, average number of beetles during 2 hr sampling period = 110).

DISCUSSION

By increasing the average number of visits and decreasing the average duration of each visit, a higher internal temperature greatly increased the rate of arthropod visitation. Chrysomelidae, which we observed most frequently on *Z. aethiopica*, showed consistently high turnover rates throughout the day. The effects of increased temperature are likely benefiting *Z. aethiopica* pollination. Because this plant species is introduced and naturalized, we cannot conclude whether this is adaptive coevolution between flowers and pollinators or an opportunistic exploitation.

Arthropods may be utilizing the *Z. aethiopica* for thermal rewards, rather than the already provided pollen source, although the true incentive of floral structure visits is still unclear. Future studies could track pollinators for longer durations and measure an arthropod's temperature change while on a flower to better determine whether pollinators are actually returning to flowers solely for a thermal reward. Chrysomelidae were also observed to move up the inflorescence and spread their wings periodically throughout the day. Future studies would be required to

elucidate the details of thermal interactions between Chrysomelidae and *Z. aethiopica*.

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LIGHT AVAILABILITY AND MULTI-LEVEL DEFENSES OF *URTICA DIOICA*

DAEWOONG LEE

Faculty Editor: Matthew P. Ayres

Abstract: *Urtica dioica* contains medically useful antiviral and anti-inflammatory agents, and thus understanding factors that influence production of such compounds may prove beneficial. In Cerro de la Muerte, Costa Rica, it is found in both shade and light conditions. I tested the hypothesis that it adjusts allocation between leaf growth and defense according to resource availability. Leaf size, stinging hair properties, and herbivory differed with light conditions. Results indicated further patterns in anti-herbivore defenses related to leaf maturation.

Key Words: light and shade, medicinal herb, plant defense, resource allocation, resource limitation, secondary metabolites, stinging nettle, Urticaceae

INTRODUCTION

Herbivory pressure has influenced plants to evolve with structural, chemical, and other forms of defenses. Among these, much attention has been given to secondary metabolites that potentially have pharmaceutical or industrial uses. Urticaceae is a stinging nettle family known for its stinging trichomes that incorporate both physical and chemical defenses. It is found in the high elevations such as around the biological station of Cerro de la Muerte, Costa Rica, and one species (*Urtica dioica*) is locally used as an anti-inflammatory aid for arthritis and rheumatism. A number of studies have reported its antiviral activity against HIV, diuretic and hypotensive effects, and medicinal usefulness for treating prostatitis and prostate hyperplasia (Lopatkin 2006, Safarinejad 2005, and El Haouari 2006). The species appears to have adapted to both light and shade environments, and understanding the nature of chemical defenses along different quality habitats may help further current understanding of how biotic and abiotic factors control the quality and quantity of plant's defense strategies.

One hypothesis is that the limited availability of light in shade may make the production of leaves more costly and cause the plants to invest more in its defense quality or quantity to reduce their losses. Alternatively, the plants exposed to more sunlight may make more anti-herbivore investments due to

the abundance of resources, while shaded plants may focus more on leaf growth and may sacrifice anti-herbivory characteristics. I predicted that to compensate for limited light, the shade plants would invest more in leaf growth, and thus have larger leaf size, show lower numbers of stinging hairs, and suffer greater herbivory, while light plants would exhibit the opposite trends.

METHODS

I. Herbivory Test

A. Feeding Trial and Selection of the Plant and Herbivores:

To determine which insects consume medicinal plants, I subjected Orthopterans, Coleopterans, and larval Lepidopteras to a 12-hour long feeding trial, using leaves from Winteraceae, Verbenaceae, and Urticaceae. Only plant species that showed signs of herbivory and the insects that consumed them were used for the feeding test. The selected herbivores were Orthoptera: Tettigoniidae (grasshoppers) and larval Lepidoptera (caterpillars).

B. Herbivory Test:

A total of 26 grasshoppers and 14 caterpillars were starved for 9 hours, and then placed individually into a 14 x 17 cm Ziploc bag blown with air, with a small wet cotton ball. Urticaceae leaves were sampled from 12 plants in sunny, open environment and 12

plants in shade environment. The species was identified as *U. dioica* (Gentry 1993 and Uva 1997). Young leaves were defined as the first sprouts on the 1st or 2nd node exceeding 2.5 cm in length, and old leaves as the first sprouts on the 4th or older node. The sizes of the old leaves in both conditions were controlled, and the sizes of the young leaves in both conditions were controlled separately. I excluded leaves previously fed upon by folivores. Four leaves were evenly distributed inside each bag: light and young, light and old, shade and young, and shade and old. Each trial lasted for 24 hours, and 12 additional hours if there was no sign of herbivory. The conditions of all subjects were observed up to 36 hours after the feeding trial to discover any visibly malignant consequences for consuming the leaves.

II. Leaf Comparison

I sampled 121 undamaged leaves from 12 plants in sunny and 12 plants in shade environments. Young leaves were defined as the first sprouts on the 1st node, adolescent leaves as the first sprout on the 2nd node, and old leaves as the first sprouts on the 4th-5th nodes. Length and width were measured for each leaf, and I counted the number of stinging hairs on one half of the lower surface of each leaf.

RESULTS

I. Herbivory Test

13 grasshoppers and 10 caterpillars did some feeding during the trial (58% of the total sample). For all 23, the favored leaves were in the order of light-old, shade-old, and young leaves in light or shade environment ($\chi^2_1 = 14.04$, $P < .001$). They also preferred the light leaves over shade leaves (binomial probability for 15 of 23 = 0.06), and the old leaves over young leaves (binomial probability for 19 of 23 < 0.001). Grasshoppers and caterpillars exhibited different preferences; grasshoppers followed the overall pattern of preference for the light and old leaves (binomial probabilities for 9 of 13 = 0.09 and for 10 of 13 = 0.03),

while caterpillars preferred old leaves (binomial probability for 9 of 10 = 0.01) but showed no preference for light or shade leaves (binomial probability for 6 of 10 = 0.2).

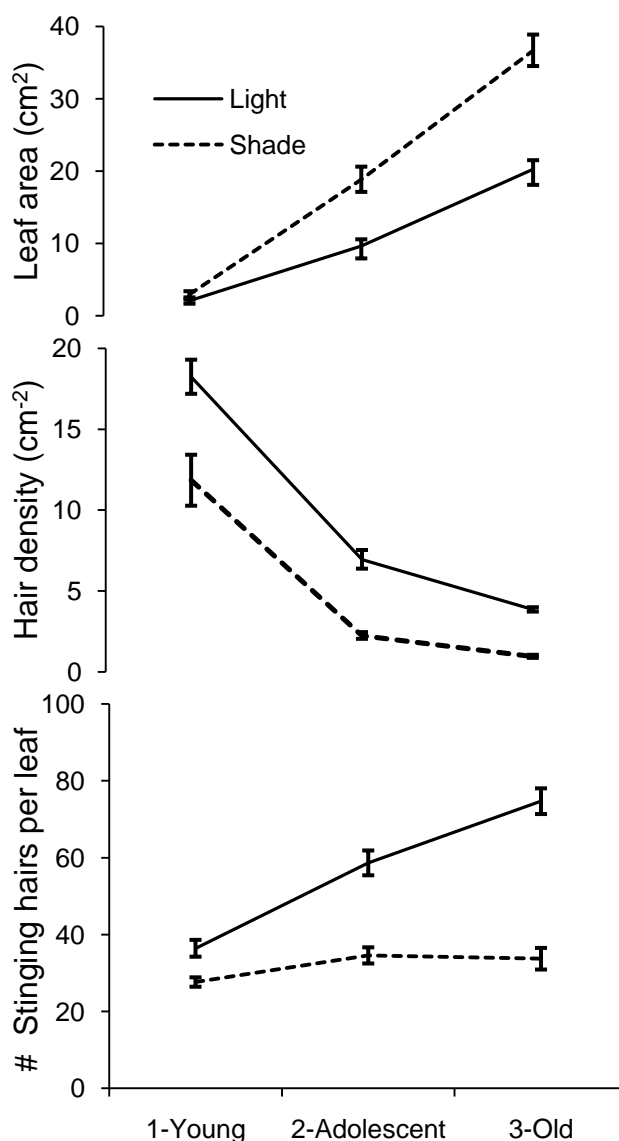


FIG. 1. Leaf comparison between the light and shade plants show that the shade leaves have smaller leaf size (top) and lower number and density of stinging hairs (middle and bottom). The slopes of increase in the number of hairs are significantly different between the two treatments (2-way ANOVA, $F_{1,115} = 11.78$, $P < 0.0001$). Data collected between January 29-31, 2010 in Cerro de la Muerte, Costa Rica. All statistical reports incorporated log-transformed data. Error bars represent ± 1 SE.

II. Leaf Comparison

Shade leaves were significantly larger than the light leaves (Fig. 1 top; 2-way ANOVA, $F_{1,115} = 44.02$, $P < 0.0001$). The stinging hair density and total number of the hairs for the light leaves were significantly higher than for the shade leaves (Fig. 1 middle and bottom; hair density: 2-way ANOVA, $F_{1,115} = 194.58$, $P < 0.0001$; total hairs: $F_{1,115} = 94.67$, $P < 0.0001$). The hair density and leaf area did not explain each other, because the shade plants increased little in the total hair counts with increasing age and leaf area (Fig. 1 top). The slopes of increase in the hair density between the two treatments differed significantly (2-way ANOVA, $F_{1,115} = 11.78$, $P < 0.0001$).

DISCUSSION

The significantly lower leaf area and stinging hair count and density in the shade plants agreed with the predictions and therefore supported the hypothesis that *U. dioica* responds to the light availability by altering its physical and chemical defense system. The differences were significant between the two treatments in all age groups, suggesting that the response may begin even before putting forth the first leaf. These results run counter to the generalization by May et al. (2006) that medicinal plants including Urticaceae lack adaptive phenotypic plasticity in regulating defense investments on the basis of light availability.

Interestingly, the number of stinging hairs increased little for the shade plants with age. One possibility is that the shade plants stalled the production of the hairs while the light leaves continued the production, likely in response to the light availability (Fig. 1 top). On the other hand, Agrawal and Spiller (2004) found that tropic silver buttonwood recovering from a disturbance allocated less towards defensive trichomes and more towards leaf growth. *U. dioica* could be similarly investing less in the hairs for the earlier leaves and more for the later younger leaves when the earlier leaves can provide photosynthates

to support the leaf production. Further studies would be needed to test this mechanism.

The herbivory test revealed little or no preference for light leaves. This ran counter to the predicted preference for shade plants with limited resource for defense investment. One possible explanation is that the stinging hairs and the associated secondary compound in the hairs are targeted to another kind of herbivore – perhaps mammals. In this case, the light plants may have produced more hairs not only because of more resource availability but also because of greater exposure to mammalian herbivores. It may also be that there are other secondary metabolites in *U. dioica* that have different patterns with respect sun and shade.

The preference of my test herbivores for old leaves shows that the physical structure of hairs is still effective and excludes them from young leaves with high density of hairs in both treatments. The herbivores did not exclude the stinging hairs in their consumption, however, and showed no sign of malignant consequences up to 36 hours after the trial, further suggesting that they may not be the intended target of the secondary metabolite in the hair.

The full complexity of *U. dioica* defense system remains unknown. My field observations indicated that the shade plants suffer from colonies of parasitic insects that did not seem to infest the light plants as much. Further studies would be required to test for the presence of other secondary metabolites and their anti-herbivore activity.

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BEAN POLLINATION BY BEES IS UNAFFECTED BY PROXIMITY TO ALTERNATE REWARDS

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Abstract: To ease pollinator limitation, farmers can cultivate additional nectar reward sources for pollinators of their agricultural crops. In this case, distance to the alternate source is likely to be crucial. Being too close or too far could even decrease pollinator success of the crop. We studied *Cubá* bean plots at the Cuericé Biological Station farm, Costa Rica, at varying distances from a clover patch (the alternate reward source). Neither the visitation rate by putative pollinators (*Bombus* spp.) nor the apparent pollination success (beans per pod) were related to the proximity of clover. This was at least partly explained because the bean plants had different pollinators than the clover. However, our results supported the premise that bean plants were pollinator limited and indicated that there can be value in developing ecological tactics to improve pollination.

Key Words: agriculture, *Cubá*, Cuericé, high elevation, pollinator limitation

INTRODUCTION

Plants often attract pollinators to their flowers by providing rewards, usually in the form of nectar or pollen. Some pollinators are generalists and may alter their foraging patterns based on the availability of particular reward sources. This has important implications for agricultural crop pollination because it suggests that landscapes can be managed to maximize pollination of crops (e.g. by planting additional reward sources around crops). There are at least four alternative theoretical models that could explain the pollination success of a particular crop species as a function of that crop's distance from an alternate reward source, assuming that pollinators prefer the alternate reward (Fig. 1). Model 1 represents the null hypothesis that an alternate reward does not affect crop pollination success. Under model 2, a crop close to an alternate reward will have higher pollination success because pollinators are primarily attracted to the alternate reward but also visit the crop flowers. Under model 3, a crop close to an alternate reward will have lower pollination success because the pollinator prefers the alternate reward and will always choose it instead of the crop. Under model 4, a crop will have maximum pollination success at an intermediate distance from the alternate reward. The rationale for model 4 is that at

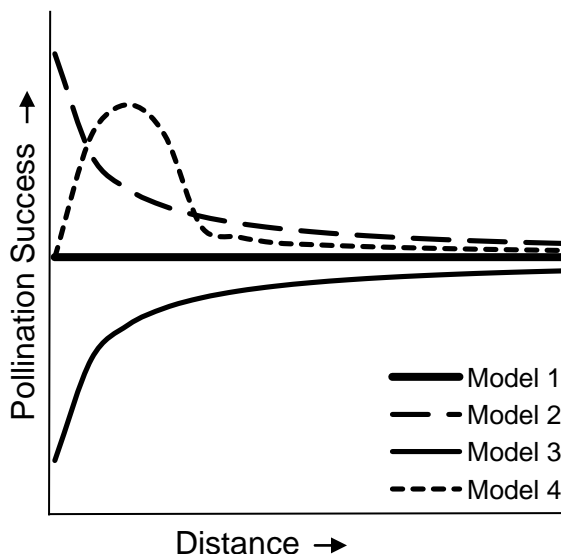


FIG. 1. Four possible models of how a plant's pollination success is influenced by proximity to an alternate reward source. (1) No relationship, (2) pollination success decreases with increasing distance, (3) pollination success increases with increasing distance, (4) pollination success is greatest at an intermediate distance.

close distances the pollinator will primarily choose the alternate reward, at far distances the pollinator will rarely traverse the intervening distance to the crop, and at intermediate distances the alternate reward is close enough to attract the pollinator to the vicinity of the crop, yet far enough away from the alternate reward so that the nearby crop pro-

vides energetic rewards. For all models, the alternate reward will not affect crop pollination success after a certain distance.

Pollinator limitation affects many agricultural systems. The high-elevation farm at the Cuericí Biological Station, Costa Rica, may experience chronic pollinator limitation due to cool temperatures and frequent cloud cover that limit the activity of insect visitors. The farm grows a high-elevation variety of bean (common name *Cubá*) that is bee-pollinated. To attract the bees, Carlos, the owner of the station, planted the clover *Trifolium* spp. (maybe *T. repens*), which is considered the bees' preferred nectar source. We measured two parameters of pollination success: (1) the number of bee visitations to bean flowers, representing a flower's potential to be pollinated, and (2) the number of beans per pod, representing the number of ovules fertilized due to previous pollinator activity.

METHODS

On 30 January 2010, we collected data at the Cuericí Biological Station farm (area: ca. 350 m²) in nine plots (Fig. 2). Each plot contained ca. 1.5 m² of bean (*Cubá*) vegetation and ca. 30 bean flowers, and was located varying distances (3.3 - 26.4 m) from the center of a large clover patch (of ca. 12 m²). We covered up other patches of clover that had more than 5 flowers, so that the large clover patch represented the majority of the clover in the site. The farm contained a heterogeneous mixture of additional flowering plant species: *Phytolacca rugosa*, *Monochaetum amabile*, *Ageratina anisochroma*, and *Monnina xalapensis*.

For each bean plot, we counted the number of pollinator visitations, measured as the number of flowers visited, and the type of pollinator over a 15-minute period. Each of the nine bean plots was observed once, from 0900 to 1200 and the clover patch was observed during all bean plot samples. We alternated sampling between near, far and middle-distanced bean plots to control for time of day.

For each bean plot we also measured the fertilization success: the number of ovules fertilized per pod. We haphazardly selected ten mature pods from each plot and counted the number of beans in each pod.

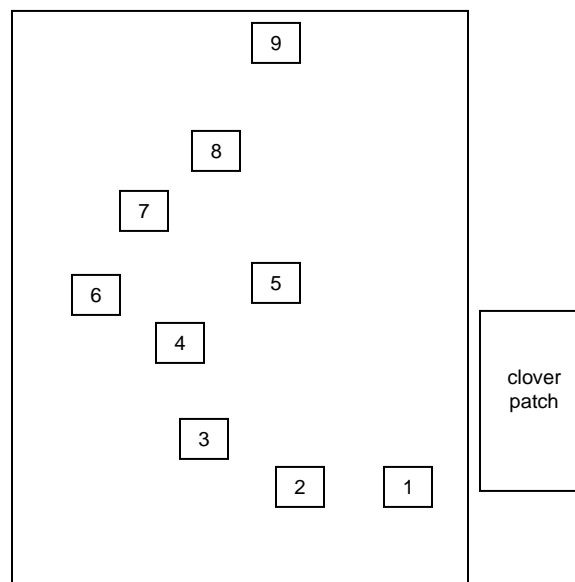


FIG. 2. Map of nine bean plots, numbered relative to distance to the clover patch from closest to furthest, at the Cuericí Biological Station farm, Costa Rica. Distance from plot to clover patch ranged from 3.3 to 26.4 m.

RESULTS

Bean and clover plants were visited by different pollinators: bumble bees (*Bombus* spp.) visited bean plants while honey bees (*Apis* spp., probably *A. mellifera*) visited clover plants. Even when bean flowers were between two clover flowers, honey bees did not stop at the bean flowers: only one of the twenty-eight bumble bee visitations observed was in the clover patch. The number of bumble bee visitations to bean plants was unrelated to the distance from the clover patch (Fig. 3).

The average number of beans per pod was also unrelated to distance to the clover patch (Fig. 4). The maximum number of beans per pod was five but the majority of pods only had three beans (Fig. 5). Although there was significant variation in the number of beans per pod across plots (Random effects ANOVA: $F = 2.13$, $df = 8, 81$, $P = 0.04$), plot only explained ten percent of the variation.

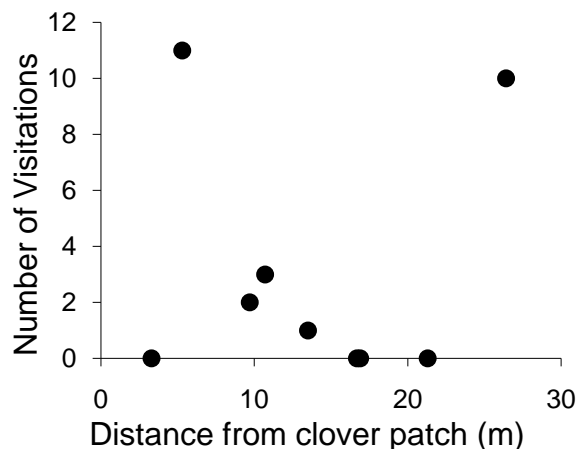


FIG. 3. Number of bumble bee visitations in 15 minutes to bean flowers, in 9 plots at varying distances from a clover patch at the Cuericé Biological Station farm, Costa Rica, in January 2010.

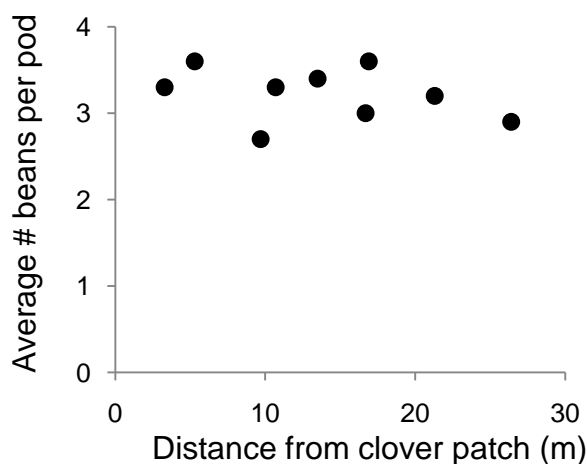


FIG. 4. Average number of beans per pod for nine different bean plots of varying distance from a clover patch at a farm 1 km from the Cuericé Biological Station, Costa Rica, in January 2010.

There was no evident spatial pattern in number of beans per pod across plots.

It appeared that temperature and weather conditions affected pollinator activity. Fewer bees visited either the clover patch or bean plots when it was cloudy and misty.

DISCUSSION

Bean and clover plants did not share the same bee pollinator species. Thus, it was not surprising that bean pollination success

(number of bee visitations and average number of beans per pod) was unrelated to proximity to clover (model 1, in Fig. 1). The lack of spatial pattern in bean pollination success (average number of beans per pod), implies that other flowers species in the vicinity also did not influence bean plant pollination by bumble bees.

On the other hand, our results supported the premise that bean plants in this setting were generally pollinator-limited because almost all pods had less than the five maximum possible beans. Frequent cloud cover and cold temperatures in Cuericé presumably contribute to pollen limitation by constraining periods of insect activity. Resource limitations of the plants could further limit bean pod production, but future studies would be needed to compare pollinator and resource limitation.

Our results do not preclude the possible benefits of propagating alternate reward sources near agricultural crops. A first step in evaluating candidate alternate reward sources would be to identify species that are attractive to the crop pollinators. Alternative tactics could include cultivating larger pollinator populations and/or growing crops in sunny, warm locations that are desirable habitats for pollinators.

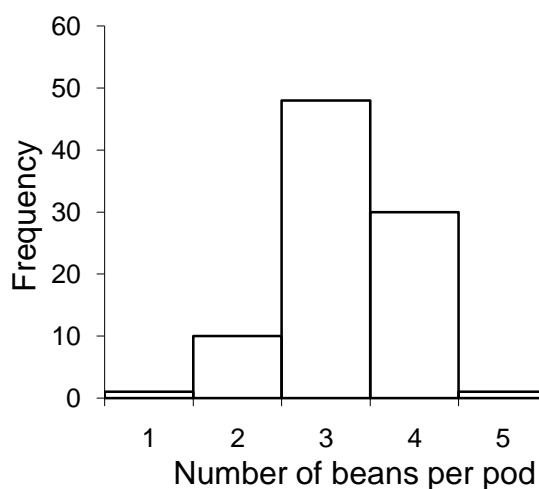


FIG. 5. Frequency distribution of the number of beans per pod for 90 pods collected from nine different bean plots at the Cuericé Biological Station farm, Costa Rica, in January 2010.

NICHE DIFFERENTIATION AS AN EXPLANATION FOR THE CO-OCCURRENCE OF TWO HIGH ELEVATION BAMBOO SPECIES IN COSTA RICA

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Faculty Editor: Matthew P. Ayres

Abstract: We tested the hypothesis that two species of bamboo (*C. longifolia* and *C. talamencensis*) exist together because of niche differentiation at Cerro de la Muerte, Costa Rica. We compared relative success (using culm height, percent dead culm, and average number of culms per clump as proxies for success) and tested for environmental differences across the ranges of the two species. We found that the success of each species tended to decrease at the edge of their ranges, supporting the niche differentiation hypothesis, but environmental gradients of elevation and soil moisture did not differ as we predicted. With more data, our results could more strongly support niche differentiation as the mechanism behind species co-occurrence.

Keywords: *C. longifolia*, *C. talamencensis*, differential survival, species range

INTRODUCTION

The co-occurrence of ecologically similar species is among the oldest problems in ecology. Co-occurrence can result from niche differentiation or reflect non-equilibrium between speciation and extinction (Begon et al. 1990). Niche differentiation in plants can yield differential survival, where offspring survival rates in different abiotic conditions determines species distribution. Plant species that

survive in a larger range of conditions tend to show greater morphological plasticity as their growth rate differs depending on the conditions (Craine 2008). At Cerro de la Muerte, Costa Rica, two species of understory bamboo, likely *Chusquea longifolia* and possibly *Chusquea talamencensis* (Widmer 1994), exist parapatrically. *C. talamencensis* has distinct requirements for soil conditions (Widmer 1998), which may help define its niche. We tested the hypothesis that these two species co-occur in the region of Cerro de la Muerte because they occupy different niches. We predicted that soil moisture would differ between the ranges of the two species, that each species would experience less success at the edge compared to the center of their range, and that the species with the larger range would show greater morphological plasticity.

METHODS

On 28-30 January 2010, we collected measurements of plant growth success for *C. longifolia* and *C. talamencensis* along a loop trail north of Cuerici Biological Station in Cerro de la Muerte Costa Rica. The western side of the loop runs in the valley of two hills, while the eastern side has an open face towards the Pacific. We used culm height (measured from the base to the tip in centimeters), percent dead culm (number of dead culms divided by total culm per clump), and

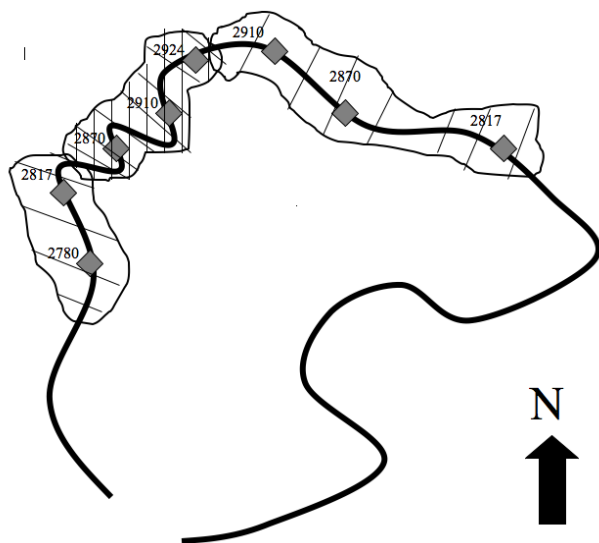


FIG. 1. Map of the loop trail at Cerro de la Muerte, Costa Rica. The diamonds indicate sites where we measured percent dead culm, average culm number per plant, and soil moisture. The area marked with hash marks shows the habitat range of *C. talamencensis* while the two surrounding areas show the lower elevation range of *C. longifolia*.

average number of both alive and dead culms per clump as proxies for plant success. When measuring height in both species, we sampled the right and left side of the trail at every 10 m increase in elevation. We measured the closest clump on the right and left side of the trail and used a stopwatch to generate a random number, counting from left to right to select our focal culm. We ended our sampling zone on the eastern side of the loop (low trail) when we no longer found any bamboo clumps (Fig. 1).

We collected percent dead culm and average number of culms per clump at eight elevation sites: 2780 m, 2817 m, 2870 m, 2910 m, and 2924 m on the high trail, and 2817 m, 2870 m, and 2910 m on the low trail. We also measured soil moisture to see if abiotic factors explained differential bamboo success in the two species (Fig. 1).

RESULTS

The height of culms increased significantly with altitude in *C. longifolia* on the high trail ($r^2_{46} = 0.24$, $P = 0.0004$), but did not show significant trends on the low trail or in *C. talamencensis* (Fig. 2). The average percent of dead culms per plant was higher in areas with one species than areas with two species (Fig. 3), but the difference was not significant ($t_{16} = -1.93$, $P = 0.07$). Variance in culm height was significantly greater in *C. longifolia* than in *C. talamencensis* (Fig. 4), and the coefficient of variance was higher in *C. longifolia* than in *C. talamencensis* (41 vs. 31).

We did not find a difference in soil moisture between sites, which ranged from 21–54% (ANOVA, $F_{2,5} = 0.27$, $P = 0.78$). We saw very distinct boundaries between species, and observed that the average number of culms in the edge area was 23.4% lower than in the average center of the range of *C. longifolia*, but there was no variation between the number of culms in the center and edges of the range of *C. talamencensis*.

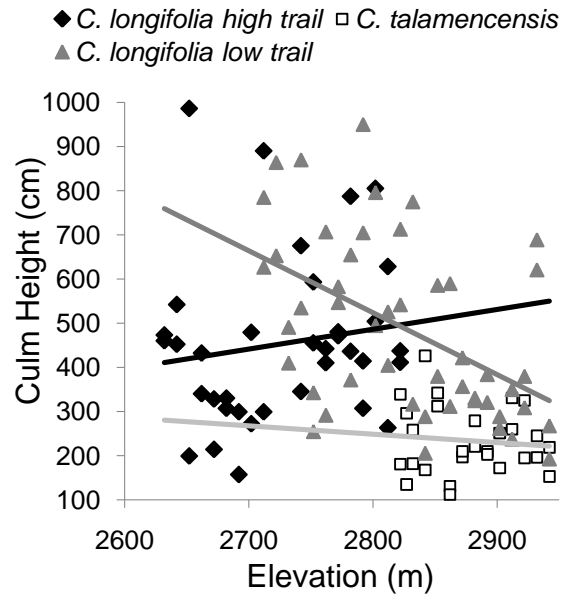


FIG. 2. Linear regression of stem stalk height at different elevations between *C. longifolia* on the high trail, *C. talamencensis*, and *C. longifolia* on the low trail on Cerro De La Muerte in Costa Rica.

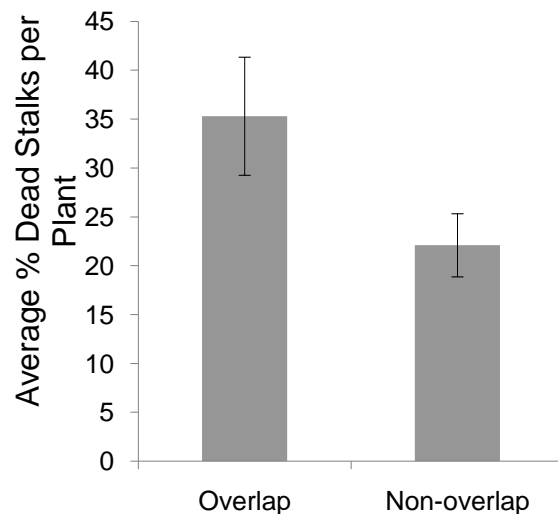


FIG. 3. Average percent of dead stalks per plant in areas with two species present (Overlap) ($n = 4$) and areas with one species present (Non-overlap) ($n = 14$) on Cerro de la Muerte in Costa Rica. Bars represent \pm one standard error.

DISCUSSION

C. longifolia tended to show lower success near edges of its range and greater morphological variation across a larger range of conditions (elevations), which supports the niche

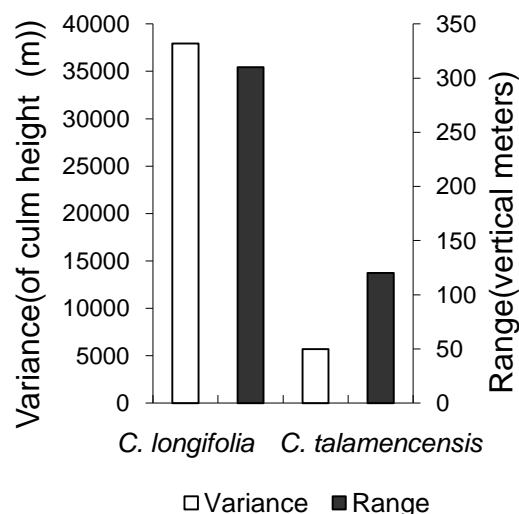


FIG. 4. Comparisons of variance in culm length and elevational range in two bamboo species found at Cerro de la Muerte, Costa Rica on January 28-30, 2010. *C. longifolia* had significantly greater variance than *C. talamencensis* ($F_{83,27} = 6.69$, $P < 0.0001$). Ranges were determined by observation on two trails NE of Cuerici Biological Station at Cerro de la Muerte.

differentiation hypothesis. Lower success on the edge of its range suggests that *C. longifolia* experiences suboptimal conditions there. Since we did not find this same abiotic limitation in *C. talamencensis* at the juncture with *C. longifolia*, the two species may differ in physiological responses to similar conditions, which may determine their niches and distributions. Also, *C. longifolia* may survive in a range of optimal to poor conditions (high morphological plasticity), while *C. talamencensis* may only be able to survive in its optimal set of conditions. Even though we observed *C. longifolia* dominating much of the understory, *C. talamencensis* may have greater survival in areas where it persists.

Although our analyses revealed some suggestive trends, the data were quite limited, and we cannot be sure that the trends are valid. Also, we did not find soil moisture or elevation differences between the ranges of the two species, which failed to support the niche differentiation hypothesis. Further stu-

dies are needed to clearly resolve the explanation for co-occurrence of these two bamboo species.

Our study focused on a specific system, but the question of plant species distribution is universal. If simple measures of differential success can test for niche differentiation, our research tactics may be useful in the study of other species in other environments.

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MECHANISMS DRIVING BILL LENGTH VARIATION IN HUMMINGBIRDS

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Faculty Editor: Matthew P. Ayres

Abstract: Hummingbirds at Cuerici Biological Station in Costa Rica exhibit a variety of bill lengths. This may be due to hummingbirds partitioning flower species by bill length or due to selection for longer bills that allow access to more flowers, with shorter bills as the basal condition. By comparing the number and overlap of pollen morphospecies found on hummingbirds with different bill lengths, we found that hummingbirds with longer bills may have access to more flowers, suggesting that niche partitioning is not what is driving variation in hummingbird bill length.

Keywords: Cuerici, green violet-ear, magnificent hummingbird, morphospecies, niche partitioning, pollen, white-throated mountain-gem, volcano hummingbird

INTRODUCTION

Hummingbirds and the flowers they feed on have coevolved, such that both flower and hummingbird benefit from a longer corolla and a longer bill, respectively. Hummingbirds' unique bill morphologies allow them to enjoy the nectar rewards of flowers inaccessible to other types of pollinators (Temeles and Kress 2003). This specialization may come at a cost; a long bill takes more energy to develop, and the extra weight may reduce flight efficiency. However, longer-billed hummingbirds can take advantage of flowers with both short and long corollas, whereas short-billed hummingbirds are limited to flowers with short corollas.

We were interested in what drives the wide variety of hummingbird bill lengths. We investigated two opposing hypotheses. (i): Hummingbird bill length variation is driven by niche partitioning, such that species with different bill lengths specialize on different species of flowers (the niche partitioning hypothesis). Alternatively, (ii): there has been selection for longer bills since longer-billed birds are able to take advantage of both short and long flowers, with short bills as the basal condition (the larger is better hypothesis). If the niche partitioning hypothesis were true, we would predict that hummingbirds of different bill lengths would visit a similar number of flower species but have few in common. From the larger is better hypothesis, we

predicted hummingbirds with longer bills would be capable of visiting a greater number of flower species than hummingbirds with shorter bills and hummingbirds would have many flower species in common.

METHODS

We collected pollen from mist-netted hummingbirds as one means of assessing the flower species visited by individuals.

We sampled for hummingbirds during 206 mist-net-hours at Cuerici biological station, Costa Rica (ca. 2600 meters elevation) on 29-31 January 2010. We used 2 x 6 m mist nets placed a minimum of 15 m apart in open fields and primary and secondary forest. We recorded the bill length of each hummingbird and collected a pollen sample from the forehead, bill, and throat using clear tape and adhered it to a microscope slide. We identified pollen grains to morphospecies using a compound microscope and recorded all morphospecies found on each bird. We rarified the total number of pollen morphospecies found on each bird population in order to correct for uneven sample sizes (EstimateS, Chao2 model; Colwell 2006).

In addition to mist netting, we opportunistically observed the foraging behavior of several hummingbirds, recording the species of flower visited by each bird. We collected pollen samples from flowers that we observed birds feeding from in order to match them to

pollen samples from hummingbirds.

RESULTS

We captured 35 hummingbirds of four species representing a range of bill lengths. Volcano Hummingbirds (*Selasphorus flammula*) had the smallest bills, Green Violet-Ears (*Colibri thalassinus*) and White-throated Mountain-gems (*Lampornis castaneiventris*) had medium length bills, and Magnificent Hummingbirds (*Eugenes fulgens*) had the longest bills (Table 1). We identified 32 morphospecies of pollen, each presumably corresponding to a different plant species. We found a similar number (1.5 to 2) of pollen morphospecies on individual hummingbirds regardless of bill length (ANOVA $F_{3,31}=0.26$, $P=0.85$; Fig. 1). However, hummingbird species appeared to differ in total richness of flower species visited by the population. Rarefaction suggested that the total community of flower species visited by our short-billed hummingbird population was barely half that of the longer-billed species (12 vs. 21-31) (Fig. 2).

Comparisons of pollen load composition between pairs of individual hummingbirds in different bill length categories suggested that the least overlap in flower resources occurs between hummingbird species with the greatest difference in bill length (Fig. 3). For short-medium, medium-long and short-long category pairs, we calculated overlap by averaging the number of pollen morphospecies each possible pair of individual birds had in common.

From direct observation, it was difficult to assess the range of flower species visited by our hummingbird populations. We observed *S. flammula* visiting 17 flowers of *Bomarea* spp., *Fuschia* spp., a small unidentified yellow flower, and an unknown light green flower; *C. thalassinus* visiting 2 flowers of *Bomarea* spp.; *L. castaneiventris* visiting 10 flowers of *Fuschia* spp., a large green bat-pollinated flower, *Bomarea* spp., and an unidentified small white flower; and we observed no *E. fulgens* feeding events. However, information

gleaned from observations added very few flowers not already represented by pollen collection.

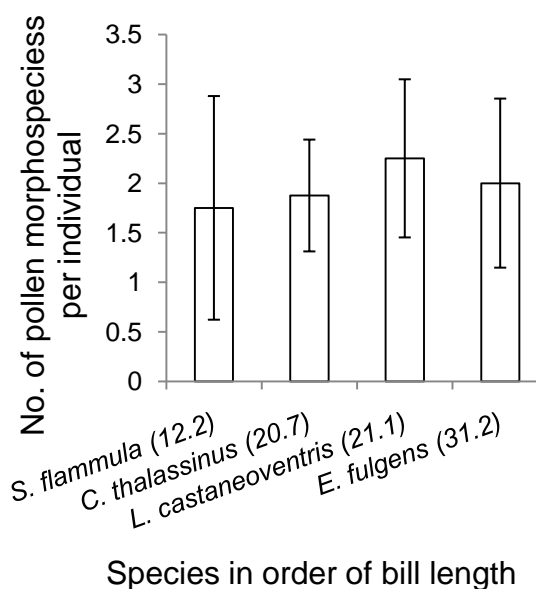


FIG. 1. Mean number of pollen morphospecies found on individual hummingbirds Cuericí Biological Station, Costa Rica. Numbers in parentheses are species mean bill length (mm). Bars represent 95% confidence intervals.

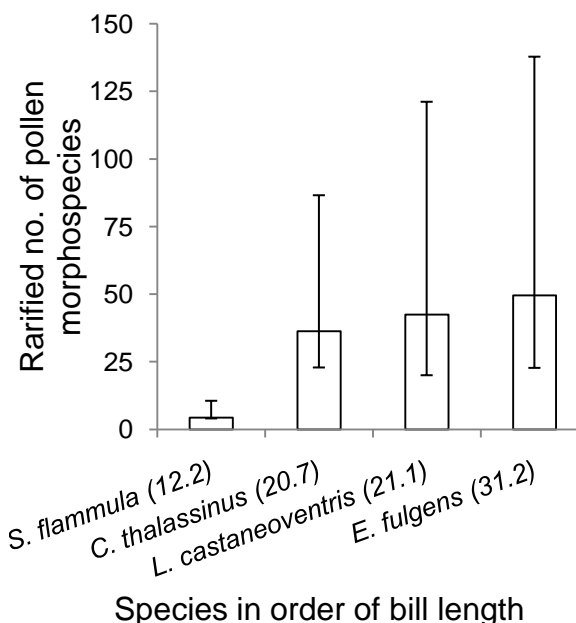


FIG. 2. Rarefied total number of pollen morphospecies found on all hummingbirds of each species tended to increase with bill length. Numbers in parentheses are species mean bill lengths (mm). Bars represent 95% confidence intervals. Data collected at Cuericí Biological Station, Costa Rica.

TABLE 1. Raw number of pollen morphospecies found on captured hummingbirds of different bill lengths at Cuericí Biological Station, Costa Rica (mass values from Stiles and Skutch 1989).

Species	Mass (g)	Mean bill length (mm) \pm 1 SD	Total # pollen morphospecies found on species	# birds captured
<i>S. flammula</i>	2.5	12.2 \pm 0.62	4	4
<i>C. thalassinus</i>	5	20.7 \pm 0.62	18	16
<i>L. castaneiventris</i>	male:6.2 female: 5	21.1 \pm 0.57	11	8
<i>E. fulgens</i>	male:10 female: 8.5	31.2 \pm 1.17	11	7

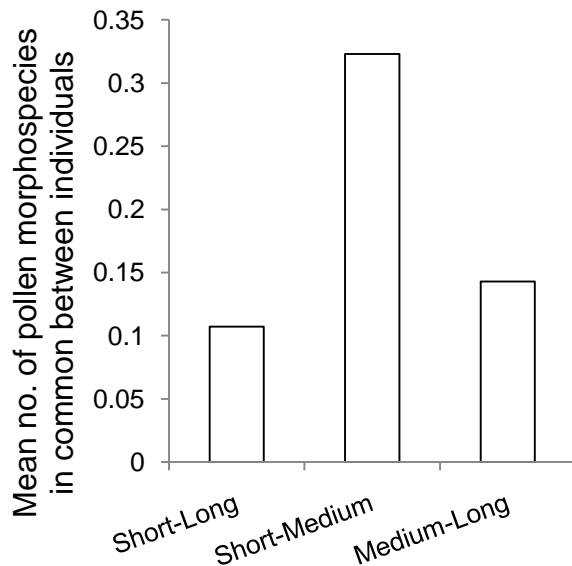


FIG. 3. Mean number of pollen morphospecies in common for all possible pairs of individuals between paired bill length categories. Short = *S. flammula*, Medium = *C. thalassinus* and *L. castaneiventris*, long = *E. fulgens*. Pairs non-independent (for short-long N = 28, for short-medium N = 96, for medium-long N = 168). Error bars omitted due to non-normality of data. Data collected at Cuericí Biological Station, Costa Rica.

DISCUSSION

We found a similar number of pollen morphospecies on individual hummingbirds, which contradicted the longer is better model, but this may have been due to insufficient power. Data showing the lowest overlap in pollen morphospecies between hummingbirds with the greatest differences in bill lengths offers support for niche partitioning. However, the pollen load data grouped by hummingbird species supported the longer is better hypothesis. With the shortest bills, *S. flammula* may not be able to access nectar in

the longer flowers. This is not to say that selection might be driving all hummingbirds to evolve longer bills: we observed *S. flammula* chasing intruding birds from the vicinity, suggesting that aggressively defending a territory may allow *S. flammula* to compete alongside the species with longer bills. Although other studies have shown that hummingbirds often specialize on particular flowers (Temeles and Kress 2003; Temeles et al. 2000) we found evidence supporting both hypotheses we tested, neither of which may completely explain mechanisms behind hummingbird bill length variation.

APPENDIX A

TABLE 2. Number of pollen morphospecies found to overlap among four hummingbird species caught in mist nets at Cuericí Biological Station, Costa Rica.

	<i>S. flammula</i>	<i>C. thalassinus</i>	<i>L. castaneiventris</i>
<i>C. thalassinus</i>	2		
<i>L. castaneiventris</i>	2	3	
<i>E. fulgens</i>	2	3	4

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FACTORS INFLUENCING DISSOLVED OXYGEN LEVELS IN A TROUT HATCHERY

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Faculty Editor: Matthew P. Ayres

Abstract: Dissolved oxygen is crucial to the functioning of aquatic ecosystems. Understanding which factors influence dissolved oxygen is important in natural and managed systems, including successful aquaculture management. Major factors that influence dissolved oxygen in the rainbow trout farm at the Estación Biológica Cuericí include trout respiration, photosynthesis, microorganism respiration, and diffusion of oxygen into the water. Understanding how these factors influence dissolved oxygen levels will inform trout farm management techniques and elucidate general principles of ecosystem functioning.

Keywords: aquaculture, aquatic ecosystems, diffusion, metabolism, microorganisms, *Oncorhynchus mykiss*, photosynthesis, rainbow trout, respiration

INTRODUCTION

Aquatic ecosystems are shaped by complex interactions between biotic and abiotic factors. The resulting properties influence which species can inhabit the ecosystem. An understanding of these interactions is especially important in human managed systems. Successful fish farms must maintain suitable temperatures and adequate levels of dissolved oxygen (DO) to raise commercial numbers of fish with low mortality rates. Falling DO levels can result in fish mortality within hours and can have a detrimental effect on the taste of the fish.

The Estación Biológica de Cuericí in Costa Rica maintains a rainbow trout farm. Among the various biotic and abiotic factors that determine the survival and quality of the fish, one of the most important is the dissolved oxygen content of the water. We sought to explain the abiotic and biotic factors

that determine dissolved oxygen concentration.

Rainbow trout, *Oncorhynchus mykiss*, are poikilotherms and thermal conformers. Their metabolic rates and oxygen requirements increase with rising water temperature (Black et al. 1991). In addition, increasing water temperature decreases the concentration of DO at saturation. Thus, water temperature, trout respiration, and their interactions may be strong drivers of dissolved oxygen in the water of a fish farm. If so, water temperature should be predictably related to dissolved oxygen levels. If not, it would imply the importance of other factors such as photosynthesis, microbial respiration, or DO input via water flow.

METHODS

We studied the trout farm on 29-30 January 2010 from 16:30 to 15:30. The farm is at

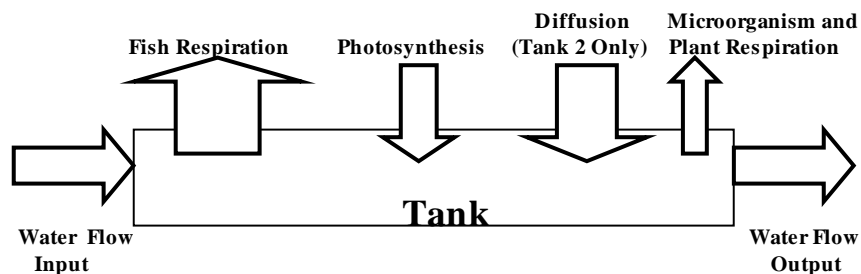


FIG. 1. Schematic of oxygen inputs and outputs for an artificial fishpond in a trout farm located at Cuericí Biological Station, CR. Arrow size reflects estimated importance in Tank 2. Tank 1 had much smaller fluxes due to fish respiration and diffusion.

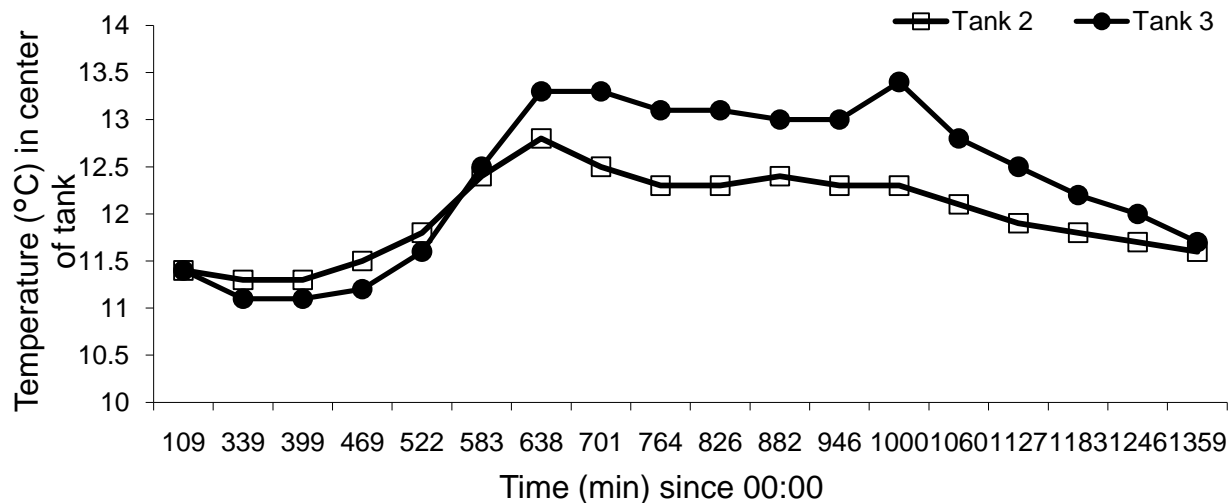


FIG. 2. Diurnal temperatures in two fish tanks at Cuerici Biological Station, CR on 29-30 January, 2010.

ca. 2500 m elevation, resulting in generally cool temperatures. We measured dissolved oxygen (DO , $\text{mg O}_2 / \text{L}$) and temperature at hourly intervals in six natural and artificial trout tanks connected by pipe. The tanks are fed by underground spring water.

We focused our analysis on two tanks. Tank 1 contained ca. 50 trout that weighed ca. 1500 g each. Tank 2 contained ca. 5000 trout that weighed ca. 200 g each. Tanks 1 and 2 were both dugout pools with no linings, and appeared similar with respect to water flow, light conditions, canopy coverage, levels of algae, and substrate.

We measured the flow rate of water through the system by calculating the amount of time it took to fill a 10 L bucket at one of the water sources (average taken from 10 repeats). In addition, we determined DO and temperature at the water inputs and outputs for both of our study tanks.

We determined rates of DO into and out of the system by multiplying the flow rate by the DO concentration at the input and output, converting mg O_2 into mL O_2 . The difference between these input and output rates was the rate at which oxygen was lost from the system, the empirical DO loss. Our equations, conversion rates and sampling schedule are detailed in the Appendix.

We calculated theoretical trout respiration rate (TTRR) using an interspecies func

tion for poikilotherm metabolic rates as a function of body mass and temperature (Peters 1983).

In Tank 1, if the difference between empirical DO loss and TTRR was greater than zero, more DO was lost from the system than could be accounted for by TTRR. At nighttime, we attributed this difference to respiration by microorganisms living in the water and soil, the microorganism/plant respiration rate (MPRR).

If the difference between empirical DO loss and TTRR was less than zero, less DO was lost from the system than should have

TABLE 1. Estimates of empirical oxygen loss, theoretical trout respiration, microorganism respiration, photosynthesis, and diffusion in a trout farm at the Estacion Biologica de Cuerici. Tank 1 contained 50 1500-g trout, Tank 2 contained 5000 200-g trout.

	Day		Night	
	Tank 1	Tank 2	Tank 1	Tank 2
A. Empirical O_2 Loss	922	11732	3243	10376
B. Theoretical Trout Respiration	1789	36366	1565	34075
C. A-B	-711	-24643	1678	58356
D. Microbial and Plant Respiration	1678	3574	1678	3574
E. Photosynthesis Addition of O_2	2389	5098	N/A	N/A
F. Diffusion of O_2	NA	-23119	N/A	-27273

been from TTRR. During daylight hours we attributed this difference to the combination of MPRR and the addition of oxygen via photosynthesis by aquatic plants.

In Tank 2, trout were theoretically consuming much more oxygen than was actually being lost from the system. This indicated that there was another factor adding large quantities of oxygen to the system that was not present in Tank 1. We attributed this to O_2 diffusion from the atmosphere. Tank 2 had between 1000-2000 kg of fish, and their high cumulative respiration rates caused decreased partial pressure of O_2 in the water, causing O_2 to diffuse into the water. Since there was twice as much water in Tank 2 as in Tank 1, we doubled Tank 1's photosynthesis and microorganism respiration rates, then used them to approximate the additional oxygen input into Tank 2, the diffusion rate. Fig. 1 summarizes our conceptual model of DO flux in this system.

RESULTS

Our data refuted the importance of water temperature as a driver of DO levels in this trout farm system, because water temperature varied by less than 2 °C (Fig. 2). Trout respiration was the most important factor, followed by diffusion, water flow, photosynthesis, and microorganism respiration.

Dissolved oxygen values were generally higher during the day (Fig 3).

DISCUSSION

Contrary to our initial expectations, trout respiration, diffusion of atmospheric O_2 into water, photosynthesis, and microorganism respiration were much more important than temperature in determining dissolved oxygen concentration in this system. When changes in temperature are negligible, respiration rates in aquatic organisms do not change substantially, and thus any differences in dissolved oxygen between night and day are the result of differing rates of photosynthesis, respiration, and in the case of large trout populations, diffusion.

It is important to consider these four factors in management of trout farms. Photosynthesis can have a substantial effect on the amount of O_2 being produced in a tank, and it may therefore be beneficial to maintain an aquatic plant population in a tank. In contrast, as microorganisms are an additional source of respiration, removal of sediment may remove a portion of microorganisms and increase the amount of O_2 available to trout. It seems unlikely that an increased water input would substantially increase levels of dissolved O_2 in the water, as trout respiration and O_2 diffusion rates can be many times

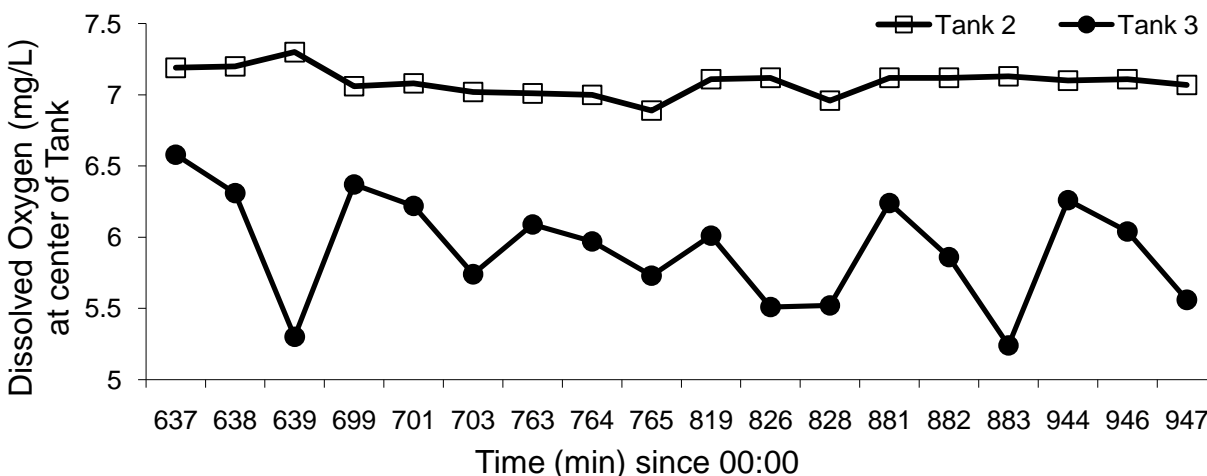


FIG. 3. Diurnal patterns in dissolved oxygen in two artificial fish tanks at Cuerici Biological Station, CR on 29-30 January, 2010.

higher and thus more influential. Because diffusion rate appears instrumental in maintaining sufficient dissolved O₂ levels, it would be beneficial to house fish in large, shallow pools in order to maximize diffusion at the surface of the water. In contrast, if too many fish are placed in a single pool, their respiration rate may be greater than the ability of O₂ to diffuse into the pool, and create a hypoxic environment that could cause fish mortality and

compromise the taste of the fish. Further studies could determine the maximum number of fish a tank of certain dimensions could sustain, based on models of diffusion.

By studying management of specific aquaculture systems, principles pertaining to ecosystem function can be explained. At the same time advances in the understanding of ecosystem functioning can allow for new insights into successful aquaculture.

APPENDIX

$$1 \text{ mg O}_2 \frac{1 \text{ g}}{1000 \text{ mg}} \frac{22.4 \text{ L O}_2}{1 \text{ mol O}_2} \frac{1 \text{ mol O}_2}{32 \text{ g O}_2} \frac{1000 \text{ ml}}{1 \text{ L}} = 0.7 \text{ mL}$$

$$1 \text{ mg O}_2 = 0.7 \text{ ml O}_2$$

$$\text{Input Rate and Output Rates} = 4.88 \text{ L s}^{-1} = 17,568 \text{ L hr}^{-1}$$

$$\text{O}_2 \text{ Input Rate} = 17,568 \text{ L hr}^{-1} * (\text{mL O}_2 @ \text{input})$$

$$\text{O}_2 \text{ Output Rate} = 17,568 \text{ L hr}^{-1} * (\text{mL O}_2 @ \text{output})$$

$$\text{Empirical O}_2 \text{ Loss} = (\text{O}_2 \text{ Input Rate}) - (\text{O}_2 \text{ Output Rate})$$

$$\text{O}_2 \text{ Consumed by kg of fish per hour (mL O}_2 \text{ kg}^{-1} \text{ hr}^{-1}) = 0.067 * g^{-0.24} * 2.71828^{(0.051 * T)} \text{ (Peters 1983)}$$

$$\text{Theoretical Trout Respiration Rate (TTRR)} = (\text{O}_2 \text{ Consumed by kg fish per hour}) * (\text{total kg of fish})$$

$$\text{Empirical - TTRR} = \text{Empirical O}_2 \text{ Loss} - \text{Theoretical Trout Respiration Rate}$$

$$\text{Night} = 18:30-6:29$$

$$\text{Day} = 6:30-18:29$$

$$\text{Diffusion} + \text{Photosynthesis} - \text{Microorganism Respiration and Plant Respiration} -$$

$$\text{TTRR} = \text{Input O}_2 - \text{Output O}_2$$

$$\text{Microorganism Respiration and Plant Respiration Tank 2 (mL/ hr)} = (\text{Avg. Night TTRR}) - (\text{Avg. Night Empirical-Theoretical O}_2)$$

$$\text{O}_2 \text{ Produced by Photosynthesis Tank 2 (mL/ hr)} = (\text{Empirical O}_2 \text{ Loss}) - (\text{TTRR} + \text{Microorganism Respiration and Plant Respiration})$$

$$\text{Diffusion} = \text{Input O}_2 - \text{Output O}_2 - \text{Photosynthesis} + \text{Microorganism Respiration and Plant Respiration} + \text{TTRR} \\ (\text{Calculated for Avg. Night Values and Avg. Day Values})$$

$$\text{Microorganism Respiration/ Plant Respiration Tank 3 (mL/ hr)} = 2 * [\text{O}_2 \text{ Consumed by Microorganisms Tank 2 (mL/ hr)}]$$

$$\text{O}_2 \text{ Produced by Photosynthesis Tank 3 (mL/ hr)} = 2 * [\text{O}_2 \text{ Produced by Photosynthesis Tank 2 (mL/ hr)}]$$

$$\text{Volume Tank 2} = 1.5\text{m} * 22\text{m} * 0.6 = 19.8 \text{ m}^3 * 1000 \text{ L m}^{-3} = 19,800 \text{ L}$$

$$\text{Volume Tank 3} = 2.5\text{m} * 22.5 * 0.75 = 42.2 \text{ m}^3 * 1000 \text{ L m}^{-3} = 42,200 \text{ L}$$

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CONTROLS ON THE ABUNDANCE OF ANOLE LIZARDS (*NOROPS POLYLEPIS*) ON THE OSA PENINSULA, COSTA RICA

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Faculty Editor: Matthew P. Ayres

Abstract: The forces that influence abundance have consequences for organisms' life histories, evolutionary pressures, and ecosystem roles. Taxa with a large geographic distribution existing in diverse environmental conditions, such as anoles, offer interesting opportunities for study as they have the potential for substantial variation in population regulation mechanisms. We investigated an anole species (*Norops polylepis*) at Corcovado National Park, Costa Rica. A removal experiment combined with mark-resight data, aggression trials, and body metric measurements suggested top-down (predation) limitation of this anole population. Strong top-down controls tend to favor an r-selected reproductive strategy, exert strong selective pressure for predator avoidance traits (e.g. cryptic coloration), and weaken food web interactions with lower trophic levels.

Key Words: *Anolis*, bottom-up limitation, competition, Corcovado, predation, resources, top-down limitation

INTRODUCTION

Anoles are widely distributed throughout the tropics and sub-tropics of the Western Hemisphere, including over 400 species in diverse habitats (Guyer and Savage 1986). The wide range of abiotic and biotic conditions in which anoles persist has driven differential selection, leading to speciation (Calsbeek and Smith 2007), and consequently creates the potential for high variability in population regulation mechanisms between and within species. In the Caribbean, island anole populations appear to be limited by resource availability (bottom-up effects; Calsbeek and Smith 2007). Our initial observations of *Norops polylepis* in Corcovado National Park on the Osa Peninsula of Costa Rica suggested abundant prey items, few anoles relative to apparent suitable habitat, and the presence of numerous anole predators (e.g. motmots, trogons, several snakes, and large lizards; Savage 2002), which implied top-down controls on population abundance. Which population limitation mechanism predominates has broad implications: for example, the limitation mechanism may be expected to interact with the anoles' reproductive strategy and be of consequence for the anoles' role in ecosystem function.

Male anoles defend territories to maintain access to quality food resources, increase safety from predators, and increase exclusive access to females (Calsbeek and Marnocha 2006). If bottom-up forces regulate population size and territories were a limiting resource, other male anoles would be expected to quickly reoccupy habitats in which the original male was removed. In addition, with resource limitation predominating, large (socially dominant) males would be expected to hold better territories (Schoener and Schoener 1980; Calsbeek and Smith 2007), permitting them to attain better body condition. The territories of large males should thus be reoccupied more quickly (relative to those of small males) and by other large males. Further, with resources predominantly limiting population instead of predators, males would be expected to display high absolute levels of aggression towards intruders. The lack of all the above expected population characteristics and relationships would suggest a predominance of top-down instead of bottom-up limitation.

METHODS

We collected all data on 5-7 February 2010 in Corcovado National Park, Costa Rica. The site was characterized by mature wet forest with tree falls and man-made trail cuts

providing light gaps in otherwise dense canopy and under-story vegetation.

We removed 16 resident male anoles and marked their territories and original perch location. At the time of removal we searched the area within a 2 m radius (approximate territory size) of the anole's original location for two minutes and noted the number, sex, and approximate age (adult or juvenile) of any other anoles. We re-searched the territories a total of three times between 24 and 48 hours after the removal and recorded the presence and snout-vent length (SVL) of any reoccupying males.

We marked nine other resident males with green permanent marker on both sides of the head and both hind limbs and left them in their territories. At the time of marking and three times between 24 and 48 hours after, we searched in a 2 m radius for two minutes and noted the number, sex, and approximate age of any other anoles, in addition to whether the marked males were re-sighted.

We measured SVL and mass of all removed lizards and eight additional lizards. Body condition data were calculated as the residuals of mass about the known general allometric equation for anoles (Stamps *et al.* 1994) adjusted to our study species ($\text{mass} = (\text{SVL} / 35)^{2.94} - 0.46$).

We conducted aggression trials with 11 resident males. We placed another male as an intruder in sight of the resident male, 30 cm below him on the same stem. The five intruder males used had SVL of 49.0, 49.0, 43.9, 49.4, and 49.0 cm, equivalent to or smaller than the mean SVL of measured male anoles. We observed the behavior of the resident male for five minutes, recording the number of head bobs and dewlap extensions and the time at which they occurred. We also measured the time to attack, and if it occurred within five minutes, immediately separated the males and ended the trial. Attacks typically entailed the resident male running at the intruder and biting him, which resulted in the intruder running away.

RESULTS

We found that eight out of 16 territories from which male anoles were removed were reoccupied within 48 hours, a reoccupation rate of 50%. We re-sighted 5 out of 9 marked lizards (56%). The size of the original male did not affect the probability that a territory was reoccupied (logistic regression: $r^2_{15} = 0.11$, $P = 0.21$) nor the size of the reoccupying male ($r^2_4 = 0.58$, $P = 0.13$). For *N. polylepis* sampled, male body condition did not increase with SVL (instead it decreased with SVL: $F_{1,26} = 5.47$, $P = 0.027$, $\text{Body condition} = 1.94 - 0.04 \cdot \text{SVL}$, $r^2 = 0.17$). In aggression trials, as expected, resident males that were larger than the intruder tended to respond with aggression more quickly (including physical attack, head bob, or dewlap). However, aggression intensity was low (compared to a resource limited population: Calsbeek and Marnocha 2006), with only 2 out of 11 resident males (18%) physically attacking intruders within five minutes. The proportion of resident males attacking did not differ with the relative size of resident males (Fisher's exact test, two-tailed, $P = 0.455$).

DISCUSSION

Our findings failed to support bottom-up limitation of the *N. polylepis* population in Corcovado National Park, providing evidence in favor of the alternative, top-down limitation. Field observations suggesting high predation intensity were consistent with this conclusion. However, a stronger inference would be gained by positive tests of predator limitation, including predator-exclusion experiments and predation rate measurements.

We only re-sighted 56% of the marked anoles, which may have implications for the probability of reoccupation reported from our removal experiment. If a low re-sighting frequency was indicative of sampling flaws, there may have been a greater proportion of territories reoccupied than we reported, which would provide more evidence for resource limitation. If a low re-sighting fre-

quency were due to territory infidelity or predation, it would support the predation-limitation hypothesis. Data from Caribbean anole populations suggests that males are easy to re-sight on their territory (Calsbeek and Marnocha 2006) and in our own study we sometimes re-sighted males on their original perch. We also left two dead anoles on a log in the forest and found that they had disappeared within 24 hours, suggesting high predation pressure.

The different mechanisms of anole population limitation across anoles' geographic distribution have important implications for their life histories, evolutionary pressures, and ecosystem roles. While predator limitation would pressure anoles towards being r-selected, resource limitation would encourage k-selection. For one anole population (*Anolis sagrei*) in the Caribbean, resource competition and limitation shapes speciation through selection for large body size and competitive ability (Calsbeek and Smith 2007). In predation-limited anole populations, selection may work in the opposite direction and favor cryptic and smaller males. An anole population depressed by predation may have a weaker food web interaction with lower trophic levels (prey items) than an anole population limited by resources and therefore dependent on prey populations. Understanding the balance of population regulation mechanisms is essential to the study of ecosystems, especially in areas where environments are subject to change.

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SPATIAL STRUCTURE OF INDIVIDUALS WITHIN TROOPS OF THE MANTLED HOWLER MONKEY (*ALLOUATTA PALLIATA*)

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Abstract: In social animal groups spatial distribution of individuals may be important for defense and communication. We examined the distribution of male and female *Alouatta palliata* in a troop, hypothesizing that the sex of individuals would influence the spatial pattern of males and females. We hypothesized that males would position themselves closer to females to defend females from predators and rival males and that females would position themselves closer to other females to minimize time spent scanning. We observed three troops of *A. palliata* in Corcovado National Park, Costa Rica from 5 February to 7 February 2010 and recorded the sex composition of each troop and each individual's nearest neighbor every ten minutes during our observation period. We found that individuals were distributed at random with respect to sex. Our results imply that the sex of individuals is less important in determining spatial patterning within troops than the availability of leaves and other resources.

Keywords: *Corcovado, nearest neighbor, spatial distribution*

INTRODUCTION

In mantled howler monkey (*Alouatta palliata*) troops, sex is an important factor in determining dominance, with males dominant to all females (Wainwright 2002). Males scan for rival males and for predators more than females (Brown et al. 2010). Given this, it could be expected that males would position themselves closer to females than to other males to better defend females and that females would cluster together so males could defend them more easily. We tested this hypothesis by studying the spatial structure of *A. palliata* troops, with respect to the sex of individuals.

METHODS

We observed three troops of *A. palliata* in Corcovado National Park, Costa Rica. We observed the first troop from 0745 to 1015 and from 1340 to 1610 on 5 February 2010, the second troop from 1413 to 1613 on 6 February and the third troop from 0914 to 1024 on 7 February. We recorded the number of males and females present in the troop, and every ten minutes we recorded the sex of each adult monkey and the sex of its nearest neighbor.

We categorized nearest neighbor groupings as M:F (a male whose closest neighbor was a female), F:M (a female whose closest

neighbor was a male), F:F (a female whose closest neighbor was a female) and M:M (a male whose closest neighbor was a male). We excluded from analysis any observations where the individual had not moved since the previous observation because those observations were not independent. We calculated the expected number of nearest neighbor groupings for each ten-minute observation, with M representing the number of male *A. palliata* observed, F representing the number of female *A. palliata* observed and T representing troop size (Equations 1-4). We then compared the observed frequencies of nearest neighbor groupings to the expected frequencies using a Chi-squared test in Excel.

$$M : F = \frac{F}{T-1} \times \frac{M}{T} \quad \text{Equation 1.}$$

$$M : M = \frac{M-1}{T-1} \times \frac{M}{T} \quad \text{Equation 2.}$$

$$F : M = \frac{M}{T-1} \times \frac{F}{T} \quad \text{Equation 3.}$$

$$F : F = \frac{F-1}{T-1} \times \frac{F}{T} \quad \text{Equation 4.}$$

TABLE 1. Number of nearest neighbor pairings observed in three *A. palliatta* troops, in categories of male closest to female (M:F), female closest to female (F:F), female closest to male (F:M) and male closest to male (M:M). We sampled from 5-7 February 2010 in Corcovado National Park, Costa Rica.

Troop Number	Total Observed M:F	Total Observed F:F	Total Observed F:M	Total Observed M:M
1	51	113	54	1
2	12	48	11	1
3	4	9	2	0
All	67	170	67	2

RESULTS

Troop size ranged from four to ten individuals, with a maximum of two males in each troop. Troop 1 had 2 males and 4-8 females, troop 2 had 1-2 males and 5-7 females, and troop 3 had 1 male and 2-3 females. Troop size varied depending on which individuals were visible during each observation period.

Spatial structure was not evidently influenced by sex in *A. palliatta* ($\chi^2_3 = 5.71$, $P = 0.13$). The observed frequencies of 67 M:F, 170 F:F, 67 F:M, and 2 M:M were generally close to the expected frequencies of 61 M:F, 176 F:F, 61 F:M and 8 M:M (Table 1). Excluding times when only one male was present, the distribution was marginally significant ($\chi^2_3 = 7.35$, $P = 0.06$).

On February 6 2010, we observed an aggressive interaction between our focal troop and a neighboring troop. During the interaction, which lasted approximately 40 minutes, we observed females physically fighting, while the males vocalized. We also observed females pushing their infants away from any aggressive interactions.

DISCUSSION

Contrary to the prediction that males would position themselves closer to females to defend them from rival males, we found that males oriented themselves near females no more than would be expected by chance, suggesting that defense may not be a consequential driver of spatial position in the troop. Based on the aggressive interaction we

observed, males *and* females both play a role in troop defense.

In contrast to the prediction that females would position themselves closer to other females than to males, we found that females did not orient themselves near other females more than would be expected by chance. Females in a troop are not usually closely related (Pope 2000), so females may be more concerned with their own fitness than that of other females in the troop.

Our results also showed a trend toward males positioning themselves further from other males than from females. This may be due to male-male rivalry over mates within troops. A more extensive study could find more evidence of males avoiding other males within the troop. However our results imply that the sex of individuals is less important for spatial distribution of individuals within a troop than the distribution of leaves and other resources.

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TEMPERATURE AS A DETERMINANT OF *ATTA COLOMBICA* METABOLISM AND FORAGING BEHAVIOR

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Abstract: Poikilotherm metabolic activity increases with temperature, until reaching a threshold at which activity rapidly decreases. We asked whether *Atta colombica* (leaf cutter ants) in their natural environment experience warm temperatures beyond their upper critical temperatures, and whether their leaf piling behavior is a symptom of high temperature stress. We measured walking velocity of leaf-carrying ants as an indicator of metabolic activity and observed leaf piling behavior at varying temperatures. The travel velocity of ants increased with ground temperature up until ~36 °C, after which ants ceased carrying leaves and the creation of piles became frequent. High temperature stress occurs in both disturbed clearings and natural light gaps, and further deforestation or climate change may detrimentally influence the behavior leaf cutter ants and other poikilotherms.

Keywords: leaf cutter ants, leaf piles, metabolic performance, Osa peninsula

INTRODUCTION

Contrasting thermodynamic models seek to explain how poikilotherm metabolic performance changes with temperature shifts. Under the climatic envelope model, organisms are adapted to function at an optimum temperature range (Pearson and Dawson 2003). An alternative view, sometimes described as the “tyranny of thermodynamics” posits that temperature increases generally benefit poikilotherm performance, even in environments that already begin as quite warm. However, there must be a certain temperature, occurring naturally or not, at which poikilotherm activity crashes (Fig. 1).

The observation of a curious foraging behavior exhibited by leaf cutter ants—making leaf piles in the sun and coming back to pick them up later—prompted us to investigate the effect of temperature on foraging activity and efficiency of *Atta colombica* (leaf cutter ants). We attempt to pinpoint an upper critical temperature for *A. colombica* at which metabolic activity begins to decline. Secondly, we asked if the observed creation of leaf piles is a manifestation of heat stress, with the prediction that ants would only make piles at or above extreme upper temperatures. Finally we compared the natural range of temperatures occurring in forested areas to those

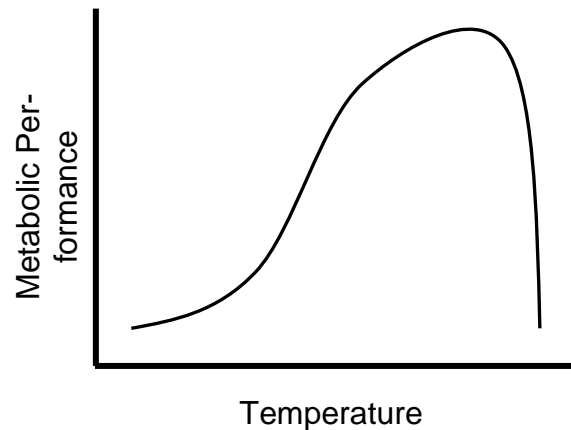


FIG. 1. The generalized model for poikilotherm metabolism as a function of temperature (Sharpe et al. 1977).

occurring in disturbed clearings to discern if naturally experienced conditions can reach the upper critical temperature.

METHODS

Experienced temperatures and temperature responses

We selected eleven active *A. colombica* trails (three in disturbed clearings) near and on Sendero Ollas at the Sirena Biological Station on the Osa Peninsula, Costa Rica. Between 0445 and 1700 on 6 February 2010 we visited each path four times to record ground

temperature (using a Raytek™ infrared temperature sensor) and to estimate average ant walking velocity as a measure of metabolic performance. We calculated velocity for five haphazardly chosen worker ants carrying leaves by recording the time it took for ants to walk 30.5 cm (1 ft). Ground temperature was measured at 15 cm from the starting point and was used as a proxy for ant body temperature.

Leaf-dropping behavior

On 7 February 2010, we observed three paths where the ants had aggregated leaves into piles the previous day, two occurring in light gaps along the Sendero Ollas in the forest, and one occurring nearby the Sirena station in an artificial clearing. We visited each path every hour (starting at 0800 and ending at 1700), and recorded the ground temperature in the clearing and whether or not a pile had been formed.

For another path occurring directly in a clearing behind the Sirena station, we manipulated the natural shade by extending it by ca. 3m using chairs. Consequently, an area that would normally have received direct sunlight at the time of our experiment was maintained in constant shade. Every half hour (from 0715 to 1715) we recorded the ground temperature at 0.75 m into the unshaded area. A pilot study showed the ants took approximately one minute to walk from the start to end of the experimental zone (0-1.5 m past the shade boundary). For two minutes we counted the number of leaf-carrying ants that entered and exited the zone, delaying the counting of exiting ants by one minute. We calculated the ratio of leaves being carried out to leaves being carried in, to see the proportion that were being dropped in a pile.

RESULTS

The travel velocity of leaf carrying ants increased significantly with ground temperature (Fig. 2; linear model: $r^2_{38}=0.16$, $P = 0.007$; second order polynomial model: $r^2_{38}=0.14$, $P = 0.06$).

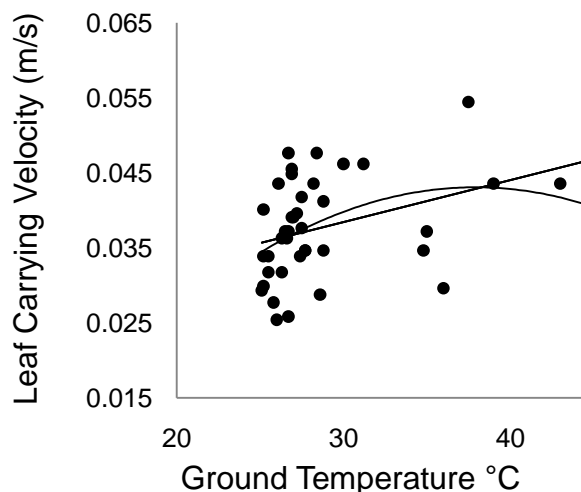


FIG. 2. Travel velocity of leaf-carrying ants as a function of ground temperature at Sirena Biological Station at Corcovado National Park, Costa Rica on 6 February, 10. Functions show linear regression and 2nd order polynomial regression.

Ants began dropping leaves when temperature exceeded about 35 °C. At temperatures above 38 °C we observed no leaf-carrying ants walking more than one meter without dropping their leaf. Even on trails that were previously noted to develop piles in sunlight, we did not observe the formation of piles the following day when the temperature did not exceed 28 °C. We also observed ant paths that became as warm as 68 °C in full sunlight (and lacked leaf-carrying ants at those times).

Prior to experimental manipulation, we observed ants dropping leaves at the natural shade boundary at 1020 on 6 February when ground temperature was 43 °C. At that same time and location on 7 February, under the shade created by our manipulation, the temperature was 29 °C and the ants did not drop their leaves, but rather proceeded to carry leaves as normal. Within the 0.75 m interval following our shade manipulation, ants abandoned leaves when temperatures exceeded 35 °C and returned to pick up the abandoned leaves when temperatures subsided (Fig. 2).

In undisturbed forest, ground temperature in light gaps reached a maximum of 51.5 °C. Ground temperature in the shade ranged from 25.1 to 29.3 °C.

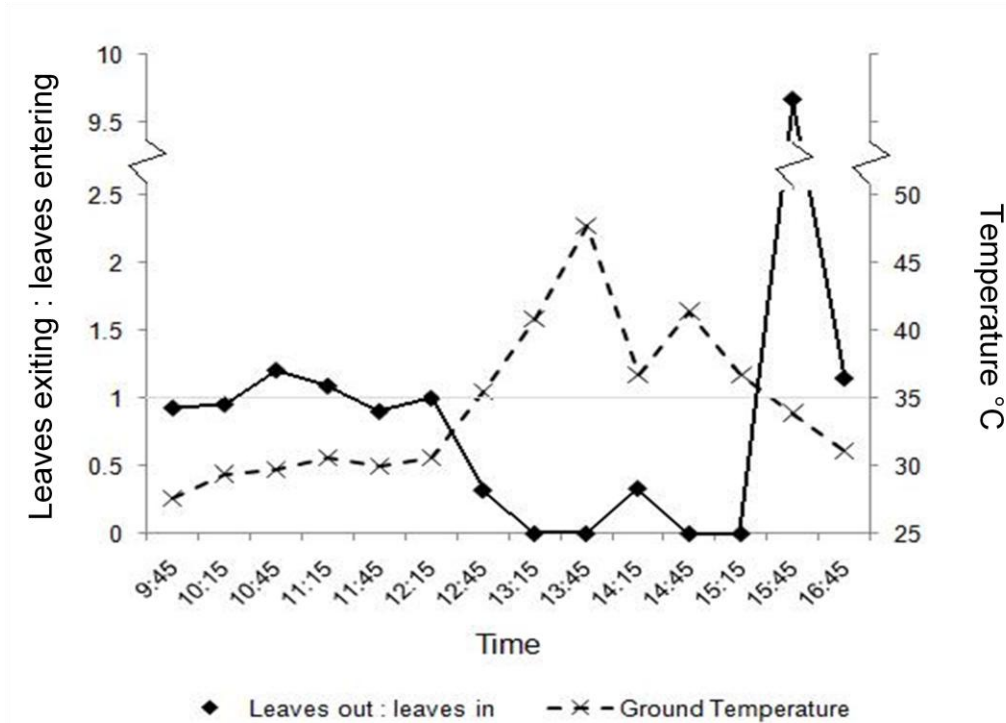


FIG. 2. The ground temperature and the leaf retention ratio of ants traveling through a sunny stretch of trail following an artificially shaded stretch of trail throughout the day of 7 February, 2010. The experiment was conducted using a trail next to a building associated with the Sirena Biological Station in Corcovado National Park, Costa Rica.

DISCUSSION

High temperatures influence the foraging behavior of *A. columbica*. As expected, ant metabolic performance, measured by walking velocity, increased with temperature (Fig. 2). Although the polynomial model did not provide as close of a fit as the linear model, it predicted a decrease in walking velocity around 35 °C, which approximated the temperature at which ants dropped their leaves. The critical upper temperature for leaf cutter ant foraging seems to be about 35 °C.

Frequently ants would place leaves into a pile immediately upon entering areas of high temperature. Our experimental manipulation of shade, as well as our observations of daily temperatures in forested areas, demonstrated that ants abandon leaves on the basis of temperature, not time of day or location. Abandoning leaves is apparently a symptom of heat stress. When temperatures dropped below about 35 °C ants began to collect dropped leaves. We hypothesize that leaf piling is an

adaptive strategy allowing ants to forage more efficiently where high temperatures would otherwise prevent them from foraging at all.

In disturbed clearings, as well as some naturally occurring light gaps, temperatures can exceed the upper critical temperature for *A. columbica*. Deforestation and climate change both have the potential to increase the frequency of critically warm temperatures in leaf cutter habitats. Leaf cutter ants are regarded as a keystone species (Hull-Sanders and Howard 2003, Fowler et al. 1989), so any decrease in foraging efficiency as a result of increasing temperature would have broader impacts for the forest ecosystem.

We provide evidence that temperatures can become too warm for poikilotherms in the tropics, which favors the climatic envelope model over the alternative viewpoint that warmer is generally better (tyranny of thermodynamics). The relatively small buffer between naturally occurring temperatures in the tropics and upper critical temperatures sug-

gests that tropical systems may be quite susceptible to climate warming and other disturbances (e.g., forest clearing) that increase experienced temperatures.

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LEAF IT ALONE: COLONY SPECIFIC PHEROMONES DETERMINE LEAF PREFERENCE IN *ATTA COLOMBICA*

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Abstract. Social insects require means of communicating between members that are particular to the target group. Our study investigated the hypothesis that *Atta colombica* use colony specific pheromones to signal which leaves should be taken to cultivate its fungal mutualist. We examined three different colonies and recorded their behavior when presented with piles of leaves cut by their own colony, a foreign colony, and the experimenters. We found that *A. colombica* preferred to use leaves cut by their colony, which supports the hypothesis that they can differentiate their colony's pheromones, which may help each colony control nutrition intake.

Keywords: *Corcovado*, *leaf-cutter ants*, *pheromones*

INTRODUCTION

Leaf cutter ants utilize chemical cues to communicate among colony members and can distinguish between communication pheromones produced by their own colony and those produced by other colonies (Hernandez 2005). In this study, we examine the hypothesis that *Atta colombica* use pheromones to signal to fellow colony members to pick up leaves and that these pheromones are colony specific. Having a colony specific leaf retrieval pheromone could enable the ants to mark their feeding territory and perhaps enable them to control what type of plant material is being taken to the fungal mutualist. If leaf cutter ants do not use leaf retrieval pheromones, they would indiscriminately pick up leaves cut by their own colony, foreign colony and humans. If *A. colombica* have a general leaf retrieval pheromone, they would pick up leaves cut by both their own colony and a foreign colony. If the ants have a colony-specific pheromone, they would only select leaves cut by members of their own colony.

METHODS

At Sirena Biological Station in Corcovado, Costa Rica on 7-8 February 2010, we selected three *A. colombica* trails separated by at least 200 m from one another to ensure that they were not the same colony (Rockwood

1976). From a utilized plant particular to each colony, we obtained leaves to be cut by the home colony, the foreign colony, and us. These three piles contained the same species of leaves, but the type of leaf differed depending on the home colony. To obtain leaves cut by a foreign colony, we placed whole leaves on the trail and collected each piece as it was cut. We minimized direct contact with the leaves to ensure that the possible ant pheromone would not rub off and conducted our study with leaves collected within two hours of the treatment.

For each colony (far, middle, and station), we ran 20 trials with three piles of 10 leaves for each treatment, placed in randomized order along the trail and separated by 5-10cm from the nearest pile. We observed the *A. colombica* for 7 minutes, and recorded the number of leaves taken along the trail (used), put aside the trail (dumped), or not picked up (ignored).

TABLE 1. Three-way ANOVA looking at the impact of two different days, three different colonies, and three different types of leaf piles on the number of leaves *Atta colombica* took back to their colony in Corcovado, Costa Rica.

Source	F Ratio	P-value
Day	0.07	0.79
Colony	84	0.0001
Day x Colony	1.94	0.15
Leaf Type	12.62	0.0001
Day x Leaf Type	3.62	0.03
Colony x Leaf Type	10.89	0.0001
Day x Colony x Leaf Type	4.18	0.003

RESULTS

We found that the far colony used the most leaves and the station colony used the least. This pattern remained constant across the two days, but *A. colombica* used more leaves overall on the second day (Table 1).

The number of leaves used also depended on the leaf type, where *A. colombica* in all three colonies used more leaves cut by their own colony than by a foreign colony or by us (Figure 1).

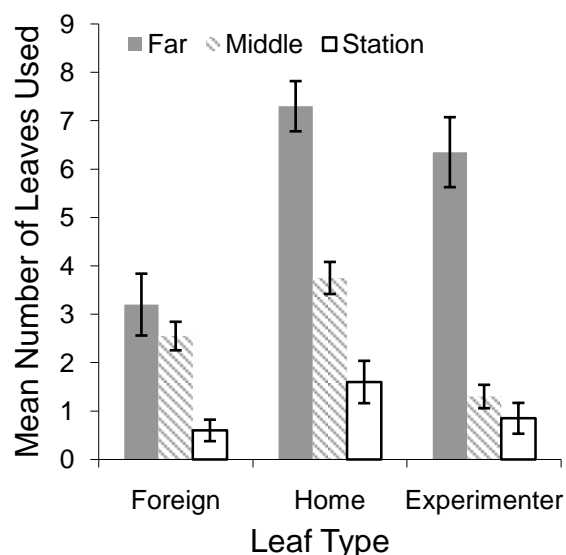


FIG. 1. Mean number of leaves used by *Atta colombica* in three different colonies in Corcovado, Costa Rica. When presented with leaves cut by their own colony, by a foreign colony, and by the experimenters, the ants preferred to use the leaves cut by their own colony ($F_2 = 12.62$, $P = 0.0001$). Error bars represent ± 1 SE.

We did not find a relationship between the order of the piles and the residuals of the average number of leaves used ($t_{178} = 1.19$, $P = 0.24$), however we did find a negative relationship between time of day and leaf usage in the station colony ($t_{58} = 2.56$, $P = 0.013$).

DISCUSSION

Our findings that *A. colombica* prefer to use leaves cut by their own colony over leaves cut by another colony support the hypothesis

that each colony has a specific pheromone to signal leaf retrieval. We also observed that *A. colombica* did not seem to differentiate between foreign or human-cut leaves, possibly because they can only detect their colony's pheromone. Unlike the other two sites, our results for the station colony varied with time, possibly as a result of larger temperature fluctuations due to direct sunlight. Between 1400 and 1700, we observed that the ants were dropping leaves and not picking up any new ones. We suggest that further studies control for temperature to better support the hypothesis.

Colony-specific leaf retrieval pheromones may be important for the development of the colony, since the nutritional needs of each colony may change depending on its life stage (Farji-Brener 2001). *A. colombica* could use these specific pheromones to ensure that the workers only collected the leaves beneficial to the colony at the time. Our study sheds light on how social insects rely on chemical cues to communicate and ensure the success of their colony.

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I'VE GOT ANTS IN MY PLANTS: THE OCCUPATION OF *APHELANDRA SCABRA* BY ANTS IN CORCOVADO NATIONAL PARK, COSTA RICA

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Abstract: We discovered several species of ants occupying inflorescences, consuming nectar from extrafloral nectaries, and sometimes attacking insect visitors on *Aphelandra scabra* plants. We tested whether the ant-*A. scabra* interactions could be a mutualism, a parasitism, or whether there was evidence of coevolutionary hotspots as predicted by the geographic mosaic model of coevolution. We compared the type and average number of ants per inflorescence with respect to number of non-ant visitors and fruiting success. We found a greater number of ants on non-fruiting plants, suggesting that the ants are either parasites or do not receive nectar from fruiting plants. We also observed an apparent preference of putative nectar robbers for inflorescences without ants, but further study is needed to characterize the nature of this ant-plant interaction.

Key Words: *Acanthaceae*, *extrafloral nectaries*, *fruit*, *inflorescences*, *Osa peninsula*, *mutualism*, *parasitism*, *pollination*

INTRODUCTION

Plant-insect interactions exist in a variety of complex forms, and provide insight into the study of coexisting and coevolving species. *Aphelandra scabra* (Acanthaceae), a plant endemic to the Osa Peninsula in southern Costa Rica, shows evidence of relationships with multiple species that have yet to be fully examined. *A. scabra* produces tube shaped corollas adapted for pollination by hummingbirds attracted to floral nectar (Zuchowski 2007). The plant's inflorescences produce nectar from extrafloral nectaries on the bracts that attract ants (Fig. 1). Different species of ants, some of which behave aggressively when disturbed, occupy different *A. scabra* plants even when in close proximity to each other, while nearby plants may not have any ants present. There are several possible explanations for the interaction between ants and *A. scabra*: (1) ants are inconsequential to plants, (2) the ants and plants have a mutualistic relationship where inflorescences provide nectar rewards and ants protect against nectar robbers or seed predators, or (3) a parasitic relationship where ants steal costly nectar rewards without providing any benefit to the plant. The nature of the interaction could vary geographically depending on local conditions, consistent with the geographic mosaic model of coevolution (Forde et al.

2004). We tested for evidence of a mutualism by comparing plants with and without ants with respect to (1) visits by potential antagonists and (2) the frequency of fruiting within inflorescences. We distributed our sampling across multiple patches to allow for spatial variation in the interactions.



FIG. 1. An *Aphelandra scabra* inflorescence exhibiting extrafloral nectaries (indicated by the arrow) on the bracts.

METHODS

We compared twelve pairs of *A. scabra* plants in the rainforest understory along the Guanacaste, Sirena, and Naranjos trails near the Sirena Biological Station in Corcovado National Park, Costa Rica on 5-7 February 2010. We sampled three pairs along both the Sirena and Guanacaste trails and six pairs along the Naranjos trail. Sites were separated from the nearest neighboring site by ca. 5 – 400 m of trail distance. Each pair included one fruiting and one non-fruiting plant matched for size and number of inflorescences. For each plant we recorded the number of visitors and inflorescences visited over a 15-minute period, as well as the type of ant present (small black, medium black, large red, or none) and average number of ants per inflorescence for five haphazardly chosen inflorescences. Because inflorescences can only produce fruit once they reach a certain size, we estimated the percentage of small, medium, and long inflorescences on each plant. As a measure of average pollination success, we collected all the fruiting inflorescences on a plant and found the average percentage of seeds that had fruited per inflorescence.

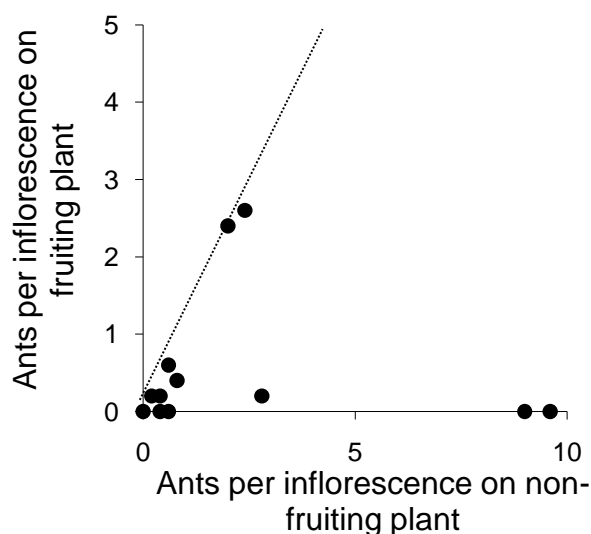


FIG. 2. Comparison of ants per inflorescence on 10 pairs of fruiting and non-fruiting *Aphelandra scabra* plants along three trails near the Sirena Biological Station in Corcovado, Costa Rica (paired $t_{22} = 1.84$, $P = 0.08$). Line of equality is indicated.

RESULTS

Non-fruiting plants tended to have more ants per inflorescence compared to fruiting plants (Fig. 2). The fruiting status of a plant did not affect the number of visitors (paired- $t_{22} = 0.34$, $P = 0.74$) or the number of inflorescences visited (paired- $t_{22} = 0.19$, $P = 0.85$). Among fruiting plants, those occupied by large red ants had the highest average pollination success, and those occupied by small black ants had the lowest average pollination success, though the difference was not significant ($F_{3,8} = 0.32$, $P = 0.81$). We observed that bees tended to visit inflorescences without ants and, if ants were present, would not land until the ants had left. We also observed a troop of squirrel monkeys feeding on nectar from inflorescences without ants. Visual examination of our data did not reveal any geographical patterns in our response variables. As the percentage of long inflorescences on a plant increased, the probability of that plant having fruit significantly increased (Fig. 3).

DISCUSSION

We were unable to conclude whether ants and *A. scabra* exhibited either a mutualistic or parasitic relationship. Since we observed no difference in the numbers of pollinators visiting fruiting or non-fruiting plants, our results do not indicate whether ants defend inflorescences from potential nectar robbers or parasitic insects. Based on our anecdotal evidence that visitors avoided inflorescences with ants, it is possible that either a mutualistic or a parasitic relationship exists (depending on whether visitors are beneficial or detrimental), but our small sample size failed to reveal either relationship. In addition, because ant-*A. scabra* interactions did not vary across a spatial distribution, there is no evidence of the geographic mosaic model of coevolution.

Although ants were more likely to be located on non-fruiting plants than on fruiting plants, we were unable to determine a causative relationship. While it is possible that the

presence of ants may in fact be detrimental to the plant's reproduction, it is also possible that fruiting plants, which have longer and older inflorescences, may have decreased nectar production and thus a decreased ability or need to attract ants.

There is still much more to learn about the ant-*A. scabra* system. While we know that hummingbirds are the main pollinators, we do not know the nature of the insect visitors and their effects on the plants. While we observed many insect visitors consuming pollen and drinking nectar when in contact with the reproductive structures of the plant, we also observed other insects bypassing the reproductive structures and reaching the nectar at the bottom of the corolla.

pollination. Future studies are needed to more accurately relate the number and type of visiting insects to the reproductive success of the plant.

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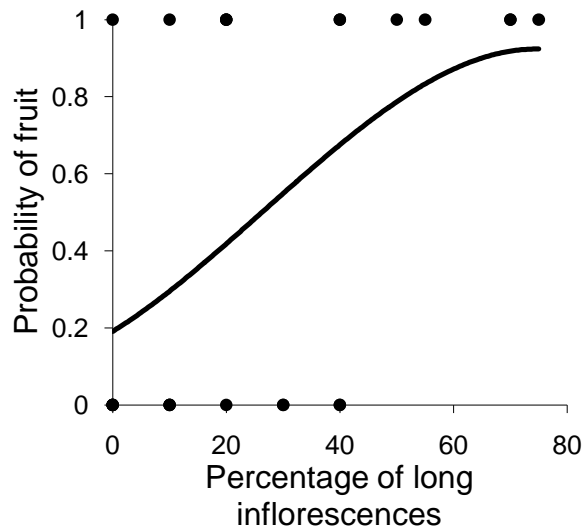


FIG. 3. Probability of an *Aphelandra scabra* plant having fruit versus percentage of long (older) inflorescences. Points are actual field observations at Corcovado, Costa Rica for fruiting and non-fruiting plants (function shows best-fit logistic regression, $\chi^2_1 = 6.74$, $P = 0.009$).

Thus, our assumption that insect visitors act as parasites may not be accurate, in which case we may not have been measuring the correct variables to determine how ants affect

DOES POOL SURFACE AREA TO VOLUME RATIO AFFECT NICHE PARTITIONING IN TROPICAL STREAM FISH?

CHASE R. RAINES AND DANIEL R. O'DONNELL

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Abstract: Competitive interactions can often drive similar species to distribute themselves in ways that reduce niche overlap. We examined the hypothesis that competitive interactions would drive two species of tetra (order Characiformes), *Hyphessobrycon savagei* and *Astyanax fasciatus* to feed in different vertical strata (e.g., surface and hypolimnion) of isolated pools in a tropical rain forest stream in Corcovado National Park, Costa Rica, and that food limitation would differ among pools with different surface area to volume ratios. We measured combined density and proportional abundances of the two species, as well as the time it took for fish to consume a provided food source (a measure of hunger). Though overall fish density was related to surface area to volume ratio, proportional abundances of the two species was not, and overall density was dominated by one species, *H. savagei*. Consumption time of a provided food source decreased with increasing surface area to volume ratio, but the trend was driven by a single point. Collectively, our results imply that the two species do not occupy entirely distinct niches, or that proportional abundances and food limitation are not strongly related to surface area to volume ratio of pools.

Key Words: Corcovado, density, food limitation, national park, niche differentiation, proportional abundance.

INTRODUCTION

Competitive interactions often lead to spatial niche partitioning among similar species. In fish, competition for food can lead to spatial niche partitioning, both horizontally and vertically (Arcifa, et al. 1991). Two species of tetra occupy the Quebrada Cameronal, Corcovado National Park, Costa Rica (Constantz *et al.* 1981). These two species are similar in size and are both highly active. Both species are pelagic, but one (*H. savagei*) appeared to occur closer to the surface, while the other (*A. fasciatus*) occurred in lower strata and often fed benthically. We examined the hypothesis that two species of tetra would distribute themselves vertically in isolated pools, such that the more surface dwelling species would rely primarily on allochthonous inputs from above for food, while the more benthic species would rely on other food sources (e.g., benthic invertebrates). Under this hypothesis, *H. savagei*, should have the highest proportional abundance in pools with high surface area to volume ratio, as these pools would trap the most allochthonous input per volume, and *A. fasciatus*, should have higher proportional abundance in pools with low surface

area to volume ratio, as they should not be as dependent on allochthonous inputs. We also tested the prediction that *H. savagei* in pools with low surface area to volume ratio would be more food limited, and should thus consume a floating food source faster.

METHODS

We measured abundances of *A. fasciatus* and *H. savagei* in pools with differing surface area to volume ratios in Quebrada Cameronal near Sirena Biological Station in Corcovado National Park, Costa Rica, on February 5-7, 2010, and quantified food limitation for *H. savagei*. We studied 12 pools ranging from 6 to 29 meters in length and from 0.15 to 0.31 m in depth, with 4 pools beginning approximately 50 m downstream of Sendero Ollas and eight pools directly upstream of the trail. We labeled pools 1-12 in ascending order beginning with the pool farthest downstream. We measured the length of each pool, five evenly spaced widths, and three depths along each width (0.5 m from each bank and in the center). We estimated total fish density and density of *A. fasciatus* on separate days by simultaneously counting the number of fish we observed in two randomly placed 0.625 m

X 0.625 m metal quadrats. We repeated counts three times at 30-second intervals on four separate occasions per pool. We estimated *H. savagei* abundance by subtracting the *A. fasciatus* abundances from the total tetra abundance as those were the only two species of fish recorded. We measured feeding rate by tossing 0.05 g of cricket food (mostly corn meal) four times into randomly selected points in each pool and measuring the time until all particles were consumed.

RESULTS

Surface area to volume ratio was unrelated to proportional abundances of the two species. Total abundance of fish decreased with increasing surface area to volume ratio (linear regression: $F_{1,10} = 26.41$, $P = 0.0004$; Fig. 1). The density of *A. fasciatus* did not change with surface area to volume ratio ($F_{1,10} = 0.01$, $P = 0.93$), while the density of *H. savagei* decreased significantly ($F_{1,10} = 31.63$, $P = 0.0002$; Fig. 2), indicating that the trend in total fish density was driven entirely by *H. savagei*. There was no relationship between the difference in proportional abundances of the two tetra species and surface area to volume ratio ($F_{1,10} = 1.87$, $P = 0.20$, $R^2 = 0.15$). Food consumption time decreased with surface area to volume ratio ($F_{1,10} = 5.97$, $P = 0.03$; Fig. 3), though the trend was mostly driven by a single point. The trend was not significant with the point removed ($F_{1,9} = 1.09$, $P = 0.32$, $R^2 = 0.11$).

DISCUSSION

The hypothesis that surface area to volume ratios of pools would affect the fish composition through niche differentiation in two species of tetras was not supported by our data. Although the combined density of tetras showed the predicted negative relationship with increasing surface area to volume ratio, the lack of a relationship between proportional abundances and surface area to volume ratio suggests that other factors may be driving fish assemblages. Also, the trend in overall density was driven primarily by the

density of *H. savagei*, indicating that *H. savagei* is simply the dominant species in every pool, regardless of surface area to volume ratio. It is possible that the fish in each pool were simply those trapped when the water level dropped at the end of the wet season, causing fish assemblages to follow no particular pattern other than being dominated by *H. savagei*.

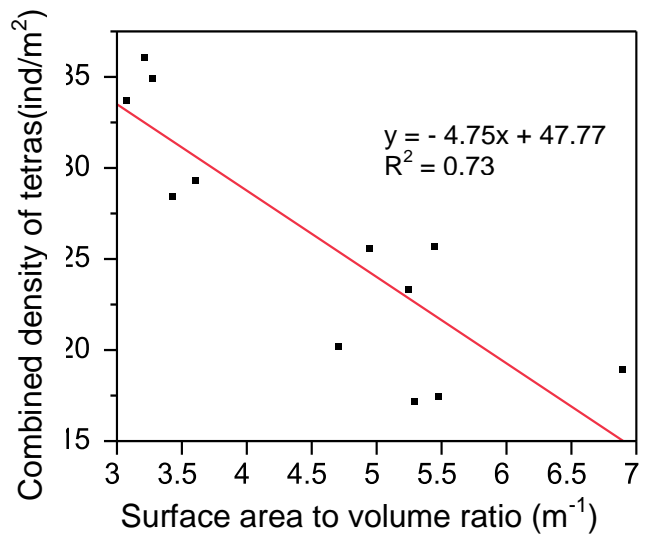


FIG. 1. Combined density of tetras decreased with surface area to volume ratio in the Quebrada Cameronal, Corcovado National Park, Costa Rica.

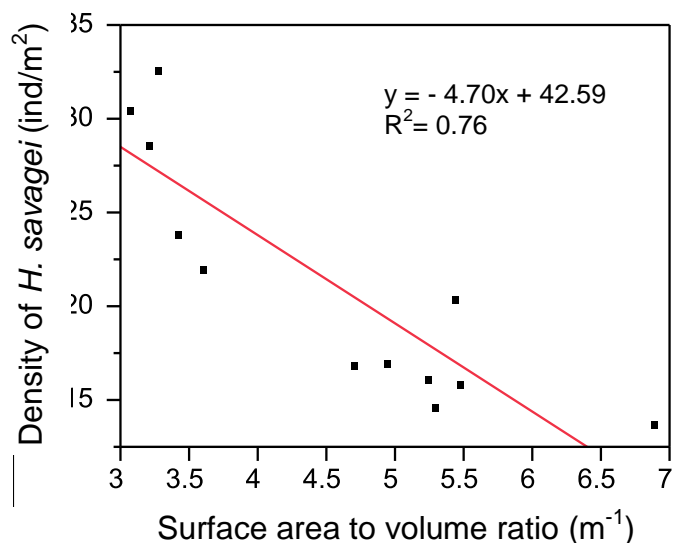


FIG. 2. Density of *H. savagei* decreased with surface area to volume in the Quebrada Cameronal, Corcovado National Park, Costa Rica.

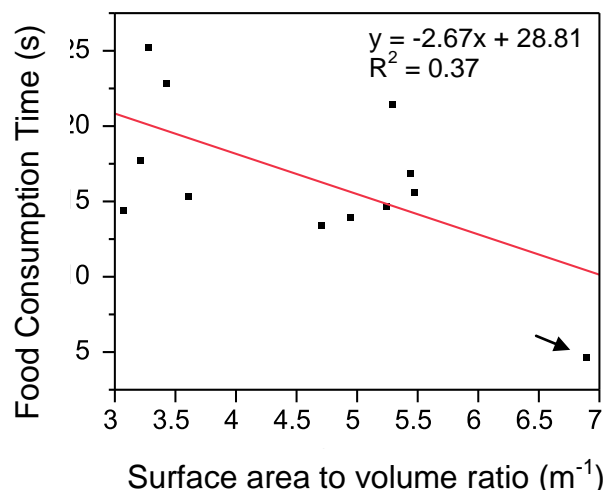


FIG. 3. In the Quebrada Cameronal (Corcovado National Park, Costa Rica), fish consumed food significantly faster in pools with low surface area to volume ratios, however the trend was driven mostly by a single point (indicated by arrow).

Other biotic and abiotic factors may be driving fish assemblages in the Quebrada Cameronal. Piscivory can affect fish assemblages (Jackson et al. 2001), and may be important in the Quebrada Cameronal, as we observed some predatory species of fish and crustaceans. The relationship between surface area to volume ratio and food limitation was not as we predicted, indicating that other factors are likely limiting food availability in the pools. We did not take into account the structural differences among pools, nor did we consider the possible differences in canopy composition above the pools. The ecological niches of the two species may not be distinct, or may be entirely different than what we had thought.

This study could have been improved by fully studying the diets of the two fish species and quantifying the food availability for each pool, as we based this vital information on anecdotal evidence and approximations. Also, fish in some pools appeared attracted to the sediment that we stirred up when placing quadrats, which may have affected the accuracy of our density estimates.

The surface area to volume ratio did not explain niche differentiation in two species of

tetra, leaving the question of their co-occurrence unanswered. Further study is needed to investigate the interactions of these species to see if niche differentiation exists and what factors might be important in determining their niches. Similar species are seen to co-occur in all ranges of environments, and though it would be convenient to explain this phenomenon with a single, quantifiable environmental factor, it is not surprising that the explanation will require a more nuanced understanding of the system.

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IRIDESCENCE IS A FLY'S BEST FRIEND: PARTITIONING OF LIGHT GAP RESOURCES BY SYRPHID FLIES

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Abstract: Males of some insect species exhibit lekking behavior. We hypothesized that male Syrphid flies in the forests of La Selva, Costa Rica were forming leks in light gaps at specific times of day to maximize visibility and energy efficiency. We also hypothesized that non-iridescent bee mimics would prefer higher light intensities because they are not as visible as iridescent morphotypes in low light conditions. We found a relationship between fly count and time, with flies decreasing over time from 0800-1200 until no additional flies were observed. Our results also supported our light intensity predictions, with the proportion of bee mimics showing a significant positive correlation with light intensity and the proportion of iridescent flies exhibiting no relationship with light. This may have implications for resource partitioning among morphotypes.

Key Words: flower flies, hover flies, La Selva, leks, mating behavior

INTRODUCTION

Syrphidae are flower flies that feed primarily on nectar as adults. In La Selva we observed several syrphid species, a bee mimic and multiple iridescent species in the genus *Ornidia*, hovering in mixed morphotype groups in light gaps in the forest. We hypothesized that the gatherings were leks and predicted that they would be composed primarily of males, that the males would engage in competitive behaviors, and that the location of the gatherings would be predictable in space and time. We examined whether or not the flies exhibited a daily rhythm, aggregating in gatherings at certain times of day. Male flies can only engage in hovering for a short time before needing to refill their crops to sustain the energetic requirements of flight and would be expected to budget their time between reproductive behaviors like hovering in leks and feeding (Gilbert 1984).

We also investigated the function of gathering in light gaps. We hypothesized that light gaps increased the visibility of male flies to females and that different morphotypes of flies would partition the light gap based on light intensity. The *Ornidia* species may be able to inhabit areas of less intense light than the bee mimics because their iridescence augments their visibility. We predicted that the composition of morphotypes would

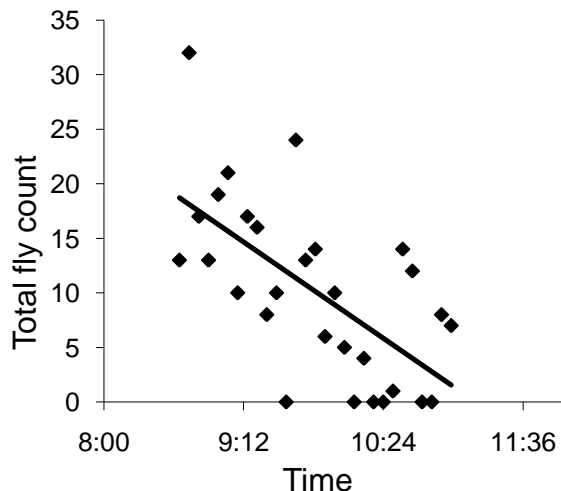


FIG. 1. Total fly count as a function of time. Fly abundance significantly decreased over time from 08:38-10:59 in La Selva Biological Station on February 16, 2010 ($r^2_{27} = 0.41$, $P < 0.01$).

reflect light intensity and that we would find bee mimics primarily during times of higher light intensity because they are less apparent than *Ornidia*. Alternatively, Syrphids may gather in light gaps for thermoregulatory benefits; Syrphids are ectotherms but may behaviorally regulate their temperature by shivering their flight muscles or basking for radiative heat gain (Gilbert 1984). If the Syrphids gathered in light gaps to thermoregulate, we would expect fly numbers to increase with temperature.

METHODS

On February 14-16 2010, we recorded average temperatures and fly presence or absence throughout the day at two light gap sites chosen after a preliminary survey for fly presence at the La Selva biological station in Costa Rica. Both sites were located within the Arboleda along the Sura trail and were approximately 50 meters apart. We also captured and sexed several individuals on each day of our study, recognizing males by their holoptic eyes.

We spent several hours on February 15 observing fly behavior. We looked for interactions between individuals as well as for feeding behavior.

On February 16, when flies were present we recorded total fly number, the number of morphotypes, the number of each morphotype present, and the light intensity on a scale from 0 to 3 (with 3 being most intense) every ten minutes for two hours. In our study we recognized two morphotypes: a dark red-eyed bee mimic about 1.5 cm in length and a green and copper iridescent fly about 1.25 cm in length.

RESULTS

Syrphid flies were only present at our sites during the morning hours. During this period, temperature and light intensity varied independently, though both were correlated with time. Temperature range appears negligible however, with a range of only 4°C between the morning maximum and minimum.

More flies were present when the light intensity was higher ($r^2_{27} = 0.28$, $P < 0.01$) and fewer flies were present later in the day (Fig. 1).

The proportion of bee mimics was significantly greater at higher light intensities (Fig. 2) while the proportion of iridescent flies did not vary significantly with light intensity (Fig. 2).

All individuals captured during the study were male. There were no flowers within the aggregating site, and so we observed no evidence of feeding behavior. We ob-

served several instances of interactions between individuals and larger groups, including chasing and position switching, within and between species.

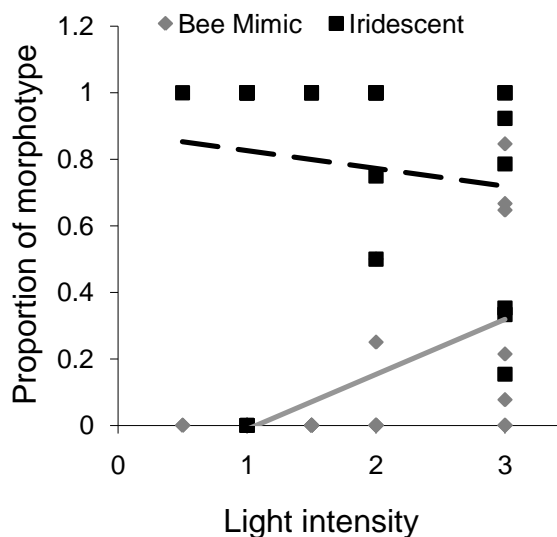


FIG. 2. Proportion of bee mimics (gray solid line; $r^2_{27} = 0.34$, $P < 0.01$) and iridescent (black dotted line; $r^2_{27} = .02$, $P < 0.52$) syrphids in the total population across light intensity at La Selva Biological Station on February 16, 2010.

DISCUSSION

The prediction that non-iridescent bee mimics would prefer brighter light gaps whereas iridescent flies would show no preference was supported by our findings. This may be a result of their iridescence, allowing them to be visible in a range of light conditions. This is perhaps an adaptation to syrphid competition in light gaps, allowing them to maximize their visibility in a habitat where direct light is rare.

There was also a significant relationship between time and total fly numbers, with the flies slowly decreasing over time and disappearing after noon. This supports our hypothesis that the flies would lek only at a specific time each day, in order to maximize their visibility and budget their energy. However, light intensity also decreased over time. Time alone does not explain the proportions of morphotypes because sites were measured simultaneously and bee mimics were only observed at one of the sites. Further studies

should be done to determine whether light intensity or time have a greater impact on lekking populations.

Syrphids have intricate behavioral patterns that are not yet well understood. However, our study has demonstrated that different syrphid species have the ability to share territory and may even be partitioning light among morphotypes. This partitioning of light resources is an example of niche-differentiation which permits the coexistence of potentially competing species and fosters diversity.

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THE ROLE OF HITCHHIKING MINIMA IN COLONIES OF *ATTA CEPHALOTA*

AMANDA M. DEVINE

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Abstract: Leaf-cutter ants exhibit "hitchhiking" behavior, in which small worker ants ride on leaf fragments carried to the colony by larger worker ants. Four hypotheses have been proposed to explain this behavior: colony energy conservation, defense against parasitoids, fungal removal and preparation of the leaf fragments, and sap consumption. In order to investigate which hypotheses may be correct, I examined frequencies of hitchhiking and characteristics of leaves, worker ants, and hitchhiker ants at La Selva Biological Station to determine whether there were nonrandom distributions of hitchhikers or correlations between different traits. I found evidence only of parasitoid defense, although several correlations and personal observations suggest that a fifth hypothesis, rapid transport back to the colony, may also be possible.

Key Words: ants, *Escovopsis*, fungus, leaf-cutting, phorids, parasitism

INTRODUCTION

The leaf-cutter ant species *Atta cephalota* exhibits several distinct morphotypes that constitute its caste system. Different morphotypes perform different jobs, such as foraging, tending to larvae, structural maintenance, or farming fungus. Intermediate sized ants, majors, are workers that leave the nest to collect leaf fragments which they bring back to nourish the fungus that feeds the colony. Another caste, minima or small worker ants, are often seen riding on the leaf fragments carried back by the majors.

There are four potential theories to explain hitchhiking minima. One theory proposes that hitchhikers walk out to the harvesting site to fulfill some unknown function, and then are carried back by the workers to conserve the total amount of energy the colony is expending (Yackulic and Lewis 2007). This would only be true if it is more energy efficient for larger ants to carry smaller ants back than for both the majors and minima to walk back. One would expect to see a relatively even distribution of hitchhikers riding on workers, as a single small additional weight may not have a great impact on a large worker but would save the hitchhiker the energy it would have used to walk back.

A second theory proposes that the hitchhikers provide a defense against parasitoids of the workers. Phorids are a family of

flies that parasitize leaf-cutter ants by landing on leaf fragments carried by workers and then ovipositing into the workers. Their larvae hatch inside the worker, consuming it from within, and emerging in order to pupate. Hitchhikers may provide defense against these parasitoids by preventing them from landing (Yackulic and Lewis 2007), and thus preventing the phorid offspring from infiltrating the colony through the bodies of the workers. Larger workers provide more food to developing fly larvae, and increase their likelihood of survival, making them attractive targets for parasitism (Erthal and Tonhasca 2000). Thus, there may be more hitchhikers on leaves carried by larger workers in order to better protect the workers.

A third theory proposes that the hitchhikers are responsible for cleaning and preparing the leaf fragment prior to return to the colony. *Escovopsis* is a parasitic fungus that can consume the nutrients of the ant fungus if introduced into the gardens, and it may be present on leaf fragments. These fragments are much less likely to carry *Escovopsis* if cleaned and prepared beforehand (Reynolds and Currie 2004) so it is possible that the hitchhikers are responsible for this preparation (Yackulic and Lewis 2007). If this is the case, then larger leaf fragments, with a greater surface area, may require more hitchhikers to be adequately cleaned.

A fourth theory proposes that hitchhikers may be responsible for obtaining sap from the leaf fragments prior to depositing them in the fungus garden. Sap from leaves is a primary food source for adult workers (Yackulic and Lewis 2007), and hitchhikers may be harvesting it from leaf fragment edges prior to depositing the fragments in the fungus garden. If this is the case, then again, larger leaf fragments, with a greater volume of sap, may require a greater number or mass of hitchhikers in order to fully harvest it.

METHODS

I looked at frequencies of hitchhiking and characteristics of workers, hitchhikers, and leaves, to determine the purpose of the hitchhikers. On 14-15 February 2010, I observed two leaf-cutter trails on two separate paths at the Estación Biológica La Selva in Costa Rica: the path heading to the Estación del Río, located near the ant colony; and 200 m down the Sendero Surá, near the tree where the ants were harvesting. It is unknown whether these two leaf-cutter trails were from the same or separate colonies. I observed each of these trails at two different times of day: morning, from 0800 - 1200; and afternoon, from 1300 - 1700.

For each observational period, I counted the number of hitchhikers on each leaf that passed a point on the trail in a 10 minute period, to determine frequencies of numbers of hitchhikers on a leaf. I then used these observed frequencies and the mean number of ants on one leaf fragment to calculate a Poisson distribution of expected frequencies if the hitchhikers were distributing themselves randomly on the leaf fragments. Using a χ^2 analysis, I determined whether my observed frequencies were more uniform or aggregated than expected under a model of random dispersion (Fig. 1).

To look at particular leaf and ant characteristics, I attempted to obtain several repli-

cates of leaves with different numbers of hitchhikers on them. I collected 41 samples, for which I measured worker ant mass, worker head width, leaf mass, hitchhiker number, total hitchhiker mass, and the amount of time it took the worker to walk 1 m carrying the leaf fragment and any hitchhikers.

RESULTS

Frequency distributions

No hitchhiker distributions differed significantly from a random distribution in the four observations. Chi-square values were <5.0 and P-values were >0.2 for all analyses.

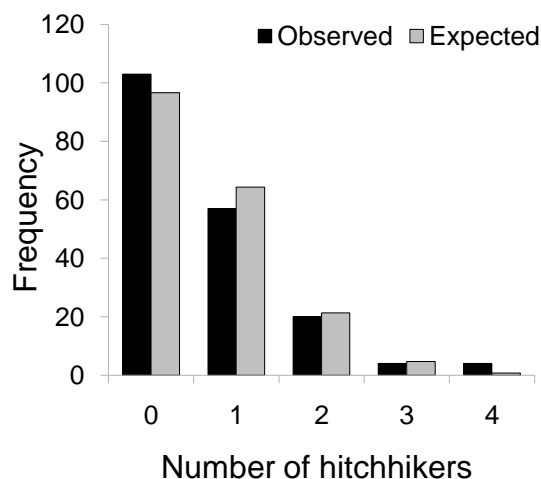


FIG. 1. An example of a comparison of observed and expected, random frequencies of *Atta cephalota* hitchhiker numbers on passing leaf fragments in a 10 minute period, in the afternoon on the Estacion del Rio trail at Estacion Biologica La Selva.

Ant/leaf traits analysis

Hitchhiker number and total hitchhiker mass were strongly correlated across all analyses ($r_{39} = 0.69$, $P < 0.0001$), as were worker body mass and worker head width ($r_{39} = 0.82$, $P < 0.0001$). Mean worker ant weight (\pm SD) was 8.4 ± 3.8 mg, while mean total hitchhiker mass was 2.7 ± 2.8 mg.

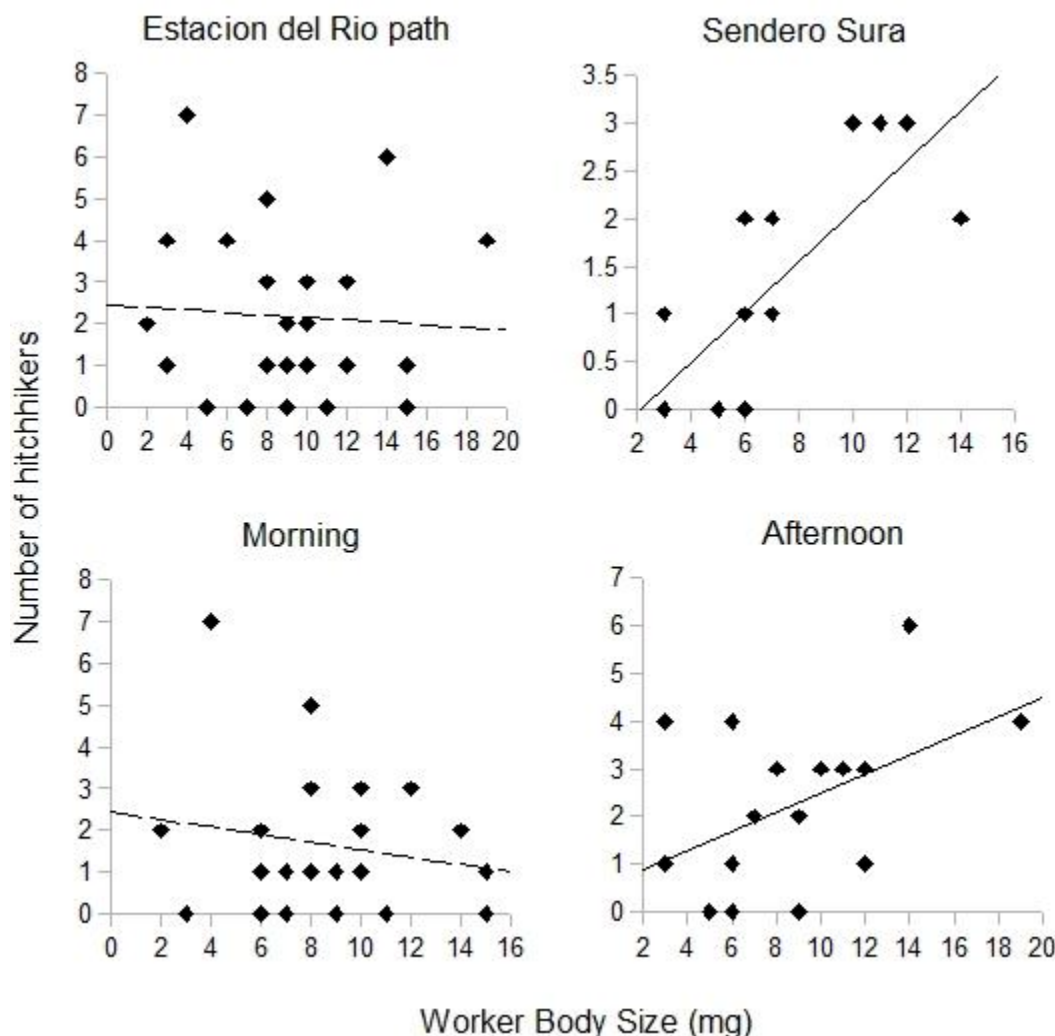


FIG. 2. Relationships between number of hitchhikers and worker body size in *Atta cephalota* at La Selva Biological Station, Costa Rica. Solid lines represent statistically significant correlations, while dashed lines were not significant.

Relationships between these variables can be modeled with Equations 1 and 2:

$$\text{Worker Head Width} = 1.14 + 0.07 * (\text{Worker Body Mass}) \quad \text{Equation 1.}$$

$$\text{HitchhikerMass} = 0.11 + 1.35 * (\text{Hitchhikers}) \quad \text{Equation 2.}$$

There was no relationship between leaf mass and worker body mass ($r^2_{12} = 0.55$, $P = 0.002$), but larger workers traveled more quickly than smaller workers ($r^2_{35} = 0.43$, $P < 0.0001$).

There were no significant overall relationships between worker body mass and number of hitchhikers ($r^2_{39} = 0.02$, $P = 0.37$) or worker head width and number of hitchhikers ($r^2_{39} = 0.01$, $P = 0.65$). There were marginally significant relationships between worker body mass and total hitchhiker mass ($r^2_{39} = 0.08$, $P = 0.07$) and between worker head width and total hitchhiker mass ($r^2_{39} = 0.08$, $P = 0.08$).

There were significant positive relationships between worker sizes and hitchhikers in the afternoon and on the Sendero Surá trail, but not in the morning and not on the Esta-

ción del Río trail (Fig. 2). Statistical results are summarized in Table 1.

DISCUSSION

Of the four potential hypotheses to explain the presence of hitchhikers, only parasitoid defense was supported by my results.

As energy conservation would be indicated by a nonrandom distribution of ants, and only random distributions were observed, it seems unlikely that hitchhikers are assorting themselves evenly onto the larger ants with the goal of total colony energy reduction. In addition, in the outgoing stream of ants there were very few, if any, instances in which a leafless worker would carry a hitchhiker out to the tree. If energy conservation were the goal of the colony, larger ants should always carry smaller ants.

Neither the leaf cleaning nor the sap drinking hypotheses were supported by my results, as the number or size of hitchhikers did not vary with leaf size. Most hitchhikers appeared to remain relatively stationary on leaf fragments, and if they did move, it was not in a manner that would suggest they were doing a thorough cleaning job on the whole leaf. It is possible that leaf cleaning is not a labor-intensive job, and that one hitchhiker could manage to adequately prepare even a large leaf. It is also possible that the leaf fragments do not contain much sap, and that one hitchhiker could consume all the sap contained in the leaf. Further analysis of leaf qualities, such as the average amount of fungus present on the leaf, or the sap content,

would be needed to determine whether many ants would be needed to perform these tasks on leaves of increasing sizes.

Parasitoid defense is a potential function of the hitchhikers, as number and mass of hitchhikers increased with worker body mass and head size in the afternoon. Phorids are more active at higher temperatures, so in the afternoon, when temperatures are higher, more phorids may be flying around and may pose a greater risk for larger-sized ants.

Significant relationships between worker ant size and hitchhiker number/mass were evident at the beginning of a leaf-cutter trail, but not the end (Fig. 2). I observed many hitchhikers relocating from one leaf fragment to another, especially when the new fragment was moving faster. Other times, a worker would drop its leaf fragment, and errant hitchhikers would swarm on while the worker was attempting to pick it up again. Thus, the distribution of hitchhikers is not fixed, but dynamic.

Based on these trends and my own personal observations, I would propose that another reason hitchhiking may be occurring is that minors may have some need to get back to the nest expediently. During the afternoon and at the beginnings of return trails to the nest, there is a greater amount of hitchhiking on leaves carried by large ants (Fig. 2.) Larger ants move more quickly. This could suggest a preference by hitchhiking ants for a more rapid return to the nest, particularly in the afternoon. My personal observations further support this hypothesis.

TABLE 1. Significant relationships between number and mass of *Atta cephalota* hitchhikers and body and head sizes of leaf-cutting workers.

	Afternoon (df = 18)		Sendero Sura (df = 12)	
	Number of hitchhikers	Total hitchhiker mass	Number of hitchhikers	Total hitchhiker mass
Worker body mass	$r^2 = 0.24$ P = 0.03	$r^2 = 0.30$ P = 0.01	$r^2 = 0.55$ P = 0.002	$r^2 = 0.49$ P = 0.005
Worker head width	$r^2 = 0.33$ P = 0.007	$r^2 = 0.42$ P = 0.002	$r^2 = 0.56$ P = 0.002	$r^2 = 0.63$ P = 0.0007

When hitchhikers were not riding on leaves, they were often trying to get on them, and as I mentioned, they would swarm on downed leaves in an attempt to secure a place. As the hitchhikers are very small, and small ants travel more slowly than large ones, it would make sense that securing a place on a leaf would enable the hitchhiker to return more quickly than if it walked back on its own. This result could be further supported by the fact that the hitchhikers will walk out to the tree, when they are in no hurry, and then ride on the leaves because they must return to the nest as quickly as possible. I would speculate that they might be harvesting some sort of substance at the tree which may degrade with time or temperature, and thus must deliver it back to the colony as soon as possible. However, there could be many explanations for this rapid return.

Since time seems to play an important role in determining this worker body size and hitchhiker abundance relationship, it would be interesting to take observations at nighttime as well, when phorids are allegedly inactive. In addition, if phorids are active at different levels at different temperatures, it would be interesting to study the effects of ambient temperature and hitchhiker frequency.

There is undoubtedly a strong evolutionary pressure acting to ensure the continuation of this hitchhiking behavior. By figuring out the cause, we can better understand which factors are most influential in shaping the ant colony population, which furthers our understanding of forest dynamics.

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RUN, FOREST, RUN? THE ROLE OF STILT ROOTS IN THE “WALKING PALM” *SOCRATEA EXORRHIZA*.

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Faculty Editor: Matthew P. Ayres

Abstract: Plants in the neotropical rain forest exhibit a wide range of morphological adaptations to compete for narrow niche space. A conspicuous example is the stilt root base of the palm *Socratea exorrhiza*, but the roots' adaptive role is not well understood. We investigated the following three hypotheses explaining their function: (a) they allow the plant to "walk" towards areas of greater light availability, (b) they serve as support to allow the plant to grow taller without investing as much in trunk diameter, or (c) they allow the plants to exist at greater lean angles than plants without stilts. We measured plant lean, light availability and root growth away from and towards the direction of lean, and the height to diameter ratio of *S. exorrhiza* at La Selva Biological Station, Costa Rica on February 13-16, 2010. We found greater height to diameter ratios in *S. exorrhiza* compared to another species of palm (*Welfia regia*), supporting hypothesis (b). Although we found light availability and root growth data supporting hypothesis (a), observations in the field led us to believe that this hypothesis was incorrect. Although *S. exorrhiza* does not "walk," its stilt roots represent an important and unique adaptive solution for competing in the neotropical rain forest.

Key Words: height to diameter ratio, light availability, phototropism, subcanopy, *Welfia regia*

INTRODUCTION

In neotropical rain forests, intense competition may drive high morphological diversity and fine niche partitioning. Plants employ numerous strategies to compete with other species for their particular environmental niche. The adaptive role of the stilt roots of the common subcanopy palm *Socratea exorrhiza* (the “Walking Palm”) is still not well understood, and has been the subject of much debate. *S. exorrhiza* create a cone of spiny stilt roots where new roots grow from the stem above the existing cone and elongate quickly toward the ground. There are several theories as to the adaptive advantage of this root growth strategy, including the idea that *S. exorrhiza* saplings use roots to right themselves (“walk”) to escape from under fallen logs (Bodley and Benson 1980), the theory that the roots allow the palms to anchor better into sloping ground (Goldsmith and Zahawi 2007; Avalos et al. 2005), and the theory that the fast-growing roots allow palm saplings to grow vertically quickly to out-compete other trees (Schatz et al. 1985).

We investigated whether (a) *S. exorrhiza*'s roots allow them to “walk” toward better light conditions by leaning in the direction of

greater light and growing greater numbers of new roots in that direction while allowing the old roots anchoring them in their old spots to break and die.

As palms lack a secondary cambium, they cannot stiffen their stems as effectively as dicot trees, and a thick, supportive stem is a large energy investment. This makes stem thickness the limiting mechanical factor for the height of most palms (Goldsmith and Zahawi 2007). We hypothesized that (b) *S. exorrhiza*'s fast-growing and energetically inexpensive root cone provides the structural stability to enable walking palms to reach a great height without investing in as thick a stem as other similar palms without stilt roots.

Lastly, we tested whether (c) *S. exorrhiza*, after some disturbance causing them to lean, are able to use their unique roots to survive at lean angles greater than those that other trees would be able to withstand.

METHODS

To address hypothesis (a) we sampled 20 leaning *S. exorrhiza* trees at La Selva Biological Station, Costa Rica on 13-16 February 2010, determining the lean (angle deviated from

vertical) and the direction of the lean vector. Along the lean vector, we measured canopy cover 3 m in the direction of the lean and 3 m in the direction away from the lean using a spherical densiometer. We counted the number of new roots and dead roots on the halves of the root cones towards and away from the lean. We defined a new root as a root connected to the stem lacking moss and epiphytes or an old root sprouting a bundle of small new roots. We defined a dead root as one that had broken and therefore was no longer touching the ground, or a hole left on the stem by a root that had rotted away.

In addressing hypothesis (b) we derived the diameter and height of 32 haphazardly chosen *S. exorrhiza* trees and 20 *Welfia regia* palm trees. We chose to use *W. regia* to represent the height to diameter ratio of other palms in comparison to walking palms since this species is also quite common at La Selva and occupies a similar subcanopy niche. We measured circumference at breast height for *W. regia*, and measured circumference of *S. exorrhiza* at the base of the stem immediately above the root cone, since in many cases the top of the root cone far exceeded the standard of breast height, and used the circumference of the stems to derive stem diameter. We stood 3 m away from the stem and used an inclinometer to determine the angle above horizontal at which the top of the tree could be seen, then calculated tree height using trigonometry, correcting for the eye-level height of the observer. We then used these data to calculate mean height to diameter ratios for *S. exorrhiza* and *W. regia*.

To test hypothesis (c) we quantified the angle of lean of 30 randomly selected *S. exorrhiza* trees and the angle of lean of the nearest neighboring tree greater than 2 m in height regardless of species.

RESULTS

In testing hypothesis (a), we found that *S. exorrhiza* do lean in the direction of light (paired- $t_{19} = 2.17$, $P = 0.04$; Fig. 1) and that there were significantly more new roots in the

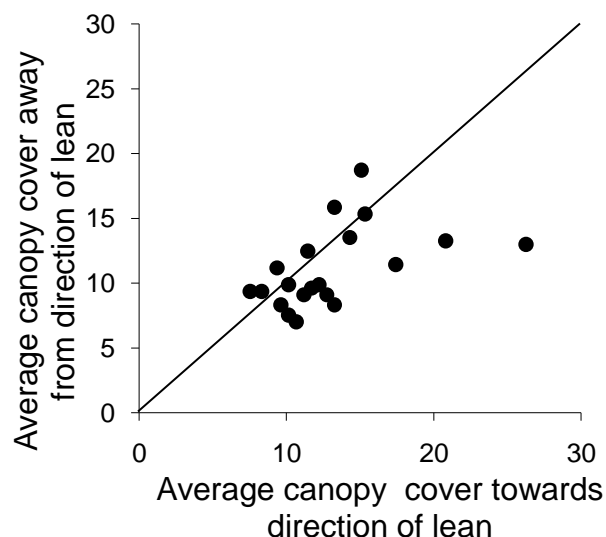


FIG. 1. Comparison of understory canopy cover 3m away in the direction of tree lean versus away from the direction of lean in 20 *S. exorrhiza* at La Selva Biological Station, Costa Rica, on February 13-16, 2010. Line of equivalence is shown, where canopy cover in the direction of lean is equal to canopy cover away from the direction of lean.

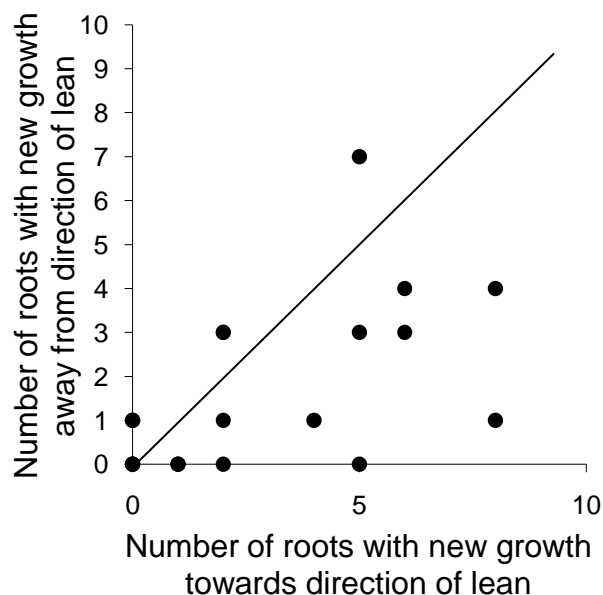


FIG. 2. Comparison of number of root shoots with new growth on the side in the direction of tree lean versus the side away from tree lean in 32 *S. exorrhiza* at La Selva Biological Station, Costa Rica, on February 13-16, 2010. Line of equivalence is shown, where the number of roots with new growth in the direction of lean is equal to the number of roots with new growth away from the direction of lean.

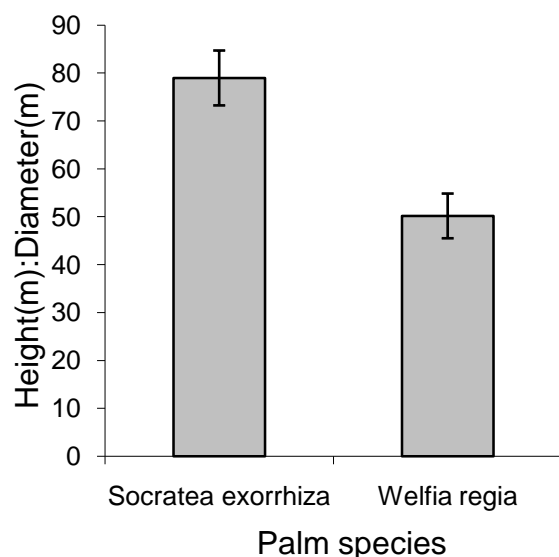


FIG. 3. Measurements of 32 *S. exorrhiza* and 20 *W. regia* comparing of height to stem diameter ratios of the two subcanopy palm species at La Selva Biological Station, Costa Rica on February 13-16, 2010. Bars represent ± 1 SE.

direction they lean (paired- $t_{19} = 2.56$, $P = 0.02$; Fig. 2). However, the number of dead roots did not vary in relation to lean orientation (paired- $t_{19} = 0.80$, $P = 0.43$). We also observed that roots near the bottom (the earliest roots grown) appeared still attached in every plant we observed. We found that the height to diameter ratio in *S. exorrhiza* was significantly greater than in the palm species *W. regia* (Simple t-test, $t_{50} = 3.60$, $P = 0.0007$; Fig. 3). We did not find that *S. exorrhiza* lean to a greater extent than other trees in the forest (paired- $t_{29} = 0.21$, $P = 0.83$).

DISCUSSION

The result that *S. exorrhiza* had a greater height to diameter ratio than *W. regia* supported hypothesis (b), that the stilt roots of *S. exorrhiza* are an adaptation for stability which enables greater maximum vertical height with less resources devoted to expansion of the plant stem as compared to palms without stilts. This may mean that once the root base is established, *S. exorrhiza* are free to spend much more energy on vertical growth than stem expansion, thus out-pacing other trees in the race to the canopy.

The results did not support hypothesis (c) as we did not find any difference between *S. exorrhiza* lean and the lean of trees in the forest in general, indicating that the support for leaning provided by the roots is not the adaptive force behind the evolution of the stilts.

Although the data supported parts of our predictions for hypothesis (a) in respect to phototropism and the location of new shoot growth, our observations in the field lead us to believe that *S. exorrhiza* do not "walk". We found that the earliest roots produced nearest the bottom of the plant were intact in nearly every plant we sampled, meaning that the plants had not moved since their first early roots were created. If *S. exorrhiza* do in fact "walk," one would expect that the root cone would lose roots near the bottom and originate further and further up the stem as the tree moved, which was never observed in the field. Additionally, studies have shown that root cone diameter and volume are allometrically related to plant height to diameter ratio, indicating that plants continually add roots for more support and are not replacing roots to move towards light (Goldsmith and Zahawi 2007). Although *S. exorrhiza* leans towards light, it may be a phototropic response similar to that of many other plant species and the new roots may be added to support this lean, but not to move the plant in that direction. It does not appear that *S. exorrhiza* roots allow the plant to lean more towards light than other plants as indicated by our result for hypothesis (c).

This study could have been improved had it employed a technique that measured the canopy cover in the subcanopy where *S. exorrhiza* photosynthesizes rather than in the understory. Our canopy measurements were often greatly affected by understory plants that did not block light for *S. exorrhiza*.

It would be interesting in further studies to examine how *S. exorrhiza* allocates resources to root growth. Many stems had a large proportion of their understory surface area covered in dead root bases of unsuccessful

ful roots. It seems to be a large energetic investment to produce these large roots when many of them die before they reach the ground. Other stilt-rooted plants we observed did not appear to have many unsuccessful roots.

The root structure of *S. exorrhiza* may be an adaptation that helps explain its niche in the tropical rainforest. If its root base allows it to grow higher and faster than other palms, it can exploit greater light availability near the top of the canopy and not be shaded by as many other plants, which may explain its great success in the tropical rainforest. Sometimes, even simple, single adaptations such as the stilt roots of *S. exorrhiza* can allow plants to greatly differentiate themselves from competitors and achieve great success.

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EFFECTS OF PREDATION RISK ON THE COST OF HOLDING A TERRITORY: *OOPHAGA PUMILIO* AND *HEMIDACTYLUS FRENATUS*

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Abstract: Physiological fitness may decrease with increasing territory quality for species that invest substantial amounts of energy in defending high-quality territories. *Oophaga* (formerly *Dendrobates*) *pumilio* and *Hemidactylus frenatus* both vocalize to defend territories, but face differing predation risk due to high toxicity of *Oophaga* species. Predation risk may affect the energy expended for territory defense because species with high predation risk will call less than species with low predation risk. One theoretical model predicts that species with low predation risk will have lower physiological fitness with higher territory quality because of the energy expended in territory defense. An alternative theoretical model predicts that physiological fitness will increase with increasing territory quality, regardless of predation risk. We collected 23 *O. pumilio* individuals and 6 *H. frenatus* individuals at La Selva Biological Station, Costa Rica and measured their mass and length and assessed their territory quality. For *O. pumilio*, physiological fitness increased significantly with territory quality, and *H. frenatus* showed a similar but non-significant trend. Predation risk does not appear to affect the relationship between territory quality and physiological fitness, and physiological fitness increases with territory quality.

Key Words: Costa Rica, *Oophaga* (*Dendrobates*) *pumilio*, house geckos, La Selva, lowland rainforest, strawberry poison dart frogs, territoriality, vocalization

INTRODUCTION

Males holding the best territories must often expend greater amounts of energy for territory defense than males holding poorer quality territories. In these cases, physiological fitness can, counter-intuitively, decrease with increasing territory quality due to the stress of holding a high-quality territory, which for males is defined primarily by opportunities for mating. For example, when testosterone levels were elevated in territorial lizards, aggressiveness towards intruders increased while survival decreased (Marler et al. 1995). Poison-dart frogs (*Oophaga pumilio*, formerly *Dendrobates pumilio*) and house geckos (*Hemidactylus frenatus*) use vocalizations as a territory defense strategy. Vocalization for attracting potential mates and marking a territory is among the most energetically demanding activities for herpetofauna and can require 1.5 times more energy than vigorous locomotion (Taigen et al. 1984). However, vocalizations also expose individuals to predators. Since calling rate increases with territory quality (Gardner and Graves 2005), species under different levels of predation

pressure may exhibit different relationships between physiological fitness and territory quality. While *O. pumilio*'s chemical defense protects it from most predators, *H. frenatus* does not exhibit chemical defense and faces high predation risk (Saporito et al. 2007).

We compared territorial males of *O. pumilio* and *H. frenatus* and tested the hypothesis that species under low predation pressure can afford to vocalize more than species under high predation pressure, but the increased calling reduces physiological fitness because of its high energetic investment. Under this hypothesis, we predicted that for species with low predation pressure, territory quality increases as physiological fitness decreases, because individuals may constantly call without increasing predation risk. We predicted that highly predated species would show the opposite trend because individuals cannot afford to vocalize as actively. Alternatively, we hypothesized that the fitness benefit provided by better quality territories could override the cost of vocalization. Under this model, predation risk should not affect the relationship of physiological condition to territory quality based on how much each species can afford to

call. According to this hypothesis, we predicted that physiological condition increases with territory quality for all species.

METHODS

To assess the relationship between physiological fitness and territory quality for *O. pumilio* and *H. frenatus*, we captured 23 male frogs and six male geckos on 14 and 15 February 2010, respectively, at La Selva Biological Station.

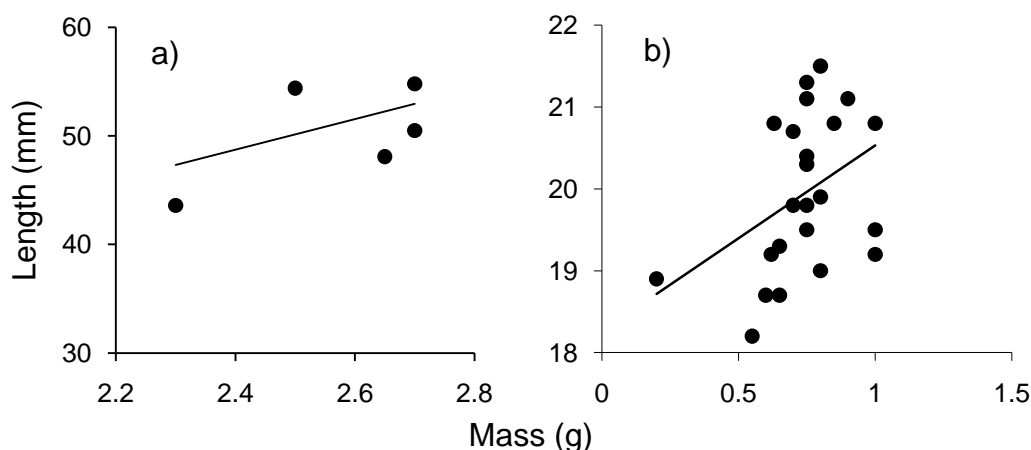
We captured frogs from 0-850 m along the STR trail, and for each individual measured its mass, length from snout to hind end, and flagged the location where we first saw it so that we could return the next day to assess territory quality. Indicators of a high-quality territory were deep leaf litter as a source of protective cover from predators and desiccation, a high perch site from which to vocalize, openness of surrounding vegetation for sound to carry, and the presence of a female. Assuming that a 1.5 m radius circle about the flag encompassed the frog's territory (Bunnell 1973), we averaged leaf litter depth from three points: at the flag, at a point that best represented the 20 cm radius around the flag, and at the deepest point in the territory. We measured perch site height as either the

height of the site where we had previously observed the frog perching or the highest horizontal perch in the territory. We qualitatively assigned a score of the territory's openness where 1 = very dense vegetation, 2 = intermediate openness, and 3 = very open space. We searched each territory for one minute to determine presence or absence of female frogs. For each territory we combined these metrics into an index of territory quality using Equation 1, where L = average leaf litter depth Z-score, P = perch height Z-score, O = openness Z-score, and F = 1 for presence of female and 0 for absence of female.

$$\text{Frog Territory Score} = L + P + O + 2F \quad \text{Equation 1.}$$

Prey is not limiting for *O. pumilio* in Costa Rica (Lotters et al. 2007) so we did not include a prey availability parameter in the territory score.

Similarly, we measured the mass and length from snout to proximal end of hind legs for six geckos found on building exteriors. We assessed geckos' territory quality by measuring proximity to nearest light source (lights attract insects, which geckos eat) and presence or absence of females. We calculated



an index for gecko territory quality using Equation 2, where R = proximity to light Z-score, and $F = 1$ for presence of female and 0 for absence of female.

$$\text{Gecko Territory Score} = R + 2F \quad \text{Equation 2.}$$

For each species, we ran a regression for length by mass and calculated residuals for each point (Fig. 1). We used the residuals, a body condition index of how relatively fat or thin an individual is, in analyses of physiological fitness compared to territory quality.

We also assessed the aggressive responses of frogs and geckos to conspecific calls to determine whether (i) animals holding better territories would expend more energy to protect themselves and whether (ii) animals expending more energy to protect territories are thinner. For frogs, we returned to each territory on 15 Feb. assuming the male occupying the space was the same as had been measured the previous day. At each territory, we played a ten-second-long recorded *O. pumilio* call (procured from “Voices of Costa Rican Frogs and Toads”) three times at five-second intervals. If the frog showed any response to the first three calls, we played it three additional times. For geckos, we performed the playback experiments two minutes after releasing them from the original capture. We quantified response as 1 = no response, 2 = demonstrated movement in awareness of the call, 3 = aggressive approach towards the call and/or vocalization in response to call.

RESULTS

Fatter frogs occupied significantly higher-quality territories than thinner frogs (Fig. 2). Geckos also exhibited a positive correlation between physiological fitness and territory quality but this relationship was not significant (Fig. 3). Frogs occupying higher-quality territories were significantly more responsive to playbacks ($r^2_{21} = 0.20$, $P = 0.03$), while no relationship was found between territory quality and response to playbacks for geckos

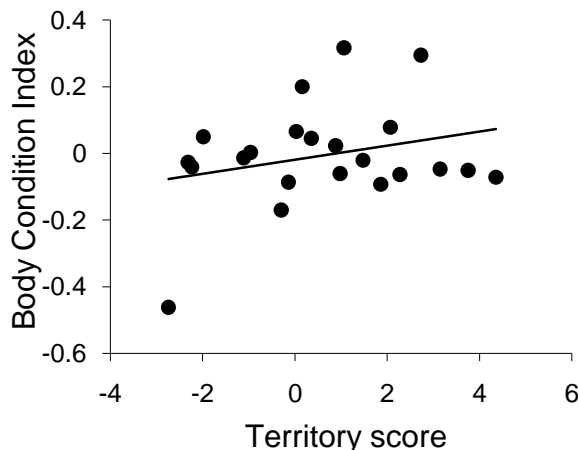


FIG. 2. Relationship between territory score (higher scores indicate better quality territories) and residuals of body mass to length ratios for 23 *Oophaga* (previously *Dendrobates*) *pumilio* males occupying different territories along the STR trail at La Selva Biological Station, Costa Rica ($r^2_{22} = 0.19$, $P = 0.04$).

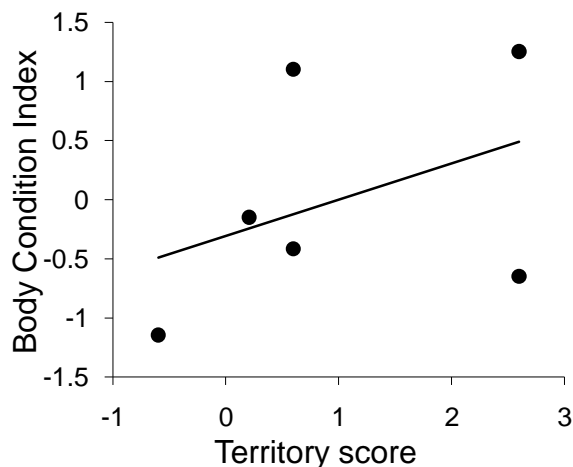


FIG. 3. Relationship between territory score (higher scores indicate better quality territories) and residuals of body mass to length for six *Hemidactylus frenatus* males occupying different territories at La Selva Biological Station, Costa Rica ($r^2_5 = 0.27$, $P = 0.29$).

($r^2_5 = 0.12$, $P = 0.49$). For both frogs and geckos, there was no relationship between body size and responsiveness to playbacks ($r^2_{22} = 0.06$, $P = 0.27$; $r^2_5 = 0.11$, $P = 0.52$).

Although the majority of frogs displayed no response to playbacks, four out of the 23 responded aggressively. After each playback these frogs responded by moving closer to the source of the playback (sometimes as close as 0.5 m from the recording device) and then

vocalizing. For unresponsive frogs, the male was neither visually present nor vocally responsive at the time the playback recording was played. Overall the geckos were much less responsive to playbacks and rarely vocalized in response to the recording. We also observed a bird (Tyrannidae) eating one of the captured geckos immediately after we returned it to its territory and never observed a frog predation event, supporting the assumption that the geckos are at higher predation risk than the frogs.

DISCUSSION

O. pumilio physiological fitness was positively related to territory quality, and we found a possible positive trend between territory quality and physiological fitness in *H. frenatus*. This supports our alternate hypothesis that predation risk does not drive the relationship between body condition and territory quality. Because *O. pumilio* are territory limited (Prohl 2005), individuals of higher physiological fitness may outcompete those in lower physiological condition, leading to individuals in better condition inhabiting higher-quality territories. Although calling is energetically costly, high-quality territories may contain resources that provide an energetic benefit that absorbs the cost of calling. Additionally, territory turnover rate may be high enough that when a frog becomes physiologically compromised, a frog in better condition takes its place. In *H. frenatus*, territory quality was determined partially by proximity to a light source, which attracts arthropods. Proximity to a food source may be driving the positive relationship between territory quality and physiological fitness.

We observed that *O. pumilio* males ceased calling as we approached them during our study, suggesting that although they are at a low predation risk, they may still reduce calling when disturbed. *O. pumilio* males in higher-quality territories responded more aggressively to playbacks of *O. pumilio* calls, moving toward the sound source while calling in response, even if they had not been

calling previously. Aggressive responses may be more important than continuously calling to defend high-quality territories, which would be a lower metabolic investment. The greater response to rival calls by individuals in higher-quality territories suggests that our metric for assessing territory quality was effective. *H. frenatus* did not respond to playbacks of gecko calls, suggesting that predation risk reduces their willingness to vocalize (Marcellini 1974). Since we measured their playback response shortly after releasing them, our handling may have affected their response. However, we measured the playback response of *O. pumilio* after assessing territory quality, which disturbed them, and we still observed a number of aggressive responses.

Further studies with greater statistical power may find a more definitive relationship between physiological condition and territory quality in *H. frenatus*. We also are not confident that our assessment of territory quality for geckos was biologically accurate, but from our observations, predation risk does not appear to affect the relationship between territory quality and physiological condition. The similar pattern between territory quality and physiological condition in low and high predation risk species indicates that the energetic cost of vocalization does not substantially decrease physiological fitness.

ACKNOWLEDGMENTS

We thank Kenneth Alfaro and Eli Hornstein for their contributions to our project.

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WHERE'S THAT DAMN BIRD? THE EFFECT OF HARMONICS ON LOCALIZATION OF BIRD CALLS

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Abstract: Sound with fewer harmonics is believed to be harder for humans to localize. Birds may have evolved calls with fewer harmonics in order to reduce predation risk. In light of this hypothesis, we predicted that bird calls lacking harmonics would be harder to localize. We asked blindfolded human test subjects to localize recorded bird calls with or without harmonics. Contrary to our prediction, birdcalls of certain species were harder to localize with harmonics. However, the dominant frequency and number of harmonic bands in calls also affected subjects' ability to localize the call. These arboreal birds employ a combination of higher frequencies and harmonics, which may bounce off of the dense foliage, altering predators' perception of sound.

Key Words: *Electron platyrhynchum*, *La Selva Biological Station*, *localization*, *predation*, *Thamnophilus atrinucha*, Trogon Massena, Trogon violaceus

INTRODUCTION

Animals vocalize for a variety of reasons—to warn others about potential predators, to establish and maintain territory boundaries, and to attract mates, among others. Male birds often call to attract mates, but calling also increases predation risk. Cryptic coloring, flocking (Page and Whitacre 1975), calling in sheltered areas, and calling for short time periods are adaptations that may lower predation risk. Calls containing fewer harmonics (frequency bands at equal intervals above the dominant frequency band of the call) may also be harder for predators to localize (Goodridge 1997). Forest guides and biologists around La Selva biological station, Costa Rica expressed difficulty in localizing the calls of certain bird species, such as Trogons (pers. corr. Kenneth Alforo). We examined the hypothesis that having a call with fewer harmonics decreases predation risk. Since humans and predators of birds both use aural cues to localize birds, the theoretical model predicts that human subjects would experience more difficulty determining the direction of a call with fewer harmonics compared to a call with more harmonics.

METHODS

We recorded birdcalls on 13 February and conducted experimental trials on 14-15

February, 2010, at La Selva Biological Station, Costa Rica. We recorded the calls of three bird species (Western Slaty-Antshrike (*Thamnophilus atrinucha*), Broad-billed Motmot (*Electron platyrhynchum*), and Slaty Tailed Trogon (*Trogon massena*)), representing a wide range of harmonic characteristics and dominant frequencies, using a 22" Telinga parabola with a Sennheiser ME62 microphone running on a K6 power module and a Marantz 661 solid state digital recorder sampling at 24 bits and 96 kHz. We also used the pre-recorded call (from audio recording by Ross 1998) of a Violaceous Trogon (*Trogon violaceus*), a species often found at La Selva, as we were unable to record one ourselves. Using R statistical programming language and Raven Lite 1.0 Interactive Sound Analysis Software, we altered the calls, removing harmonics from *T. atrinucha*, *E. platyrhynchum*, and *T. violaceus* and adding harmonics to *T. massena*, which had weak natural harmonics. We standardized volume and duration of all call clips.

We conducted experimental trials in the forest around the *Arboleda* trail roughly 20 m from the laboratory building at La Selva Biological Station. To test subjects' ability to localize bird calls, we asked our human subjects (Dartmouth undergraduates and other scientists) to listen blindfolded to bird calls played 8.8 m from the subject in a random direction. We played each manipulated and unmanipulated

lated call once (8 total calls) using an Apple iPodNano connected to Radio Shack fold-up, portable speakers, held over a researcher's

head. We constructed a 360° protractor out of cardboard, and placed it on a pole roughly 0.5 m above the ground.

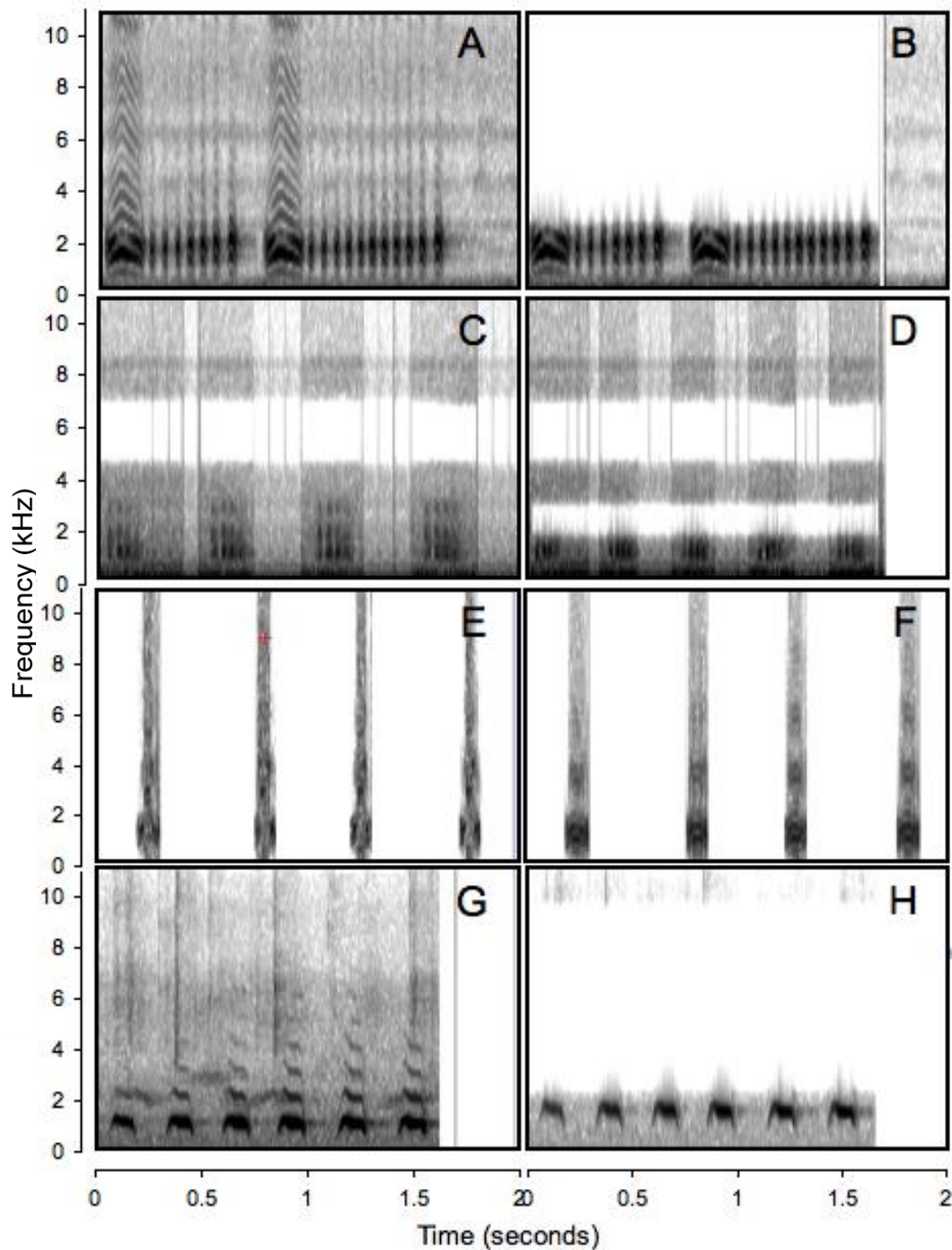


FIG. 1. Spectrograms of calls of four different bird species: *T. atrinucha* (1A. Harmonics, 1B. No Harmonics), *E. platyrhynchum* (1C. Harmonics, 1D. No Harmonics), *T. Massena* (1E. Harmonics, 1F. No Harmonics) and *T. violaceus* (1G. Harmonics, 1H. No Harmonics). La Selva Biological Station, Costa Rica, February 2010.

Upon hearing the recorded call, subjects aimed an arrow on the protractor towards the perceived direction of the call. Using a string stretched tightly from the navel of the researcher holding the iPod to the center of the protractor, we measured and recorded the angle between the actual call and the direction indicated by the subject.

RESULTS

The natural calls of the four focal bird species had the following number of harmonic bands above the dominant frequency: *T. atrinucha* 13, *T. violaceus* 5, *E. platyrhynchum* 2, *T. Massena* 0 (Fig. 1). The manipulated calls of *T. Massena* had two harmonic bands above the dominant frequency, and the manipulated calls of all other species had zero. The domi-

nant frequency of the four species' calls were: *T. atrinucha* 1.6 kHz, *T. violaceus* 1.5 kHz, *T. Massena* 1.4 kHz, *E. platyrhynchum* 1 kHz.

T. atrinucha and *T. violaceus* were more difficult to find with harmonics (Fig. 2). Harmonics did not affect people's ability to locate the calls of *E. platyrhynchum* (natural harmonics) and *T. Massena* (added harmonics). Harmonics and the interaction between harmonics and the bird species affected the ability of the test subject to localize the bird call (Table 1). Although there appeared to be no effect of test subject, we observed variability in subjects' ability to localize calls, which could be due to subjects' previous acoustic experience. The calls with higher dominant frequencies and a greater number of harmonics tended to be harder to localize (Figs. 3 and 4).

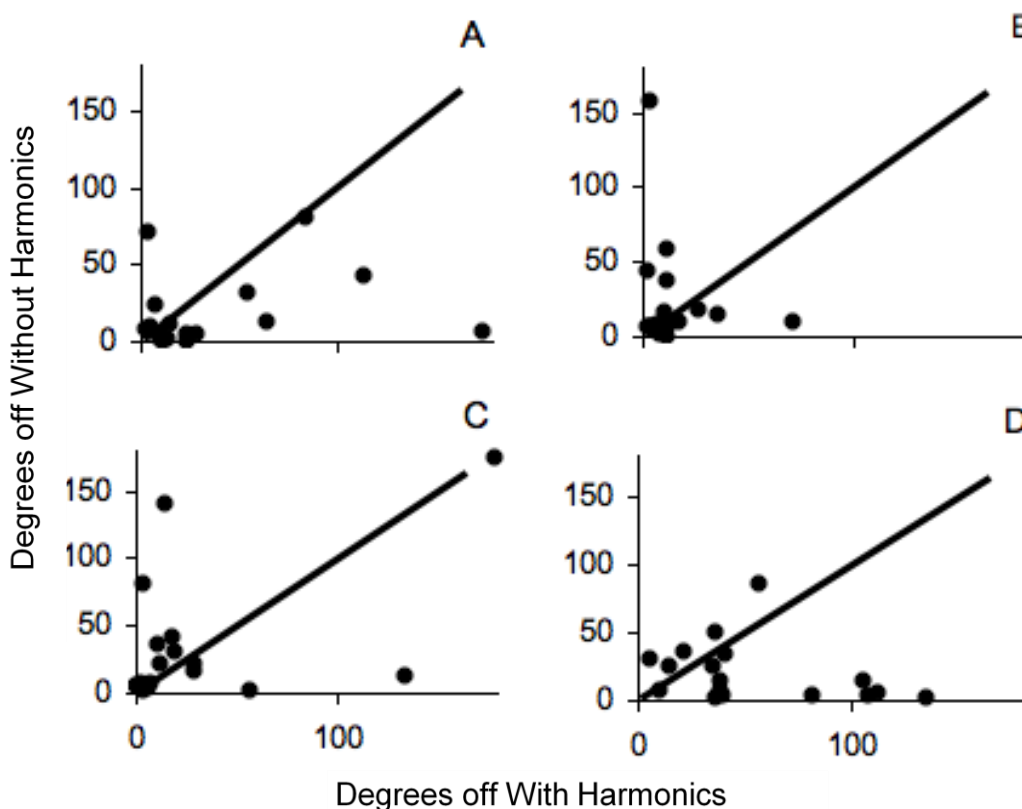


FIG. 2. The angle between the location of a bird call (A: *T. atrinucha*, B: *E. platyrhynchum*, C: *T. Massena*, D: *T. violaceus*) and the subject's perceived location of the bird call (Degrees off) of calls with no harmonics compared to the Degrees off of calls with harmonics, with equivalence line shown ($n=18$). La Selva Biological Station, Costa Rica, February 2010.

TABLE 1. General linear model of the effects of bird species, bird call harmonics, the interaction between bird species and bird call harmonics, and test subject on ability to localize the bird call. La Selva Biological Station, Costa Rica, February 2010.

Source	DF	MS	F	P
Harmonics	1	2.93	2.19	0.093
Bird	3	6.34	4.75	0.031
Harmonics*Bird	3	4.18	3.14	0.028
Person	16	1.38	1.03	0.43
Error	112	--	--	--

DISCUSSION

Although sounds with more harmonics are believed to be easier to localize, our results suggest that bird calls with more harmonics are actually harder to localize. We hypothesize that this finding is due to an interaction between vegetation density and harmonic structure. The dominant frequency of the call and the number of harmonic bands may also affect how easy it is to localize a bird call: the two bird species calls with a higher dominant frequency and a greater number of harmonic bands (*T. atrinucha* and *T. violaceus*) were harder to localize with harmonics than without harmonics. In wooded areas, harmonics and higher frequencies may bounce off vegetation and become distorted, confusing the listener. Comparing the ability to localize bird calls in dense vegetation versus open areas may shed light on this phenomenon.

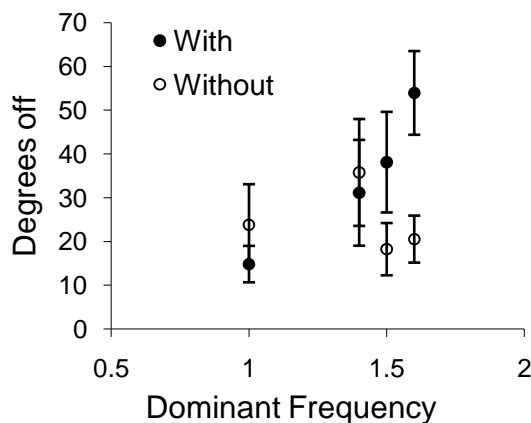


FIG. 3. The angle between the location of a bird call and the subject's perceived location of the bird call (Degrees off) according to the dominant frequency of the bird calls. Closed circles represent calls with harmonics, and open circles represent calls without harmonics. Bars are ± 1 S.E. La Selva Biological Station, Costa Rica, February 2010.

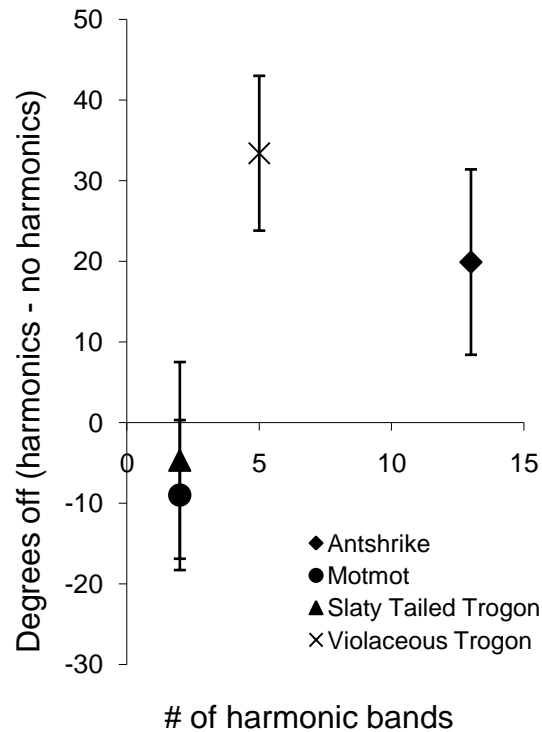


FIG. 4. The difference in Degrees off (the angle between the location of a bird call and the subject's perceived location of the bird call) between a bird species call with harmonics and without harmonics as a function of the number of harmonic bands in the call with harmonics. Bars are ± 1 S.E. La Selva Biological Station, Costa Rica, February 2010.

As a result, harmonics may be an adaptation to decrease predation risk in some bird species. However, for two species we studied (*E. platyrhynchum* and *T. Massena*) the presence of harmonics did not affect a person's ability to localize the call. In these species, female preference for calls with purer tones could exert a stronger selective pressure than predation. Variation in the number and frequency of harmonic bands may also be an example of niche partitioning where acoustic space is a limited resource. Though it is conventionally suggested that harmonics make sound easier to localize (Goodridge 1997), en-

vironmental factors such as vegetation may alter the perception of sound.

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EFFECTS OF DISTURBANCE FROM PATHS ON FOREST COMPOSITION IN LA SELVA, COSTA RICA

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JING JING ZHANG

Faculty Editor: Matthew P. Ayres

Abstract: Disturbance in a forest, both human and natural, can cause changes in plant composition. However, the effects may differ depending on whether the forest is primary or secondary growth. The Homogocene model theorizes that human disturbances create a more homogenous species composition by favoring a subset of species that tend to be less sensitive to disturbance. This model predicts higher plant abundance in secondary growth forest because those species are more adapted to disturbance. In La Selva, Costa Rica, the maintenance of paved and unpaved trails through the forest creates small but continual disturbance. Though our hypothesis predicted there would be changes in forest composition depending on proximity to the trails, the changes were on a smaller scale than expected. In secondary forests relative to primary forests, overall abundance of plants was higher and there were more small plants close to the trails.

Key Words: Homogocene model, human disturbance, paved trails, primary forest, secondary forest, unpaved trails

INTRODUCTION

Secondary and primary forests may respond differently to different levels of disturbance, particularly to human changes to the environment. One possible generalization is that human disturbances create a more homogenous species composition because the more resilient species out-survive the less resilient species, lowering overall number of species per total number of plants. This has been described as the Homogocene model. At La Selva, Costa Rica, human disturbances include the maintenance of 40-year-old paved and unpaved trails through both previously cleared (secondary) and old-growth (primary) forests. Under the Homogocene model, sec-

ondary forests tend to have higher overall plant abundance because plants found in secondary growth have a higher inherent resilience to disturbances. Another prediction of the Homogocene model is that secondary forest will have a lower number of species per total number of plants compared to primary forests, since only the highly resilient species survive. Conversely, we may observe higher number of species per total number of plants in the secondary forest if invasive species fill niches left open from an anthropogenic disturbance.

Extending the Homogocene model, we predicted that paved trails would have a greater negative effect on vegetation in pri-

TABLE 1. Results of a 3-way ANOVA testing the effects of trail type (paved or unpaved), forest type (primary or secondary), and meter (1, 5, or 10 m off trail) on the number of small plants, total number of plants, and number of species per total number of plants encompassed in 1m² quadrats at La Selva, Costa Rica. Asterisks (*) represent significant effects.

	Number of Small Plants		Total Number of Plants		Number of Species/Total Plants	
	F	P	F	P	F	P
Trail Type	0.35	0.55	1.14	0.29	2.94	0.09
Forest Type	41.07	<0.01*	38.61	<0.01*	53.51	<0.01*
Meter	5.39	0.02*	7.83	0.01*	1.95	0.16
Trail Type*Forest Type	0.04	0.84	0.63	0.43	1.13	0.29
Trail Type*Meter	3.06	0.08	1.67	0.20	0.49	0.48
Forest Type*Meter	0.46	0.50	0.69	0.41	0.32	0.57
Trail Type*Forest Type*Meter	0.34	0.56	0.09	0.77	0.02	0.88

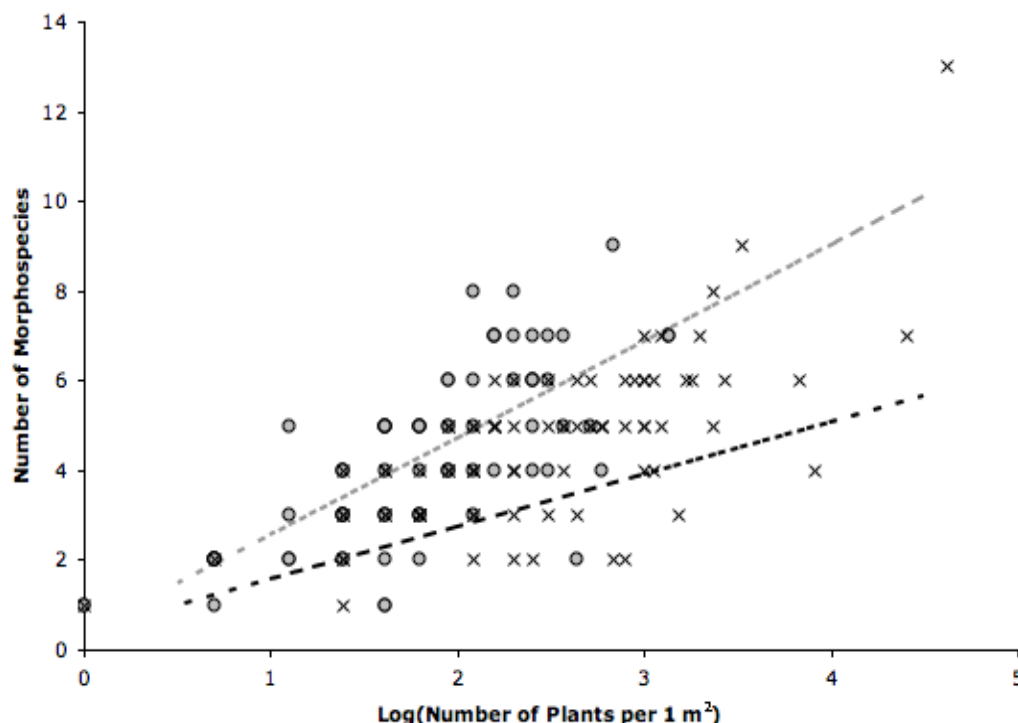


FIG. 1. The number of different morphospecies versus the logarithm of the observed number of total plants, in both primary and secondary growth forests in La Selva, Costa Rica. Primary forest is shown with grey circles and the grey dotted line while secondary forest is shown with the black Xs and black dotted line. Species diversity was higher in primary than in secondary forest, but the rate of morphospecies accumulation with increasing number of plants sampled did not differ between forest types (ANCOVA, $df = 1,160$, forest type: $F = 18.23$, $P < 0.0001$; $\log(\# \text{ of plants}/\text{m}^2)$: $F = 164.21$, $P < 0.0001$; interaction: $F = 2.38$, $P = 0.12$).

mary forests than in secondary forests, with a greater increase in sapling abundance and number of species per total number of plants as distance from the trail increases. In secondary forests, we expect sapling abundance to be highest closest to the paved trail because those plants are better able to take advantage of the light gap. We predict to see similar trends near the unpaved trails but to a lesser extent because the level of disturbance is not as great.

METHODS

To assess the impact of man-made trails, we selected trails on the basis of location in either secondary or primary forest, the degree of path disturbance (paved vs. unpaved), and proximity to the La Selva Biological Station. On each focal trail, we chose sampling sites at a randomized distance (between 0 and 49 m) from each pre-existing 50 m marker. In this

way, we selected 28 sites (7 secondary/ paved, 7 secondary/ unpaved, 7 primary/ paved, 7 primary/ unpaved). At each, we conducted two transects perpendicular to the trail (left and right), on which we assessed a forest floor 1 m^2 quadrat at 1, 5, and 10 m distance from the edge of the trail. In each quadrat, we 1) estimated % cover of leaf litter, 2) measured and averaged litter depth at the four corners, 3) counted live stems $< 1 \text{ m}$ and $> 1 \text{ m}$ in height, and 4) counted the number of plant morphospecies present. We calculated an index of diversity for each quadrat as the number of plant morphospecies divided by the total number of plant stems.

RESULTS

The number of small plants per quadrat (median = 7, IQR = 8.75) and total plants per quadrat (median = 8, IQR = 8.75) were both greater in secondary forests than in primary

forests (Table 1), and the number of species observed per number of plants was greater for primary forests (Table 1, Fig. 1). In secondary forests, the number of small plants decreased logarithmically with distance from the trail (Fig. 2), with the median number of small plants dropping by 52% in the first 5 m.

The median number of small plants was similarly low at both 5 m (median = 4) and 10 m (median = 4), compared to a higher number at 1 m (median = 5). The median number of total plants showed similar trends, with equal numbers at 5 m and 10 m (medians = 8) and a higher number 1 m away from the trail (median = 10.5).

DISCUSSION

The Homogeneous model predicts that species adapted to take advantage of disturbance will colonize in secondary forests, and therefore the plants found in secondary forest

will be more successful in dealing with additional, smaller-scale disturbance than primary forest plants, which are not adapted to deal with disturbance. On the paved trail in secondary forest, the density of small plants was higher closer to the trail, suggesting that those plants are adapted to take advantage of disturbance. The density of small plants was higher in secondary forest than primary forest, which makes sense in light of the Homogeneous model's prediction that the plants that colonize secondary forests are particularly resilient and fast growing.

The effect of the trail on plant abundance and richness was much smaller than predicted. While we did not look at the direct effects of trail construction (which occurred ca. 40 years ago) or trail maintenance on vegetation, it appears that the spillover effects of

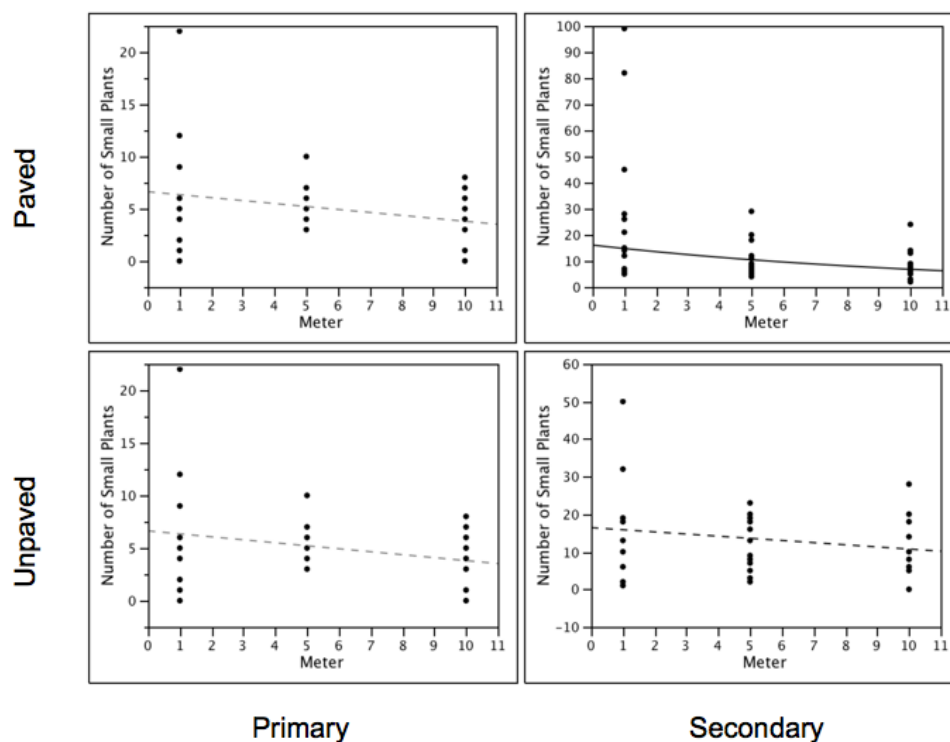


FIG. 2. The number of small plants near paved and unpaved trails in primary and secondary forest. The solid line indicates a significant decline with distance off paved trails in secondary growth forests ($r^2_{41} = 0.15$, $P = 0.01$; $\text{Log}(\text{Small Plants}) = 2.78 - 0.09 \times \text{Meter}$).

that maintenance and construction are minimal. Additionally, we observed important differences between trails (amount frequented, width of path, species composition) even within the same forest type, so it is possible these factors played a role in what we observed.

The effects of disturbance on vegetation varied depending on the physical and temporal scale of disturbance, with different trends appearing between the small-scale, continual disturbance of maintaining a trail and the large-scale disturbance of clearing a forest ca. 20 years ago. Future studies could look at how the effects of large-scale disturbance change with time, and how that change over time influences the effects of continual small-scale disturbance. It also may be interesting to investigate how these different scales of disturbance affect number of species per total number of plants in light of differing models, such as the Intermediate Disturbance Hypothesis.

Although there was a significant effect of distance from the trail on forest composition, we observed that this difference was mainly between one and five meters, while there was very little difference between five and ten meters, suggesting the effects of the trail dissipate quickly with distance. Therefore we conclude that the construction and maintenance of trails does not have a detrimental effect on forest health. By supporting the Homogocene model, our results concerning the difference between primary and secondary forest give credence to the idea that human-modified environments have more and faster-growing plants, as well as lower diversity, than untouched environments, which has global implications for future species composition as more and more land becomes affected by human activity.

THE EFFECT OF DISTURBANCE ON TOP-DOWN CONTROL OF EPIPHYTIC DIATOM COMMUNITIES BY THE SNAIL, *CERITHIUM LITTERATUM*

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Faculty Editor: Brad W. Taylor

Abstract: Grazers such as snails can be important top-down controls on diatom communities in marine systems. This is especially true in high-productivity systems, where diatoms can be epiphytic on macrophytes such as sea grass. We studied seagrass beds at two sites on Little Cayman, Cayman Islands; Preston Bay had high wave disturbance, close proximity to a reef, and very low snail density while South Hole Sound had lower wave action and high snail density. We tested the hypothesis that greater disturbance in Preston Bay would have a negative effect on the snail population, and thus indirectly increase diatom density. We measured the baseline diatom density and compared it to densities of diatoms after 24 hours in cages with snails added or removed. To assess the effect of wave disturbance, we observed the disappearance of snails from quadrats after 24 hours. Our results suggest that diatom density was higher in Preston Bay; however there was no effect of the snail density manipulations on diatom density. In contrast to our prediction, losses of snails from populations at South Hole Sound were higher than Preston Bay. Though our manipulations did not show an effect of snail presence on diatom density, future studies conducted over a longer time period may reveal spatially dependent top-down effects of snails on diatom communities around Little Cayman Island.

Key Words: herbivore density, herbivore exclosure, *Thalassia testudinum*, top-down control, wave disturbance.

INTRODUCTION

Diatoms play a crucial role as primary producers in marine food webs (Tiffany 1968). Many diatoms are epiphytic, and are important as a food source for gastropod and echinoderm grazers in near-shore areas, where plants are abundant (Morgan & Kitting 1984, Moncreiff & Sullivan 2001). Density and efficiency of foraging gastropods are negatively affected by many factors, such as predation (Halpern et al. 2006) and wave action (Menge 1978, Etter 1995, Schanz 2004), which indirectly affect plant communities by reducing top-down effects.

The near-shore areas of Little Cayman Island support abundant communities of epiphytic diatoms, often found growing on Turtle Grass, *Thalassia testudinum*. In South Hole Sound, an area protected from high surf by the coral reef, the snail *Cerithium litteratum*, is abundant in turtle grass beds (*personal observation*). In Preston Bay, an area exposed to high wave disturbance from northwesterly winds and lacking a well-defined lagoon, *C. litteratum* is rare or absent from the turtle grass. We tested the hypothesis that wave disturbance, gastropod predators, or both would

limit populations of *C. litteratum*, allowing diatom communities to flourish, whereas in South Hole Sound high snail density would suppress epiphytic diatom communities. We predicted that 1a) compared to ambient, enclosures with snails added would show a decrease in diatom density in Preston Bay, but would show no difference in South Hole Sound where snails are naturally abundant; 1b) compared to controls, snail exclosures would show an increase in diatom density in South Hole Sound, but would show no difference in Preston Bay where snails are naturally absent. 2) due to waves and predation, snail population losses over a 24-hour period would be greater in Preston Bay than in South Hole Sound.

METHODS

We collected approximately 380 snails from South Hole Sound, Little Cayman Island on 28 February, 2010 and held them in sea water for several hours. We marked 180 of the snails with red nail polish.

In the sea grass beds in South Hole Sound and Preston Bay, we haphazardly placed nine 0.5 m x 0.5 m quadrats, and placed 10 marked snails in each quadrat.

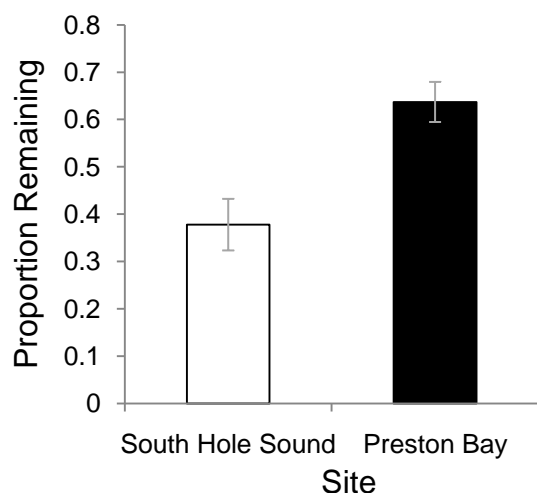


FIG. 1. Two-tailed t-test comparing proportion of snails remaining in 0.5 x 0.5 m quadrats after 24 hours in South Hole Sound and in Preston Bay on Little Cayman Island, 1 March, 2010. Error bars are ± 1 standard error of the mean.

After 24 hours, we recorded the number of marked snails remaining within the quadrats. We tested for differences using a two-tailed t-test assuming equal variances.

At both sites, we staked 20 fiberglass mesh, open-top cages (52 cm in circumference x 22 cm in height) into the sea grass beds, with the bottom edge touching the sediment. We stratified the locations of the cages across the study site and randomly selected which cages would be snail enclosures or exclosures. We placed 10 snails into 10 of the enclosures and excluded snails from the other 10 enclosures.

We collected a random blade of turtle grass from each cage and 10 random blades from outside the cages as a control at each site. We measured the width of each blade and marked out 15 cm of length. We scraped along both sides of the grass blade with a razor from the 15 cm mark to the tip into a weigh boat containing 1 mL of tap water. We washed the contents of the weigh boat into the original sample container with 4 mL of water, shook them for 5 seconds, then pipetted 100 μ L of the fluid into a microcentrifuge tube. We spun the tubes for 7 seconds in an Eppendorf Minispin Plus centrifuge using the “Short Spin” button (max. 9000 rpm), and

then discarded 90 μ L of the supernatant. We vortexed the precipitate and placed 4 μ L of the sample onto a microscope slide. We counted the number of diatoms along one transect of each slide and found the number of diatoms per square millimeter of blade area. We compared the natural log of diatom densities among treatments and between sites using a general linear model with Location, Treatment, and Location*Treatment as explanatory variables.

RESULTS

We observed approximately 20 species of diatom, of both the Pennales (elongate) and Centrales (radially symmetric) orders. The effect of treatment on diatom density varied significantly by location, and there was no effect of addition or exclusion of snails on diatom density (Table 1, Fig. 2). The results of the open quadrat snail movement experiment were opposite our predictions; 22% more snails remained in quadrats in Preston Bay than in South Hole Sound ($t_{18} = 2.32$, $P = 0.03$; Fig. 1).

TABLE 1. General linear model of the effects location, treatment, and the interaction between location and treatment on diatom density in Preston Bay and South Hole Sound, Little Cayman Island, March 1, 2010.

Source	df	MS	F	P
Location	1	54.93	68.39	<0.0001*
Treatment	2	1.83	2.28	0.11
Location*Treatment	2	4.40	5.47	0.007*
Error	54	--	--	--

DISCUSSION

Though the effect of treatment on diatom density varied significantly by location, the results strongly suggest that the diatom density in Preston Bay may be higher than in South Hole Sound. We did not find support for the hypothesis that a difference in diatom density between South Hole Sound and Preston Bay was driven by snail density. However, we suspect that the lack of response in diatom density to the addition or exclusion of snails was due to the short duration of our experiment. Moreover, our exclosures/ encl-

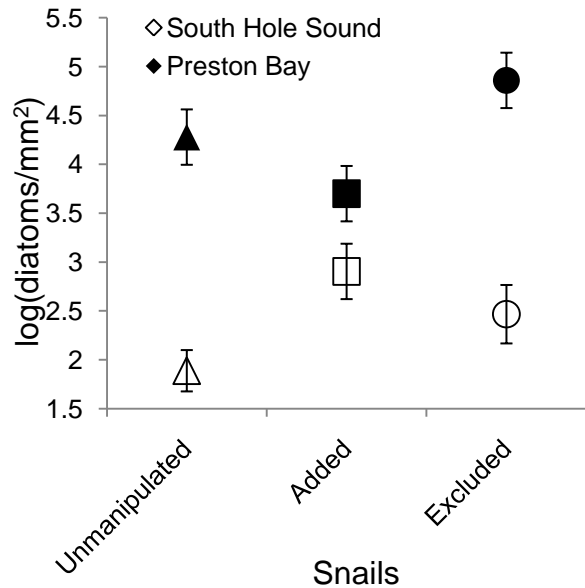


FIG. 2. General linear model showing the effects of snail enclosures and exclosures on diatom density compared to controls in Preston Bay and South Hole Sound, Little Cayman Island, March 1, 2010. Error bars are ± 1 SE.

losures were ineffective in maintaining the desired snail manipulations. We observed snails inside exclosures in South Hole Sound and directly outside the enclosures in Preston Bay.

The results of the disturbance component of our study were opposite of our prediction, with more snails remaining in their quadrats in Preston Bay relative to South Hole Sound. Disturbance may not prevent snails from maintaining their position, but still may interfere with their feeding in some way. Snails in South Hole Sound may have moved out of their quadrat because they were in control of their movement, whereas snails in Preston Bay may have clung on to the nearest blade so as not to be swept away. These findings do not support predation as a cause of the snail distributions, but do not rule out waves as a mechanism. Hydrologic effects have been shown to dislodge snails, causing them to seek more protected locations (Holomuzki and Biggs 1999), which may explain their presence in South Hole Sound and absence from Preston Bay. Preston Bay is located on the side of Little Cayman most affected by hurricanes, so it is also possible that more in-

tense disturbances such as hurricanes rather than everyday wave action are responsible for lower snail density.

Snail and diatom density appeared to be negatively correlated between the two study sites, but none of the tested mechanisms could explain a difference. Further study is needed to test whether abiotic factors such as waves or top-down control by predators from the reef decrease snail abundance and thus increase diatom abundance through cascading trophic interactions. In many ecosystems, the degree of top-down control by herbivores is highly variable (Cyr and Pace 1993), and herbivory can play a large role in shaping a system (Williams 1988). Thus, in high-productivity systems such as sea grasses, understanding what factors drive the top-down control of diatoms may help to more clearly describe the local system as a whole.

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THE SPATIAL IMPACT OF TERRITORIAL DUSKY DAMSELFISH (*STEGASTES ADUSTUS*) ON A CARRIBBEAN CORAL REEF

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Abstract: Some species of damselfish, including *Stegastes adustus*, defend territories against herbivores, which can negatively impact coral growth. Territory size and *S. adustus* density may be good indicators of this species' impact on coral reefs. Potentially important factors for *S. adustus* density and territory size include algal growth rate and interspecific competition. To assess which of these factors were driving *S. adustus* impacts on the coral reefs of Little Cayman, we measured *S. adustus* density, territory size, herbivore density, and the number of interspecific aggressive interactions as they varied by depth (a proxy for light availability). *S. adustus* density decreased and territory size increased with depth while herbivore presence and aggressive interactions were similar, suggesting that light availability or algal growth rate may strongly contribute to *S. adustus* spatial distribution. Relative area controlled by *S. adustus* and the percent algal cover within their territories did not differ between shallow and deep sites, suggesting that *S. adustus* has similar impacts on coral growth across their depth range.

Key Words: algal garden, algal growth rate, coral growth, herbivory, interspecific competition, territory defense, territory size

INTRODUCTION

In light of recent coral declines, understanding the factors impacting coral growth has become urgent. Some species of damselfish, including *Stegastes adustus*, aggressively defend territories against herbivores on coral reefs and cultivate algal turfs, farming epiphytes on the algal lawns. Because they promote macroalgae growth, prevent herbivore grazing, and actively damage live coral, damselfish can inhibit coral growth and increase bioerosion (Ceccarelli et al. 2001; Risk and Sammarco 1982). The territory size and density of *S. adustus* indicate the amount of area over which they may influence coral growth. In order to understand the factors influencing variation in the territory size and density of *S. adustus*, we looked at several metrics across depth, a strong environmental gradient. Fac-

tors that may increase territory size include decreased competition from heterospecific herbivores, allowing *S. adustus* to expend similar energy defending a larger area, and lower algal growth rate, requiring more area to provide similar food resources. The opposite trends in competition from heterospecific herbivores and algal growth rate may decrease territory size. Algal growth rate is predicted to decrease with increasing depth due to decreasing available light. If algal growth rate represents food availability for benthic herbivores, we may expect higher abundances of potential *S. adustus* competitors at shallow sites (e.g. Schiel et al. 1986 reported finding more herbivores in shallow waters). Increased competition may be expected to decrease local *S. adustus* density due to its negative impact on overall habitat quality in-

TABLE 1. Hypothesized factors affecting *Stegastes adustus* density and territory size could be algal growth rate (represented by depth) or interspecific competition (represented by herbivorous fish density and frequency of aggressive interactions).

Driving Factors	Depth	<i>S. adustus</i> Density	Territory Size	Herbivorous Fish Density	Frequency of Aggressive Interactions
Algal Growth Rate	Shallow	High	Low	No Difference	No Difference
	Deep	Low	High	No Difference	No Difference
Interspecific Competition	Shallow	Low	Low	High	High
	Deep	High	High	Low	Low

dependent of intraspecific competition. We expect decreased competition to have the opposite effect. Lower algal growth rate could also decrease *S. adustus* density, because it would make habitat less desirable at greater depth. Either of these two factors (heterospecific competition or algal growth rate) may be most important in structuring *S. adustus* spatial distribution (Table 1).

METHODS

We recorded depth, *S. adustus* density, and *S. adustus* territory size, herbivore fish density, the frequency of aggressive interactions, and percent algal cover in territories at two shallow and two deep coral reef sites surrounding Little Cayman Island (Preston Bay (0.78 m), Jackson's Point (0.76 m), Grundy's Garden (7.96 m), and Cumber's Cave (6.81 m)) from 28 February to 2 March, 2010. Preston Bay and Grundy's Garden were on the south side of the island while Cumber's Cave and Jackson's Point were on the north side of the island. We snorkeled at Preston Bay between 0941 and 1100 and between 1441 and 1630 on 28 February, 2010 and at Jackson's Point between 1236 and 1413 on 2 March 2010. We used SCUBA at Grundy's Garden between 1406 and 1504 on 1 March 2010 and at Cumber's Cave between 1500 and 1550 on 2 March 2010.

To quantify *S. adustus* density at deep and shallow sites, each researcher pair recorded the number of *S. adustus* sighted while swimming for 10 or 15 minutes. We averaged the *S. adustus* counts of each researcher to find number of fish sighted per minute, henceforth referred to as density. We used *S. adustus* density multiplied by territory size to ascertain the relative amount of reef area influenced by *S. adustus* algal farming.

We measured herbivorous fish density twice prior to and twice after *S. adustus* density time transects as an indicator of interspecific competition. For herbivore fish density, each pair of researchers held a 4 m rope between them and recorded the number of herbivorous fish sighted in 1 min within the cir-

cle diameter formed by the rope. We averaged the herbivore fish counts recorded by each researcher. We observed 4-5 haphazardly chosen individual *S. adustus* within the area covered by the time transect. Each pair recorded the maximum number of aggressive interactions (chases) between an individual *S. adustus* and heterospecific herbivorous fish (Surgeonfishes, Parrotfishes, Wrasses, heterospecific Damselfishes) observed in 5 min as an additional indicator of interspecific competition. We measured territory size by placing a rope marked at each half meter across the longest section of territory. At shallow sites, we measured territory depth by stretching the rope from the surface to the center of the *S. adustus* territory. At deep sites we used a dive computer to quantify depth. We measured percent algae cover by placing a 0.5 m by 0.5 m quadrat in the center of the individual's territory. We computed the average of each researcher's estimate of the percent algal cover within the quadrat.

We used a one-tailed t-test to test differences between depths in factors for which we had unidirectional predictions, and a two-tailed t-test for *S. adustus* density and percent algal cover between depths (Table 1). We used Levene's test to test for unequal variances, and if this test was significant we performed unequal variance t-test.

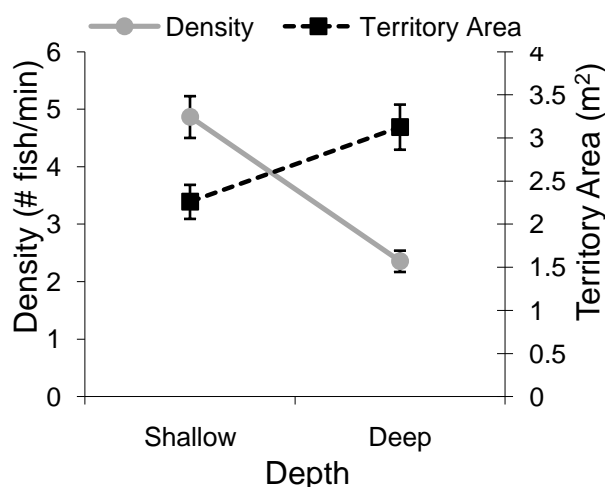


FIG. 1. *S. adustus* density and territory size in two shallow and two deep reef areas at Little Cayman Island from 28 February to 2 March, 2010. Error bars represent ± 1 SE.

RESULTS

S. adustus relative density was 107% greater at the shallow sites, Preston Bay and Jackson's Point, than at the deep sites, Grundy's Garden and Cumber's Cave (Fig. 1; $t_{39,76} = 6.15$, $P < 0.0001$). Territory area was 28% smaller at the shallow sites than at the deep sites, (Fig. 1; one-tailed t-test, $t_{43} = 2.65$, $P = 0.006$). Herbivore density and number of aggressive interactions were not significantly different between shallow and deep sites (For herbivore density, one-tailed t-test, $t_{39,90} = 0.67$, $P = 0.25$; for aggressive interactions, one-tailed t-test, $t_{35,46} = 0.01$, $P = 0.50$).

Relative *S. adustus*-controlled area (average observed territory area multiplied by *S. adustus* time density for each transect) and percent algal cover for each observed territory did not differ significantly between deep and shallow sites (For *S. adustus*-controlled area, $t_{7,87} = 0.44$, $P = 0.67$; for percent algal cover, $t_{43,90} = 0.79$, $P = 0.43$).

DISCUSSION

The spatial impact of *S. adustus* on coral reefs did not vary along the depth gradient: between shallow and deep sites there was no difference in the amount of reef area controlled by *S. adustus* and in algal cover within territories. Frequencies of aggressive interactions and herbivore densities did not vary across depth, suggesting similar levels of heterospecific competition, yet we still detected differences in *S. adustus* density and territory size across depth. This suggests that a factor that varies across depth, algal growth rate, may be the primary factor determining *S. adustus* spatial distribution (Table 1). Similar percentages of algal cover could be driven by the similar herbivorous fish densities observed at shallow and deep sites. However, we rarely observed herbivores successfully grazing within *S. adustus* territories, although invasions of herbivorous competitors could occur primarily in isolated large-scale events that we were unable to quantify (e.g. outside of data collection, we observed a large school

of chub briefly grazing a series of *S. adustus* territories). Intraspecific competition may play an important structuring role, but our anecdotal observations did not support this, as *S. adustus* rarely interacted aggressively with conspecifics. However, it is possible that intraspecific competition is important but not readily observable. Alternate explanations for the decrease in density at depth may be higher direct space competition from other territorial herbivores (for example, we observed high densities of bicolor damselfish at our deeper sites), lower availability of shelter (Wellington 1982), or greater predation pressure on *S. adustus* with increasing depth.

Our findings suggest that changes to algal growth rate, whether naturally along gradients or by anthropogenic forces may not alter *S. adustus* spatial impact on the reef, as density and territory size may reach some equilibrium keeping the *S. adustus*-controlled area relatively constant. We did not find variation in the frequency of aggressive interactions and herbivore density across depth, therefore the relative importance of this factor remains unclear. Any disturbance that alters heterospecific competition may have the potential to greatly affect the *S. adustus* impact on the reef.

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CORAL STRENGTH IN DIFFERING LEVELS OF WAVE INTENSITY

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Abstract: Coral reefs are greatly affected by wave disturbance, which can harm but also disperse broken coral fragments as new recruits. We examined whether the strength of coral species was affected by the shape, size, and density of their corallites by testing breaking strength of dead corals at Jackson's Point and Preston Bay, Little Cayman. We estimated the relative abundance of six species at the reef crest, the fore reef, and the lagoon to determine the location of corals in relation to their breaking strength. We found that coral strength varied among coral species and by location. Weaker corals tended to be found in the reef crest and fore reef, while the stronger corals were found in the lagoon. Because strong corals were observed in both high- and low-intensity wave locations, our results suggest that wave intensity may not be the driving factor in determining breaking strength. Future studies should address other influences on coral strength and distribution, such as parrotfish predation, food availability, weathering, or coral shape.

Key Words: coral skeleton, corallite density, Little Cayman Island, polyp, reef crest

INTRODUCTION

The physical stress of waves is an important factor affecting coral reef communities (Dollar 1982, Tunnicliffe 1982). Waves cause coral mortality through abrasion, breakage, and dragging debris onto corals. Breakage decreases the topographical complexity of the reef, which can lead to lower diversity and abundance of coral and other reef organisms (Aronson and Precht 1995). Coral fragmentation is also a mechanism for reproduction (Dollar 1982, Tunnicliffe 1982). Coral strength may affect which areas of the reef a coral species can colonize and how that species is impacted by hurricanes, grazing by parrotfish and other organisms, and human physical disturbance (e.g., boat anchors, tourist activity).

Stony corals (order Scleractinia) have a rigid aragonite skeleton that breaks after a certain stress threshold (Tunnicliffe 1982). Stony coral species vary in corallite size, shape, and density. We tested the effect of corallite size and density, along with skeletal density, on the strength of six common boulder-shaped stony corals found at Little Cayman Island (LCI).

Here we test two possible models explaining the distribution of coral in relation to

wave intensity. One model predicts stronger corals in areas with high wave intensity because they are able to withstand the physical stress without breaking. The other model predicts weaker corals in high wave intensity areas because they are able to fragment instead of having the entire colony overturned. Since corals exhibit phenotypic plasticity in shape and structure (Bruno and Edmunds 1998) and may adapt to habitats with different physical stresses, we compared the strength of dead coral at two reefs with different average annual wave intensities. We then estimated the distribution of live coral at different reef zones that varied in wave intensity.

METHODS

We collected coral specimens on 28 February and 1 March 2010, along the beach at Jackson's Point and Preston Bay of LCI. Preston Bay is on the southwest of the island, receives more dominant winds, and is directly hit by more hurricanes compared to the north, centrally located Jackson's Point. We collected 14 samples per 6 species of coral at each beach: *Diploria strigosa* (Smooth Brain Coral), *Diploria labyrinthiformis* (Grooved Brain Coral), *Stephanocoenia intersepta* (Blushing Star Coral), *Solenastrea bournoni* (Smooth

Star Coral), *Siderastrea radians* (Lesser Starlet Coral), *Agaricia humilis* (Low Relief Lettuce Coral). Specimens were flat and circular, 10-15 cm wide and 2-4 cm in depth. We measured the mass to the nearest gram using a balance and volume by water displacement and calculated their density.

For star and starlet corals, we measured corallite size using a 5 x 5 cm quadrat placed haphazardly on the coral, averaging the diameter of four randomly selected corallites. For brain corals, the corallite diameter was estimated as the distance between the ridges.

We counted the number of corallites in the 5 x 5 cm quadrat to calculate corallite density in *S. intersepts* and *A. humilis*. For *S. bournoni* and *S. radians* we used a 2 x 2 cm quadrat. Large quadrats were used to accommodate large corallites. For *D. strigosa* and *D. labyrinthiformis* we used a 1 x 5 cm quadrat and counted the number of valleys. All densities were converted to corallites per square centimeter.

To estimate breaking strength, we used breaking height as an approximation. We placed the coral on a cement block and dropped a 2.27 kg lead weight on the coral at successive heights until the coral broke. A break was determined as a crack through the entire coral specimen. We dropped the weight from heights of 0.5 m (Force, or $F = 34.82$ N), 1.0 m ($F = 49.24$ N), 1.5 m ($F = 63.81$ N), 2.0 m ($F = 69.64$ N), 2.5 ($F = 77.86$ N), 3.0 m ($F = 85.29$ N), 3.5 m ($F = 92.13$ N), and 4.0 m ($F = 98.49$ N). On the rare occurrence that the coral did not break from a height of 4 m we recorded the breaking height as 4.5 m.

To estimate the distribution of live coral, we swam three 50 m transects at Jackson's Point due north of Little Cayman Research Center: one on the reef crest, one 10 m from the crest on the fore reef side, and one 10 m from the crest on the lagoon side. Two people swam each transect counting the six coral species within one meter on each side of the transect, recording the number of each species.

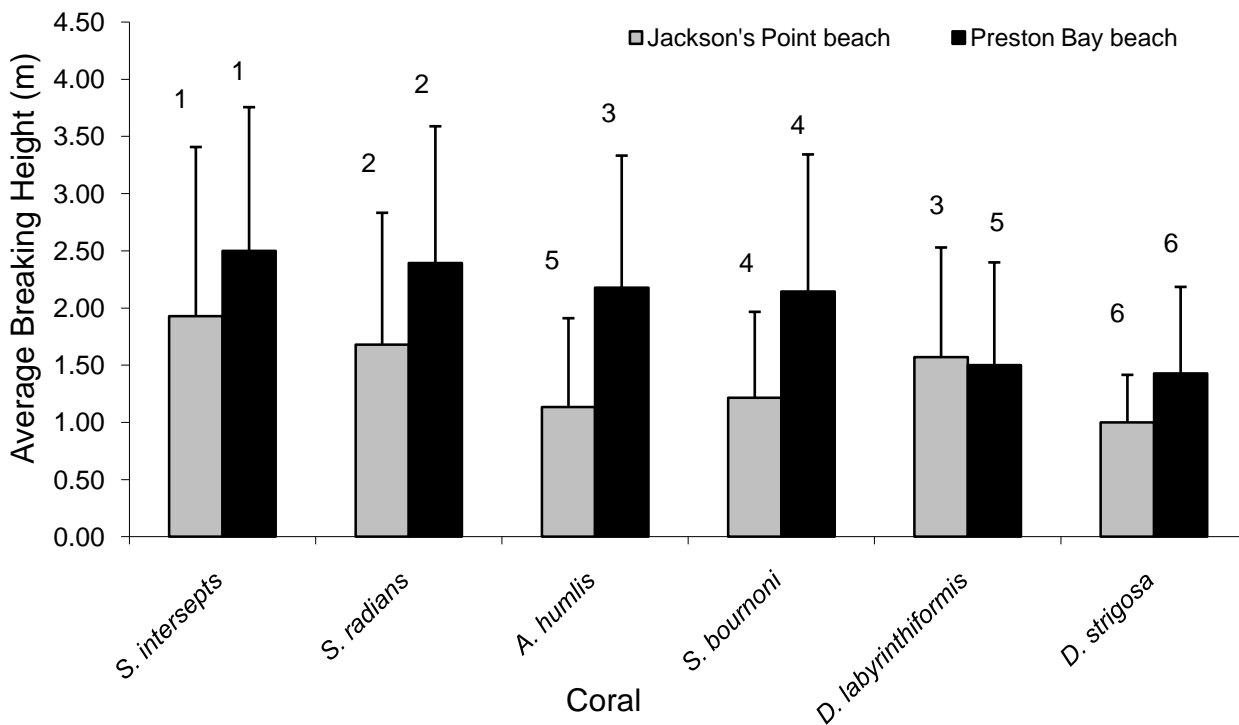


FIG. 1. Coral species breaking height at a high wave intensity site (Preston Bay beach, Little Cayman) had a higher breaking strength than coral at a low wave intensity site (Jackson's Point beach, Little Cayman) ($F_{1,5} = 13.55$, $P = 0.0003$). Numbers 1-6 indicate coral strength from strongest to weakest.

TABLE 1. General linear model of the effects of coral species, mass, and volume on breaking strength of six coral species.

	df	Sum of Squares	F	P
Coral Type	5	13.20	2.35	0.043
Mass	1	0.024	0.021	0.88
Volume	1	1.67	1.49	0.22
Error	160	--	--	--

We used a general linear model to compare coral species among the two beach sites, to test for an interaction between corallite density and species, and to test how mass, volume, and coral type affected breaking height. We tested the difference between coral species at each site with an ANOVA and student t test. ANOVA compared breaking heights between star and brain coral across all locations.

RESULTS

Dead coral found at Preston Bay beach had a higher breaking strength than dead coral found at Jackson's Point beach (Fig. 1). At Preston Bay, *S. intersepts* and *S. radians* had a significantly higher breaking strength than *D. labyrinthifo* and *D. Strigosa* ($F_{5,78} = 2.41$, $P = 0.043$). At Jackson's Point, coral breaking strengths were not significantly different from each other. Corallite density varied by coral species and by site (i.e., Jackson versus Preston), with *S. bournoni* driving the interaction effect by having a higher mean corallite density at Preston Bay beach ($F_{11,156} = 3.4051$, $P = 0.006$). There was an effect of coral species on breaking strength, but mass and volume did not affect breaking height (Table 1). Across the two sites, brain corals (*Diploria* spp.) had a significantly lower breaking strength than star corals ($F_{1,138} = 10.37$, $P = 0.0016$).

At Jackson's Point beach, stronger coral tended to be found in the lagoon area, while weaker corals tended to be found in the fore reef and crest (Fig. 2).

DISCUSSION

Breaking strength did not show a consistent pattern in relation to wave intensity. The distribution of corals within the reef at Pres-

ton Bay supports the model that the weakest coral species were found at areas of highest wave intensity (the reef crest). However, the difference in coral strength between beaches supports the model that stronger corals were found in areas of higher wave intensity (Preston Bay).

Differences in coral strength may be a response to biotic stresses, such as biological erosion due to predation by parrotfishes (Hutchings 1986), and not solely to wave action. Bioerosion and other forms of predation may vary depending on location. Future studies could examine the relationship between coral strength and these biotic factors.

Of all our measured variables, only corallite density was observed to vary by coral species between the two beach sites. This supports conclusions from previous studies that corallite spacing is a phenotypically plastic trait (Bruno and Edmunds 1998).

Our methods for testing breaking strength may not have accurately recreated the natural force applied to coral by waves

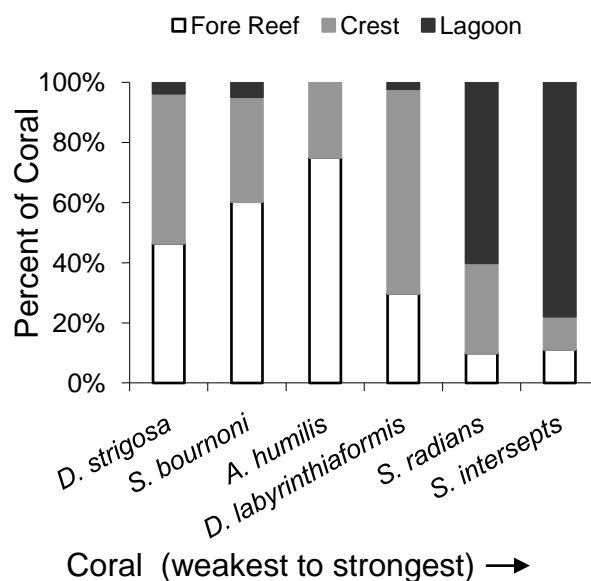


FIG. 2 Percent of each coral type found along a 50 m transect in three zones of the coral reef at Jackson's Point on 2 March 2010. The reef crest transect was taken where the waves were breaking, with the lagoon and fore reef transects ca. 10 m parallel on each side of the crest. Coral species are ordered from weakest to strongest breaking strengths.

and debris, and future experiments should try to better mimic the natural conditions of these stresses. In addition, corals that have been on the beach for long periods of time may be weaker due to longer periods of weathering, which may differ among species or between the two sites on Little Cayman. Shape (i.e., mounding or branching) of corals and how that interacts to buffer corals from wave stress was also not considered, which may explain some of the variation in strength and position of coral species in the different reef zones.

Understanding coral strength is important in the preservation of reefs, especially when coral is under stress from physical forces such as hurricanes, boat anchors, cruise ships, or SCUBA divers. Likewise, this study indicates that the physiology of coral may be much more dynamic than previously thought, and much more susceptible to abiotic factors like wave action.

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DO HERMIT CRABS USE CHEMICAL CUES EMITTED BY SHELLS AND THE TRAILS OF CONSPECIFICS?

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Abstract: Hermit crabs release and sense chemicals to gain information about their environment. In this study, I tested whether hermit crabs use chemical cues to select a new shell and whether chemical cues left by other hermit crabs' trails change the direction of their movement. Hermit crabs showed no preference for shells with *Cittarium pica* scent versus shells that were bleached to remove scent. There were size-specific changes in behavior when hermit crabs encountered small or large hermit crab trails. However, there was no significant change in reaction to the two intermediate size class trails. Perhaps hermit crabs are not sensitive to small changes in the sizes of conspecifics, as they only responded to the smallest and largest size classes.

Key Words: chemical cues, gastropods, Little Cayman, shells

INTRODUCTION

Hermit crabs have been found to use chemical cues for various purposes, such as aggregation, alarm, and shell withdrawal behaviors (Rittschot et al., 1992). Chemical cues enable hermit crabs to gain information about their environment.

Studies have shown that various species of hermit crabs use the scent of dead gastropods to identify shells suitable for habitation and to help them locate shells that are vacant (Rittschot, 1979). For my first experiment, I tested the effect gastropod scent had on shell preference by the Caribbean land hermit crab, *Coenobita clypeatus*. If gastropod scent is a strong factor in shell preference, hermit crabs should prefer scented shells versus ones that have been bleached to remove scent. However, if they prefer bleached shells, then perhaps scent left behind by other hermit crab inhabitants of the shells may make shells less appealing for habitation. If there is no shell preference, then other factors, such as shell quality may be more important than gastropod scent in selecting suitable shells.

I also explored how chemical cues influence hermit crab behavior. In the second study, I tested the effect hermit crab trails have on the behavior of other hermit crabs encountering these trails. I hypothesized that smaller hermit crabs would be more cautious

when encountering hermit crab trails, fearing conflict or cannibalism and therefore may respond by avoiding conspecific trails. Larger hermit crabs may be less cautious and thus may be more likely to cross a trail because there is less risk if there is a confrontation. Conversely, since hermit crabs in general are gregarious (Harvey, 1996), they might be more likely to follow paths left by other hermit crabs to increase the likelihood of encountering an aggregation, water, or food. If chemical cues are not associated with trails or are not recognized by hermit crabs, then there should be no response of hermit crab behavior to trails. Using chemical cues to identify hermit crab presence enables hermit crabs to assess risk before encountering a conspecific.

METHODS

Experiments were conducted 28 February - 2 March, 2010 at the Little Cayman Research Center (LCRC) in Little Cayman Island. Approximately 40 specimens of the hermit crab, *Coenobita clypeatus*, were collected near the LCRC.

To test for shell preference, I collected vacant West Indian top snail, *Cittarium pica*, shells predominantly used by hermit crabs from along the beach at Jackson's Point. I paired similar-sized undamaged shells, one shell containing gastropod, hermit crab, or

both scents (as these shells may or may not have been previously inhabited by hermit crabs) and one shell with scent removed. To remove the gastropod scent, shells were submerged in a 20% bleach solution for 30 minutes and then soaked in seawater overnight. Similar-sized hermit crabs were used if they had damaged or small shells, factors that would increase their likelihood of changing shells during the trials. Additionally, some inhabited shells were mechanically damaged with a wood file to increase the chance of hermit crabs switching shells. Hermit crabs were presented with scented and bleached shells in identical 7.5 liter plastic containers in the lab.

To test if hermit crabs respond to chemical trails left by the tracks of other hermit crabs, I selected four hermit crabs to create trails and sorted them into four claw length size classes: 1 (0.9 cm), 2 (1.4 cm), 3 (2.7 cm), 4 (4.6 cm). I used each hermit crab to make a single trail in the sand, with each of the size class trails parallel to each other, separated by approximately 2 cm. New trails were made for each focal crab. I also measured the claw sizes of each focal hermit crab. Each focal hermit crab was oriented perpendicular to each of the four different sized trails and their behavioral response was noted. Hermit crabs could turn around (encounter avoidance), pass over (ignore trail) or follow (aggregation seeking) the trails. If the focal hermit crab turned away from or followed a trail, I would pick it up and place it in front of the next trail. If the focal hermit crab passed over the trails I wouldn't disturb it and recorded how many trails it passed over before changing its behavior. Trials were performed both at night 21:00-24:00 and day 12:00-13:00, since hermit crabs were active at all times of day. A logistic regression was used to test the behavioral response to the different sized trails of the focal hermit crabs as a function of their claw size.

RESULTS

Out of ten replicates, five bleached shells were selected by hermit crabs while five

TABLE 1. Frequency of behavioral responses of hermit crabs to trails of different sized conspecifics.

Behavioral Response	Size class 1	Size class 2	Size class 3	Size class 4
Turn around	8	5	8	8
Pass through	9	9	9	8
Follow	1	4	1	2

shells with *C. pica* scent were selected. ($\chi^2_1=0.00$).

The response to trails of conspecifics by focal hermit crabs as they increased in size differed significantly between size class 1 ($r^2 = 0.21$, $P = 0.04$) and size class 4 ($r^2 = 0.23$, $P = 0.02$), with the hermit crabs increasing in turning around behavior. However, there was no significant difference in behavioral responses to trails between size class 2 ($r^2 = 0.02$, $P = .063$) and size class 3 ($r^2 = 0.04$, $P = 0.52$).

DISCUSSION

There was no preference for either the bleached or unbleached shells. This may indicate that other factors, such as shell quality or size, are more important in shell selection. Hermit crabs were observed to thoroughly inspect the shells using their legs, claws, feelers, etc., suggesting that they were not selecting shells simply by scent. However, my sample size was very small and may not be a representative sample of the hermit crab population. Also, because I collected the shells from the beach, it was impossible to tell how long shells were exposed to the environment, so perhaps variation in the strength of *C. pica* scent, perhaps along with the varying presence of hermit crab scent, among shells may have affected my results. This finding conflicts with other studies demonstrating that gastropod scent strongly attracts hermit crabs to the shells and induces them to switch into the shell (Rittschof, 1979). Further studies are needed to see which factors are the strongest in shell preference in *C. clypeatus*.

There was a relationship between hermit crab size and behavior when encountering the trails made by the smallest and largest size classes. As test hermit crabs increased in claw

size, their behavior was significantly different, with increased numbers of crabs turning away from size class 1 and 4 trails. Hermit crab behavior was not affected across claw size by trails made by intermediate size classes. This may indicate that hermit crabs are not extremely sensitive to different sized trails left by conspecifics. Also, other confounding factors, such as the gender of the hermit crabs that produced or encountered the trails may have affected the way they responded to the different trails. For example, a male hermit crab may be more likely to follow a trail made by a female hermit crab, regardless of the sizes of the two individuals.

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DIFFERING RESPONSES TO SIMULATED PREDATION THREATS BY TERRITORIAL AND NON-TERRITORIAL CORAL REEF FISHES

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Abstract: Coral reef fish respond to an increasing threat of predation using various predator avoidance behaviors, such as swimming or hiding from predators. We investigated whether the territoriality of a fish affected its anti-predator response, because these behaviors afford fish the ability to survive but may impact a territorial fish's ability to successfully hold a territory. We presented different sized fish models to four Caribbean reef fishes, two of which were territorial and two of which were not, and observed behavioral responses. We found that all fish were more likely to exhibit predator avoidance behavior with increasing predation risk and that territorial fish were more likely to hide to escape predation, while non-territorial fish were more likely to swim to escape. Within their preferred mode of predator avoidance, territorial fish were slower to respond to increasing predation threat compared to non-territorial fish. Our findings support the hypothesis that territorial fish experience a higher cost to avoiding predation than non-territorial fish.

Keywords: bluehead wrasse, coral reef, Caribbean, dusky damselfish, French grunt, Little Cayman, models, predator avoidance, squirrelfish, territoriality, trade-offs

INTRODUCTION

Many individuals face a tradeoff between predator avoidance activities and other activities that benefit fitness (Downes 2001, Cowlshaw 1997). Fish must weigh the benefit of evading predation against the opportunity cost of abandoning other fitness enhancing behaviors such as foraging, territory defense, and mate attraction (Godin 1997). As the magnitude of predation threat increases, fish exhibit progressively stronger predator avoidance behaviors (Helfman 1989). We investigated whether the differential costs that territorial and non-territorial fish face result in different magnitudes and types of predator avoidance behaviors in response to increasing threat levels. By hiding or swimming away from a predator, both territorial and non-territorial fish give up time that could be spent foraging or courting mates. However, a territorial fish gives up the ability to defend its territory from others, while non-territorial fish do not incur this cost when exhibiting the same behaviors. Therefore, the fitness cost of hiding or swimming away from a predator may be greater for territorial fish, resulting in more conservative predator avoidance beha-

viors than non-territorial fish. We predicted that both territorial and non-territorial fish would increase the time spent exhibiting avoidance behaviors with increasing predation risk, but that territorial fish would spend less time than non-territorial fish exhibiting avoidance behaviors for any given predation threat. Additionally, we predicted that territorial fish would reserve the investment in exhibiting avoidance behaviors for greater predator threats than non-territorial fish.

METHODS

On 28 February and 1 March 2010, we observed the responses of four fish taxa (Table 1) to different sized models of fish at Jack-

TABLE 1. Taxa and total body length of four target fishes, divided into size classes and territoriality behavior.

	Territorial	Non-territorial
Small	Dusky damselfish <i>Stegastes adustus</i> 7.6 - 12.7 cm	Initial phase bluehead wrasse <i>Thalassoma bifasciatum</i> 7.6 - 12.7 cm
Large	Squirrelfish (Holocentridae) 12.7 - 25.4 cm	French grunt <i>Haemulon flavolineatum</i> 15.2 - 25.4 cm

son's Point and Preston Bay, Little Cayman Island.

To simulate varying magnitudes of predation threat, we made different sized fish models out of silver duct tape, cardboard, dead coral pieces, and fishing line. Predation threat increases with size of predator; maximum prey size increases with predator size, whereas minimum prey size rarely varies with predator size (Schari et al. 2000). These models were approximately 1x, 2x, and 3x the total length of the different focal fish: for *S. adustus* and *T. bifasciatum*, the models were 10 cm, 21 cm, and 34.3 cm long, respectively; for the Holocentrids and *H. flavolineatum*, models were 21 cm, 34.3 cm, and 53.3 cm, respectively.

While snorkeling at both study sites, we haphazardly chose focal fish. We dangled a model 0.5 m from the focal fish for 90 seconds, simulating a predatory fish swimming up and down towards the focal fish. As a control, we hovered above focal fish, presenting a closed fist without a model. We used a random number generator to choose which of the three models, or control, to present. For each presentation we recorded the amount of time the fish spent swimming away or hiding (avoidance behaviors), and not responding (non-avoidance behavior). We performed five replicates of each presentation for *H. flavolineatum* and four replicates of each presentation for *S. adustus*, *T. bifasciatum*, and Holocentrids.

We analyzed the proportion of time fish spent exhibiting each behavior. We arcsine-square-root transformed the percentage data due to non-normality. The data were skewed due to a large number of zeros. We used an ANCOVA to test for the effects of fish type (territorial or not) and size of predator model on the proportion of time fish spent exhibiting avoidance behaviors. We used two one way ANOVAs to test for differences in proportion of time spent swimming away and proportion of time spent hiding, respectively, for territorial and non-territorial fish pre-

sented with different sized fish models. In both cases, we used Tukey's HSD post hoc.

RESULTS

With increasing model fish size, both non-territorial and territorial fish spent significantly more time avoiding predator models (ANCOVA $F_{1,48} = 8.26$, $P = 0.0060$; Fig. 1). The two territorial species showed similar trends, as did the two non-territorial species. This similarity between species of the same type shows that the trend we observed was not driven by a single species. In addition, there was no difference in the slope of the lines relating the proportion of time avoiding the predator model to predator model size between territorial and non-territorial fish (ANCOVA $F_{1,48} = 0.19$, $P = 0.67$; Fig. 1).

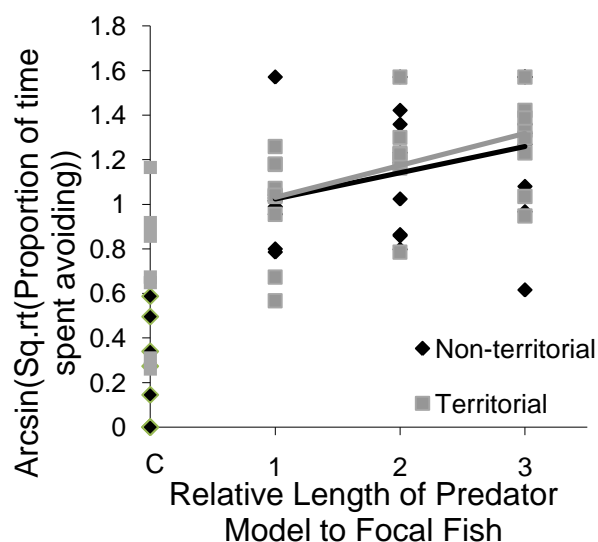


FIG. 1. At Jackson's Point and Preston Bay, Little Cayman, *Thalassoma bifasciatum* and *Haemulon flavolineatum* (non-territorial) and *Stegastes adustus* and Holocentridae (territorial) spent a greater proportion of their time exhibiting avoidance behaviors when presented with increasingly large predator models. However, territorial and non-territorial fish did not spend significantly different proportions of time exhibiting avoidance behaviors, nor was there an interaction between fish type (territorial or not) and size of predator model. 'C' on the x-axis represents the control treatment during which fish were presented with no predator model. The control values were not included in the analysis.

Although focal fish spent a similar proportion of their time avoiding predators, territorial and non-territorial fish engaged in different avoidance behaviors. Non-territorial fish spent at least twice as much time swimming away than territorial fish did, while territorial fish spent at least twice as much time hiding than non-territorial fish did ($F_{7,56} = 12.10$, $P = 0.0010$; Fig. 2). The non-territorial fish spent significantly more time swimming away from predator models compared to the control ($F_{7,59} = 4.98$, $P = 0.0038$), but the proportion of time spent swimming remained similar, even with increases in predation threat (Fig. 2). The response of the territorial fish did not differ from the control until the threat was very large ($F_{7,59} = 4.62$, $P = 0.0058$; Fig. 2).

DISCUSSION

As predicted, all fish species spent more time exhibiting avoidance behaviors with inc-

reasing predation threat, as measured by increasing fish model size, indicating that there is a trade-off between spending time doing normal activities and avoiding predators for both territorial and non-territorial fish. However, the amount of time spent exhibiting avoidance behaviors did not vary between non-territorial and territorial fish at any given fish model size. This would seem to suggest that the cost of exhibiting avoidance behaviors does not differ between territorial and non-territorial fish. However, there was a significant difference between the type of avoidance technique used by territorial and non-territorial fish, with territorial fish preferring to hide, and non-territorial fish preferring to swim away. Within their chosen avoidance technique, non-territorial fish always reacted significantly more to the models than the control regardless of the size of the model. In

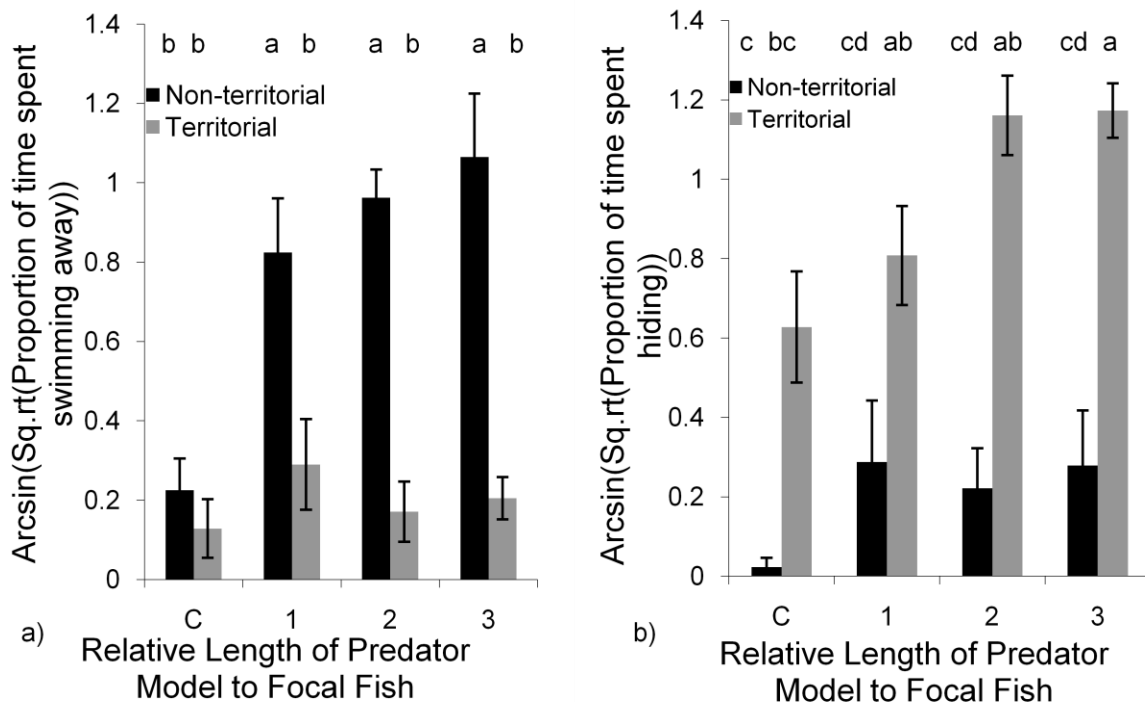


FIG. 2. Comparison of time devoted to two different types of avoidance behavior in territorial and non-territorial fish when presented with increasingly large fish predator models. 'C' on the x-axis represents the control treatment in which fish were presented with no model. In panel a), non-territorial fish spent more time than territorial fish swimming away from larger predator models and the increase in time from the control was also greater than in territorial fish. In panel b), territorial fish spent more time than non-territorial fish hiding from predators and they also spent more time hiding when the threat was largest. Different letter shows a significant difference at $\alpha = 0.05$ based on Tukey's post hoc test and error bars denote \pm one SE.

contrast, territorial fish only reacted significantly more strongly to the largest model than the control. This supports the hypothesis that territorial fish refrain from reacting strongly unless the perceived threat is high, as the risk of losing one's territory makes the cost of exhibiting the avoidance behavior greater for territorial fish than non-territorial fish. This supplements previous findings that fish will exhibit increased anti-predator responses to increased predation threat (Helfman 1989), but adds a new dimension in that we compare the relative magnitudes of costs to fish with different life styles. Additionally, we observed one instance in which *S. adustus* hid for an extended period of time from the largest model, and a smaller conspecific encroached on its territory, providing further evidence that territorial fish face the risk of losing their territory when exhibiting avoidance behaviors.

As overharvesting leads to fewer large predators (Stevenson et al. 2007), territorial fish may be at an advantage, as they tend to reserve costly avoidance behaviors for only very large threats. If they are able to spend more time doing normal activities than the non-territorial fish, they may initially out-compete non-territorial fish in the absence of large predators.

Organisms will behave in ways that reduce costs and optimize benefits when faced with a trade-off. The evolution of different techniques for dealing with such trade-offs may have led to niche partitioning and allowed species to coexist.

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THE EFFECTS OF SIZE-SELECTIVE HARVESTING ON *STROMBUS GIGAS* (QUEEN CONCH) SHELL MORPHOLOGY

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Abstract: Size-selective harvesting can lead to declines in body size and skewed sex ratios and age structures. We examined whether size-selective harvesting on Little Cayman Island for larger, thinner shelled *Strombus gigas* (queen conch) had an effect on shell morphology. By comparing the shell length to lip thickness ratios of *S. gigas* found in protected and harvesting areas and harvested shells found on the beach, we found no evidence of size-selective harvesting. This result may be due to the frequent movement of *S. gigas* between protected and harvested areas, increased predation pressure in the protected area, or the short amount of time that *S. gigas* have been harvested on this island.

Key words: gastropods, Little Cayman Island, predation, replenishment zone

INTRODUCTION

Size-selective harvesting can lead to long term declines in body size as well as skewed sex ratios and age distributions in a population (Fenberg 2008). Overharvesting of individuals with specific morphological traits can artificially select against those traits in a population. Once *S. gigas* reach adulthood, they stop growing lengthwise and begin thickening their shells (Randall 1964). Residents of

Little Cayman Island preferentially harvest large individuals with thin shells because they provide the most meat and are the easiest to break open (*pers. comm.* Lowell Forbes). On Little Cayman Island, *S. gigas* can be harvested from November through April in designated harvesting areas and are protected from all harvesting in two replenishment zones (CIDE 2008).

We examined whether the harvesting of

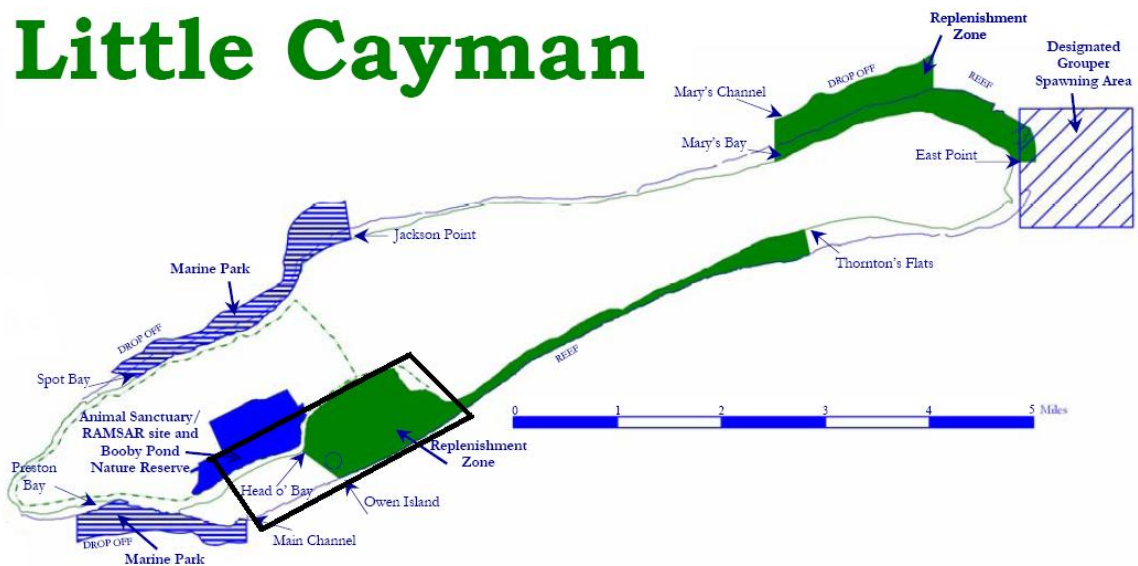


FIG. 1. Map of Little Cayman Island conservation areas from the Cayman Island Department of the Environment. South Hole Sound is outlined. Shaded areas are protected from harvesting and non-shaded areas are open to harvesting.

S. gigas has changed the population demographics at Little Cayman Island. If humans are preferentially harvesting thinner shelled individuals, we would expect to see a lower ratio of shell length to lip thickness in harvesting areas than in protected areas, indicating that shells are thicker for their length in harvesting areas. If this demographic difference between harvesting and protected areas were observed, it may result in the artificial selection of thicker shelled individuals. This assumes that the two populations have the same age structures, environmental conditions are the same in both areas, and there is a genetic basis of shell thickness.

Alternatively, the effects of human preference may not be the driving force behind shell morphology. Protected areas protect not only *S. gigas*, but also their predators, including spiny lobsters (CIDE 2008). Individuals with thicker shells have better protection against predators (Delgado et al. 2002). In this case, elevated predation in protected areas might result in the differential survival of thicker shelled individuals. Thus, we would predict a higher shell length to lip thickness ratio in the harvesting areas than the protected areas, indicating that shells are thicker for their length in protected areas.

METHODS

On 6-8 March 2010 we sampled *S. gigas* in the protected area of South Hole Sound and the adjacent harvesting area west of Owen Island, Little Cayman Island (Fig. 1). We sampled four 100 m transects parallel to shore in the harvesting area and 11 in the protected area. For each individual we measured length with a tape measure (apical spiral to siphonal groove) and lip thickness with calipers (ca. 1 cm into the lip and halfway up the shell; Fig. 2). We also recorded whether the individual was a juvenile or adult (presence of lip flange indicates adulthood), dead or alive, and if dead we noted whether the individual was killed by natural means or by human predation (indicated by a chisel hole on the apical spiral). We also collected data at the

South Hole Sound beach where local residents discard their harvested shells. We only measured shells from the beach that still had pink nacre visible (indicating minimal erosion since time of the individual's death).

Transects in the harvesting area began at the farthest western point of Owen Island and extended westward with the first transect ca. 25 m from shore and subsequent transects ca. 50-100 m apart. Seven transects in the protected area began at the farthest eastern point of Owen Island and extended eastward with the first transect ca. 25 m from shore and the next six ca. 50-100 m apart. The other five transects in the protected area began 100 m east of Owen Island's farthest eastern point and extended eastward. We sampled ca. 4 m on either side of transects. The water depth of transects ranged from 0.5 – 2 m.

We used an ANOVA to compare length:lip thickness ratios for live adult *S. gigas* from the harvesting area to the protected area and to the adult shells from the beach after log transforming length:lip thickness ratios to normalize data.

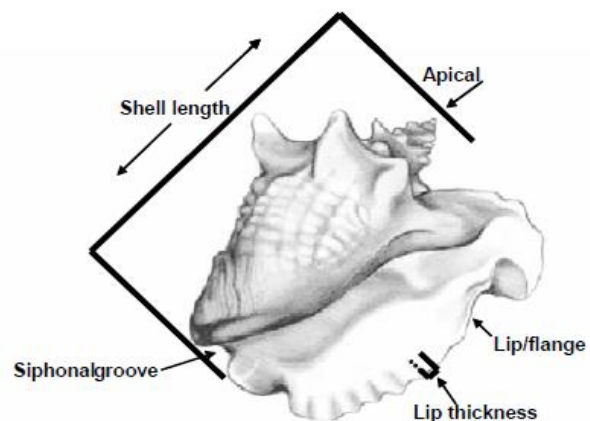


FIG. 2. Diagram (Collins and Harrison 2007) showing measurement locations for lip thickness and length of mature *Strombus gigas* (queen conch).

RESULTS

There were no significant differences between length:lip thickness ratios for harvested

shells found on the beach and for live *S. gigas* in protected and harvesting areas (ANOVA $F_{2,99} = 0.18$, $P = 0.83$; Fig. 3). There was also no significant difference among sites for shell length (ANOVA $F_{2,99} = 1.74$, $P = 0.18$) or lip thickness (ANOVA $F_{2,99} = 0.36$, $P = 0.70$). However, we found four times as many individuals per transect in the harvesting area than in the protected area (two-tailed $t_{13} = 2.16$, $P = 0.03$).

We observed three spiny lobsters and one unidentified ray in the protected area, both predators of *S. gigas*.

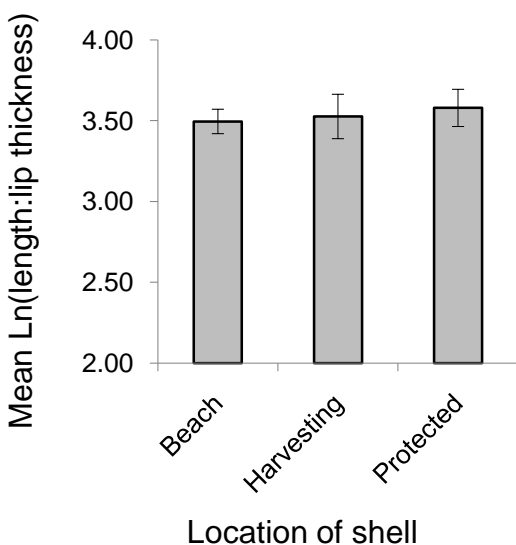


FIG. 3. Mean natural log transformed length:lip thickness ratios for adult *Strombus gigas* shells found in three locations at Little Cayman Island. “Beach” shells were harvested and discarded shells at South Hole Sound beach that still had pink nacre on the interior, indicating minimal erosion since the individual’s death. The harvesting area is west of Owen Island and the protected area is east of Owen Island. All shells from these sites were live adults. Error bars represent ± 1 SE.

DISCUSSION

There are several possible reasons why we did not find a significant difference in the length:lip thickness ratios among the individuals in the protected, harvesting or beach areas. The preferential harvesting of *S. gigas* may not be strong enough to affect population demographics between sites. When we measured the harvested shells on the beach,

we found no difference between those shells and the shells of live individuals in the bay. This indicates that humans may not be preferentially harvesting the largest, thinnest individuals, as previously believed. Additionally, we learned from a chef at the Little Cayman Beach Resort that most commercially sold conch is imported from Grand Cayman and Cayman Brac; thus, perhaps local harvesting is not strong enough to produce a measurable difference in morphology between sites. We suggest that our study be repeated at Grand Cayman and Cayman Brac to see whether harvesting produces effects on shell morphology on a broader spatial scale.

S. gigas mobility may enable them to move freely between the protected and harvesting areas, thus masking any geographic structuring of individuals with different shell length to lip thickness ratios. Individuals have been found to have a range of greater than 5000 m² (Hesse 1979). Preliminary measurements of *S. gigas* at South Hole Sound demonstrated that they can move more than 10 m in one day (unpublished observation).

Furthermore, harvesting has been allowed only in the last four years. Since the average lifespan of *S. gigas* is six years, with most reaching reproductive maturity in three to four years (Theile 2001), only one generation has been able to reach adulthood under the current harvesting rate.

Finally, the effects of predator preference for thinner shells may dampen the difference in shell morphology between the two sites, since we only observed *S. gigas* predators in the protected area.

Another finding of this study, though not directly related to our hypotheses but important to the changing *S. gigas* demographics, is the remarkable differences between our data in 2010 and a survey of *S. gigas* taken one year ago at the same sites. We found four times as many individuals per transect in the harvesting area as in the protected area, whereas the density of *S. gigas* was slightly higher in the protected area last year (Doolan et al. 2009). Individuals were 3.8 mm thicker in the har-

vesting area last year (Doolan et al. 2009), whereas we found no significant difference in lip thickness between the sites this year. These marked differences in our findings between years may be driven by the patchy distribution of *S. gigas* (Stoner and Lally 1994), or they may indicate that there are other factors shaping the population that we have not considered.

Though size-selective harvesting may not currently affect the *S. gigas* population on Little Cayman Island, the potential consequences of chronic size-selective harvesting should not be ignored by fisheries managers. Gastropods in Southern California have declined in body size due to the last century of human impact (Roy 2003). Trophy hunting of big horned rams has resulted in smaller horned and lighter body weight rams (Coltman et al. 2003). Mediating the effects of size-selective harvesting is essential to the conservation of ecosystem structure and function.

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ANY SLIPPERY DICK(S) WILL DO: THE STRUCTURE OF A REEF FISH FORAGING ASSOCIATION

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Abstract: Multi-species foraging associations are a common and important phenomenon in coral reef communities. Spotted goatfish (*Pseudupeneus maculatus*) and slippery dick (*Halichoeres bivittatus*) form conspicuous foraging associations in the backreef and lagoon areas of the Caribbean. Although the potential benefits of such associations are well established, there is little information on what factors structure the variation that exists within these groupings. We tested several hypotheses based on how the body size of fish, number of fish, and substrate over which they forage might affect the association structure. We conducted observations at Preston Bay, Little Cayman Island to test these hypotheses. There was no evidence suggesting non-random structure in the association between goatfish and slippery dick. In contrast to our results, previous work involving much larger spotted goatfish has shown body size and number of goatfish to be important factors structuring foraging associations, suggesting that the relative importance of these factors may depend on the body size of the goatfish.

Keywords: Caribbean coral reef, co-foraging, commensalism, *P. maculatus*, Spotted Goatfish

INTRODUCTION

In reef fish communities, established multi-species foraging associations (including commensalisms, mutualisms, and parasitisms) are a prominent feature of species interactions (Lukoschek and McCormick 2002a). Goatfishes (Mullidae) are frequently the nuclear species of reef fish foraging associations (Sazima et al. 2006). In feeding, goatfish vigorously disturb the substrate with their barbels and mouth (Krajewski et al. 2006), attracting a wide variety of co-foragers, including trumpetfishes (Aulostomidae), groupers and sea basses (Serranidae), tilefishes (Malacanthidae), jacks (Carangidae), grunts (Haemulidae), wrasses (Labridae), parrotfishes (Scaridae), and surgeonfishes (Acanthuridae; Sazima et al. 2006, Krajewski 2009). Further, it has been suggested that goatfish serve as ecosystem engineers by bioturbating benthic substrate and resuspending sediments, with implications for organic matter flow and filter feeder assemblages (Uiblein 2007).

In the shallow waters of the backreef and lagoon zone of Little Cayman Island's bank reef, spotted goatfish (*Pseudupeneus maculatus*) and slippery dick (*Halichoeres bivittatus*, family: Labridae) provide an abundant and easily

observable example of a multi-species foraging association. An earlier investigation of this foraging association suggests that slippery dick provide goatfish with predator detection benefits, while goatfish heighten the accessibility of slippery dick's prey items (based on behavioral observations: Pizzicchi et al. 2009). During initial observations, we frequently observed an individual slippery dick and a goatfish swimming within 1 cm of each other. However, a pair of co-foragers is only one variant of these species' foraging association: foraging groups range from one individual of each species, to numerous slippery dicks with one goatfish to numerous goatfish with just a few slippery dicks, to more than half-a-dozen individuals of both species. Slippery dicks and goatfish of a wide range of body sizes participate in these foraging groups. Additionally, individuals of both species can be seen foraging alone. There is little work investigating how this foraging association, putatively driven by predator detection and feeding facilitation, is structured.

We tested several hypotheses based on three factors of possible importance to the structuring of goatfish and slippery dick foraging associations: goatfish body size, the number of fish, and the substrate over which

the association takes place. We predicted that pairs of goatfish and slippery dick would sort by size such that the ratio of the body lengths of co-foraging fish would be relatively constant because a large goatfish may disturb a greater amount of sediment that would attract a larger slippery dick. We also predicted that larger goatfish might attract a greater number of slippery dick individuals because of a greater amount of sediment disturbance.

A single goatfish and a single slippery dick foraging together may do so to limit competition. For groups of goatfish foraging together, we predicted that larger groups would attract greater numbers of slippery dick.

Another hypothesis is that the structure of the foraging association changes based on the substrate over which goatfish forage, specifically between rugose, algae-covered and more exposed, flat sandy areas. In exposed areas, we expected individual goatfish to associate with larger groups of slippery dick in an effort to reduce predation risk. Lastly, we predicted that groups involving multiple goatfish would forage more frequently over algal cover because of higher food availability

and therefore less competition between goatfish.

METHODS

We observed goatfish and slippery dick by snorkeling March 6- 8, 2010 in Preston Bay, Little Cayman Island.

Size Sorting

We tested whether goatfish and slippery dick associated by size by measuring the lengths of both species in co-foraging pairs. To measure total fish lengths, we watched an individual until it came to rest on the bottom, estimated points on the substrate at the tips of the snout and tail, and measured the distance between those points with a ruler on the dive slate. In an effort to increase accuracy, we also visually estimated the ratio of slippery dick to goatfish length, and took the average of the estimated and measured ratios. We compared the distribution of these averaged ratios for co-foraging pairs to that of the ratios of randomly paired slippery dick and goatfish observed in the area using a two-sample Kolmogorov-Smirnov test.

On the morning of March 8, we tested whether, after being separated from slippery

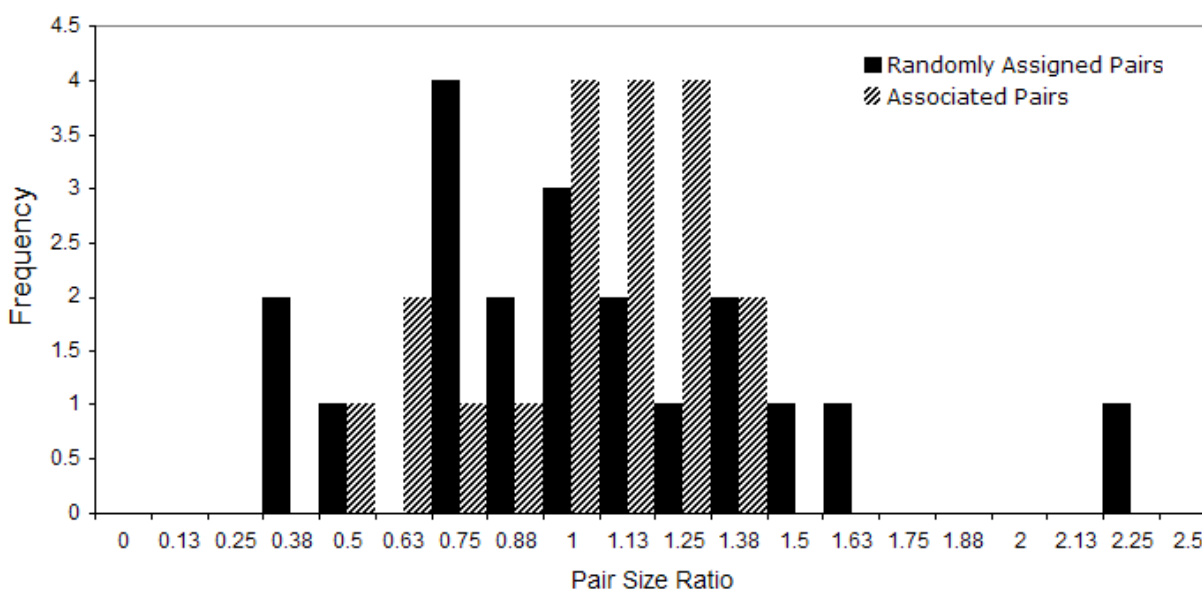


FIG. 1. Frequency distributions of the size ratios of associated (hatched) and randomly assigned (solid) pairs of spotted goatfish and slippery dick at Preston Bay, Little Cayman Island.

dick co-foragers, goatfish sought slippery dick of similar size to those with which they had previously been foraging. We frightened goatfish by sneaking up behind them and then swinging our dive slates rapidly downward above them. Immediately before and after separation, we visually estimated the size ratio of the primary (closest) slippery dick observed foraging with the goatfish and compared the two ratios using a paired t-test.

Group Size

On the afternoon of March 6, we tested whether larger goatfish were associated with larger groups of slippery dick. In pairs, we observed co-foraging groups for one minute, and recorded the maximum number of slippery dick simultaneously present within approximately 30 cm of the focal goatfish. We also measured the length of the focal goatfish, and recorded how many additional goatfish were present, if any. We excluded those goatfish accompanied by conspecifics from the regression analysis, but used the excluded data to test whether larger groups of goatfish are correlated with larger groups of co-foraging slippery dick.

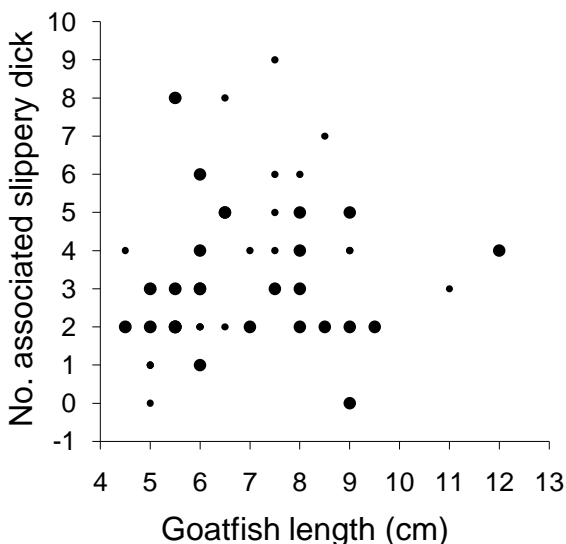


FIG. 2. The number of associated slippery dicks (*Halichoeres bivittatus*) fit by the length of the largest spotted goatfish (*Pseudupeneus maculatus*) observed in 73 foraging groups at Preston Bay, Little Cayman Island. Enlarged points indicate early data for which we did not record substrate.

Substrate

On the afternoon of March 7 we tested whether substrate type (macroalgae or sand) affected the number of slippery dick associated with goatfish by observing co-foraging groups and measuring the focal goatfish while simultaneously recording substrate type. We analyzed these data with a general linear model with substrate type and size of goatfish as explanatory variables, and number of slippery dick as the response variable. These same data (goatfish size and slippery dick group size) were also used in the regression described in *Group Size*.

Census

On the morning of March 7, we conducted a census of goatfish and slippery dick populations over sand and macroalgae substrates to control for possible differences in fish density between substrates that may affect the test of co-forager group size by substrate. In pairs, we conducted a total of six time transects over each substrate. Each researcher recorded the number of each species he or she observed within 2 m on either side, averaged their counts, and compared fish densities over the two substrates with a t-test.

RESULTS

We observed goatfish co-foraging with more than one slippery dick in only 10% of cases, and with conspecifics in 40% of cases. Goatfish and slippery dick in co-foraging pairs ranged in size from 4 to 13 cm, and 3.5 to 9 cm, respectively.

Size Sorting

We found none of the predicted patterns in the structure of slippery dick and goatfish foraging associations. There was no difference in size between slippery dick foraging with goatfish before and after scaring (paired- $t_{23} = 0.14$, $P = 0.88$). We found no support for size sorting, as the size ratio distribution of slippery dick and goatfish foraging in pairs did not differ from the pairs we randomly as-

signed (two-sample Kolmogorov-Smirnov: $D = 0.16$, $P = 0.95$; Fig. 1).

Group Size and Substrate

A linear regression did not support the hypothesis that the size of the co-foraging group of slippery dick would increase with the size of the focal goatfish ($R^2 = 0.03$, $F_{1,46} = 1.45$, $P = 0.23$; for bivariate plot, see Fig. 2). However, a general linear model analysis using a smaller subset of the data that had observations excluded because substrate type was not recorded revealed a significant relationship between goatfish size and slippery dick group size, but no effect of substrate (Table 1). Number of goatfish was not correlated with the number of slippery dick co-foragers (Pearson $R = 0.069$). Finally, census data of the two species indicated no difference in abundance between the two substrates (goatfish: $t_{7.65} = 0.70$, $P = 0.51$; slippery dick: $t_{6.08} = 1.38$, $P = 0.22$).

TABLE 1. General linear model of the effects of goatfish size and substrate type (algae or sand) on number of co-foraging slippery dick in Preston Bay, Little Cayman Island.

Source	df	MS	F	P
Goatfish Size	1	19.35	6.42	0.02*
Substrate	1	3.07	1.02	0.32
Goatfish Size*Substrate	1	7.55	2.51	0.13
Error	24	--	--	--

Observations

We often observed goatfish swimming to catch up to slippery dick co-foragers, but rarely observed slippery dick making any effort to remain in close proximity to goatfish. We observed one attempted predation event over sandy substrate by a *Cephalopholis cruentatus* on a small goatfish.

DISCUSSION

There was no effect of size of goatfish, number of goatfish, or substrate on foraging associations with slippery dick, suggesting that the magnitude of the benefit of foraging

with heterospecifics (Pizzichemi et al. 2009) may overshadow any variation in foraging group structure based on these variables. The conflicting result between the GLM analysis and linear regression analysis for the effect of goatfish size on the group size of co-foraging slippery dicks may have been due to differences in sample size, because the larger, more inclusive data set showed no effect of goatfish size on the group size of slippery dick. The lack of a difference in foraging association structure between sand and macroalgae substrates may be due to similar predation pressure across substrates.

In contrast to our results, previous research has found that among larger goatfish (11-30 cm) there is substantial structure in foraging associations with size and number of goatfish positively correlated to follower size and number (Sazima et al. 2006). We found no such correlations in foraging associations for smaller goatfish (≤ 12 cm), suggesting that the relative importance of the factors structuring foraging associations may be dependent on the size of the goatfish involved. For example, it is likely that small goatfish experience greater predation pressure, so small goatfish may especially benefit from foraging with other fish. We observed small goatfish actively following and seeking out slippery dick, while prior research involving larger goatfish considers heterospecific co-foragers to be the followers (Sazima et al. 2006). Small goatfish do not disturb the sediment as much as a larger goatfish, so benefits to co-foragers may be limited. We speculate that in small goatfish, the association may be driven by the benefit to the goatfish, which could explain the lack of any pattern in slippery dick-goatfish foraging associations. Although large goatfish may still benefit from a decrease in predation risk by foraging with other fish, the substantial substrate disturbance caused by large goatfish offers a meaningful benefit to co-foragers (Sazima et al. 2006). We suggest that the nature of the goatfish and slippery dick foraging association may change dramatically as goatfish grow, potentially shifting

from a commensalism benefiting small goatfish to either a mutualism, or a commensalism benefiting the followers of large goatfish.

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THE EFFECTS OF RUGOSITY AND FOOD AVAILABILITY OF ARTIFICIAL HABITATS ON CORAL REEF FISHES

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Abstract: Rugosity and food availability are important factors in determining the ability of artificial habitats to recruit resident fish. We tested how levels of rugosity and food availability (algae) affect the frequency at which habitats are visited and the abundance and species richness of colonizing fishes. Habitats with high rugosity and food availability were colonized faster and had higher fish abundance and fish species richness than other habitats. There was a combined effect of rugosity and food availability in determining the abundance and richness of resident fishes. These results provide information about the relative importance of habitat complexity and food resources for artificial coral reefs design.

Key Words: abundance, fish colonization, Jackson Bay, Little Cayman Island, richness

INTRODUCTION

Coral reef degradation has led to concerns about the possible effects on reef fish abundance and richness, which are both correlated to reef habitat availability (Jones et al. 2004). Most artificial reef additions have focused on increasing structural complexity, or rugosity, because reef fish are habitat-limited (Luckhurst 1978). However, other studies have suggested that food availability is the driving factor in reef fish distribution (Jones 1986). We tested the effects of differing levels of rugosity and food availability on fish colonization rates as well as the abundance and richness of fish visiting and inhabiting each habitat type.

We hypothesized that colonization rate, fish abundance, and fish species richness would all increase with increasing habitat quality, as determined by rugosity and food availability. We predicted that habitats high in rugosity with high food availability would be the most desirable habitats, and would therefore have the fastest colonization rates and attract the highest abundance and species richness of fish. Accordingly, habitats with low rugosity and low food availability would have the slowest colonization rates and attract the lowest abundance and species richness of fish, while habitats with low rugosity and high food availability or high rugosity and

low food availability would both show intermediate levels of abundance and richness. Alternatively, if high quality habitats attract the most territorial fish, high quality habitats would have the fastest colonization rate, but would have lower fish abundance and species richness, as the territorial fish may exclude other fish from the territory.

Determining the interactive effect of habitat complexity and food availability on fish richness and abundance is important for designing effective artificial reefs.

METHODS

We constructed twelve habitats; six with high and six with low rugosity. All habitats were made of PVC pipe and duct tape and were roughly 5x5x10 centimeters. The low rugosity habitats were made of two 5 cm long 5 cm diameter PVC pipes, while the high rugosity habitats were made of eight 5 cm long 2.5 cm diameter PVC pipes. We taped over all openings except those on one face of the structure, and attached a dive weight to the bottom of each habitat to prevent it from being swept away or moving with the waves.

On 6 March, 2010 east of Jackson's Point directly north of Little Cayman Research Center, Little Cayman Island, we placed artificial habitats in water ca. 1.8 m deep at least 15 m apart, with each site ca. 10 m from the nearest

reef head. All openings faced the reef (north). We placed 3 or 4 rocks 10-20 cm in diameter around each habitat. The rocks were either algae-covered or bare, depending on whether the treatment was high or low food availability. We randomized the order in which we placed the treatments along the transect.

We swam the transect three times a day, at approximately 0800, 1300, and 1700, on 7-8 March, and at approximately 0800 on 9 March, and observed each habitat for 90 seconds. We recorded the number and species of fish we observed using the habitat (including our placed rocks) and noted which fish entered the holes of the PVC structure at least once during the observation period.

We observed all fish that we saw in the area (transient), noting those individuals who were seen at the same structure at multiple time periods (resident). We also recorded which fish were seen entering the PVC structure. We used a multiple ANOVA to determine the combined effect of rugosity and food availability on observed fish.

RESULTS

We observed 30 fish visiting our habitats of five different species, including Cocoa

Damselfish (*Stegastes variabilis*), Doctorfish (*Acanthurus chirurgus*), Spotfin Butterflyfish (*Chaetodon ocellatus*), Slippery Dick (*Hali-choeres bivittatus*), and Seaweed Blenny (*Parablennius marmoreus*). Fifteen of those fish were observed inhabiting the area, five of which inhabited the PVC structure.

More fish visited the habitats with high rugosity and food availability than any other treatment, and fewer visited the habitats with low rugosity and low food, and the number of visiting fish was observed to increase over time for all treatment levels (Fig. 1).

There was no effect of food on the total number of transient fish ($F_1 = 0.42$, $P = 0.535$), however rugosity did have a significant effect ($F_1 = 6.74$, $P = 0.032$). However, for resident fishes, there was an interaction between food and rugosity (Fig. 2). Fish species richness of residents showed a very similar trend, with an interaction between food and rugosity ($F_1 = 8.33$, $P = 0.020$).

No fish were observed entering the tube structures of low rugosity habitats, but there were a total of five fish observed using the high rugosity tubes. There was a marginally significant effect of rugosity on tube residence ($F_1 = 5.00$, $P = 0.056$).

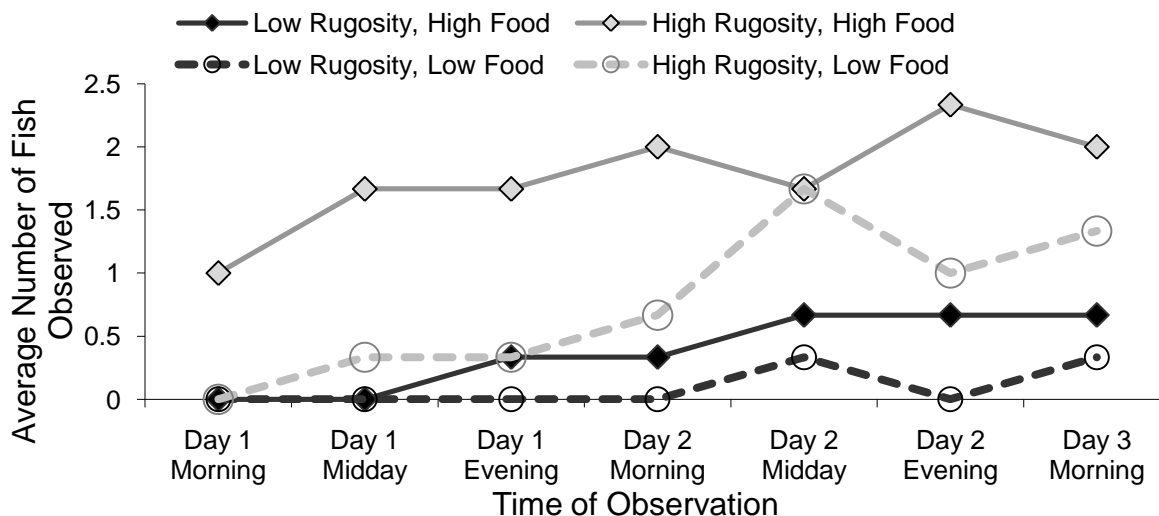


FIG. 1. Time series data for the average number of fish observed visiting each habitat type ($n=12$), collected from Day 1 (March 7 2010) until Day 3 (March 9 2010) east of Jackson's Point, Little Cayman Island. Dashed lines with open circles show low food treatments, and solid lines with closed diamonds show high food treatments. Likewise, grey lines show high rugosity habitats and black lines show low rugosity habitats.

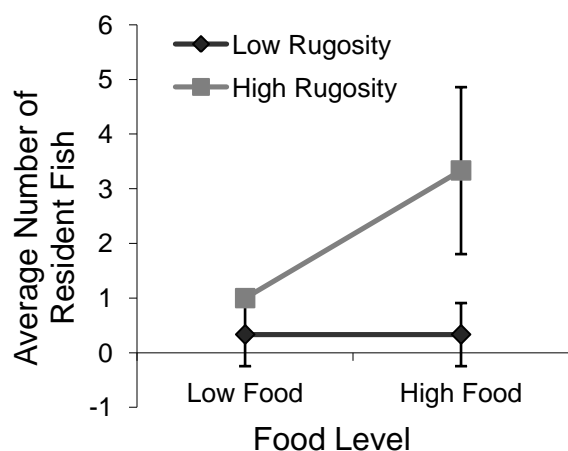


FIG. 2. The average number of resident fish observed at each habitat type placed at Jackson's Bay on Little Cayman Island. Under low rugosity conditions, the presence of food has no effect on the number of resident fishes; however, under high rugosity, the presence of food increases the number of resident fishes ($F_1 = 5.44$, $P = 0.048$).

There was no effect of either food ($F_1 = 3.00$, $P = 0.122$) or of rugosity ($F_1 = 1.33$, $P = 0.282$) on the number of resident fish the rocks placed around our tube structures.

DISCUSSION

In accordance with our hypothesis, fish preferred habitats of both high rugosity and high food abundance. The combined effect of both high rugosity and high food led to significantly higher abundance and richness of resident fishes.

We initially hypothesized that food would have an influence on fish visiting the habitat (i.e., transients) and that rugosity would not have an effect, because transient fish would be primarily driven by food availability and not shelter. However, we observed the opposite pattern: rugosity was the only variable influencing transient fishes. This suggests that wandering fish may choose to travel over areas of higher rugosity rather than areas of high food availability; an interesting finding that future studies should investigate. Additionally, we observed high amounts of algae in areas surrounding our

habitats, so it is possible our food treatments were not successful in increasing or decreasing the amount of available fleshy algae.

Our identification of individual resident fish represents a possible source of error: we could never prove that the fish we saw at one instance was, in fact, the fish we saw returning at another time period. When we observed the same species occurring multiple times at a site we assume it was the same individual. This may have increased the amount of fish we classified as residents.

Our tests support the previous finding that habitat limits fishes (Jones et al. 2004). Over time all the habitats became occupied, even the low food and rugosity habitats. Although high rugosity and food play a significant role in attracting higher numbers of fish, the severe limitation of available habitats shows that even less desirable sites will eventually become inhabited. These results are relevant to the construction of and placement of artificial reef systems, where both the abundance and diversity of resident fishes are of great concern.

Artificial reefs should be built and placed to maximize food availability as well as rugosity, since this would allow them to attract the most residents. The combined effect of increasing food availability and rugosity is far more substantial than increasing either variable alone, a finding that should be noted when constructing artificial reefs to rebuild fish populations in areas of coral degradation.

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MARINE PROTECTED AREAS: A SURVEY OF REEF FISH AND CORAL DIVERSITY ON LITTLE CAYMAN ISLAND

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Abstract: Marine protected areas are controversial, in part, because they can impact economies by prohibiting fishing. On Little Cayman Island, where fishing pressure is low, we hypothesized that there would be little difference in fish and coral species richness between protected and unprotected areas. We measured coral and fish diversity in four sites, inside and outside marine protected areas. We found that differences in fish species richness and dominance were ~10%, which we do not consider large enough to be biologically important. Parrotfish abundance was highest at Jackson's Point and Grape Tree Bay, but bar jack proportional abundance did not differ. Coral species richness and fish species richness were positively correlated. Because Little Cayman is relatively undisturbed, it is not surprising that we found small differences between protected and unprotected areas. Baseline studies like this are important for assessing the effects of future development in currently unimpacted areas like Little Cayman.

Key Words: *diversity, dominance, Little Cayman Island, marine parks, richness*

INTRODUCTION

The National System of Marine Parks was established in the Cayman Islands in 1986 (Geoghegan et. al 2001). There are two established marine protected areas in Little Cayman, where taking any marine life and anchoring boats are prohibited. Although a goal of marine protected areas is to relieve fishing pressure, fishing outside of the boundaries may still impact the populations inside. Marine protected areas also raise controversy by affecting local economies based on coral reef fisheries. We investigated the success of marine protected areas in Little Cayman, where fishing and other anthropogenic pressures are low in both protected and unprotected areas. We hypothesized that there would be little difference in coral and fish diversity between the areas inside and outside of the marine protected areas due to overall low impact. We also measured proportional abundances of bar jack (*Caranx ruber*, upper level predators) and parrotfish (Scaridae, corallivores), since these fish can impact many trophic levels in coral reefs. We studied the correlation between coral and fish species richness across sites to understand if management strategies that protect fish populations also protect coral diversity.

METHODS

We collected data on 6-8 March 2010 on Little Cayman at four sites: two on the south side of the island, within (Preston Bay) and outside of (Owen Island) a marine protected area and two on the north side of the island, within (Jackson's Point) and outside of (Grape Tree Bay) a marine protected area (Fig. 1). All of the sites have shallow reef crests approximately 50 to 200 m from shore. We excluded Owen Island from our marine park comparative study because reef damage due to Hurricane Paloma in 2008 could have confounded the differences between that site and the sites within the marine protected areas.

We identified fish species along ten-minute time transects on the lagoon side of the reef crest. At Preston Bay and Grape Tree Bay we performed eight fish transects during the day at each site and two at night at each site to ensure that nocturnal fish diversity did not differ between sites. On the same transects, we measured coral species richness in five haphazardly selected 4 m² quadrats, swimming 30 sec between choosing quadrats. At Owen Island and Jackson's Point, we collected coral and fish diversity data during the day with three and six transects, respectively.

We created rarefaction curves for each site to account for different fish abundances at

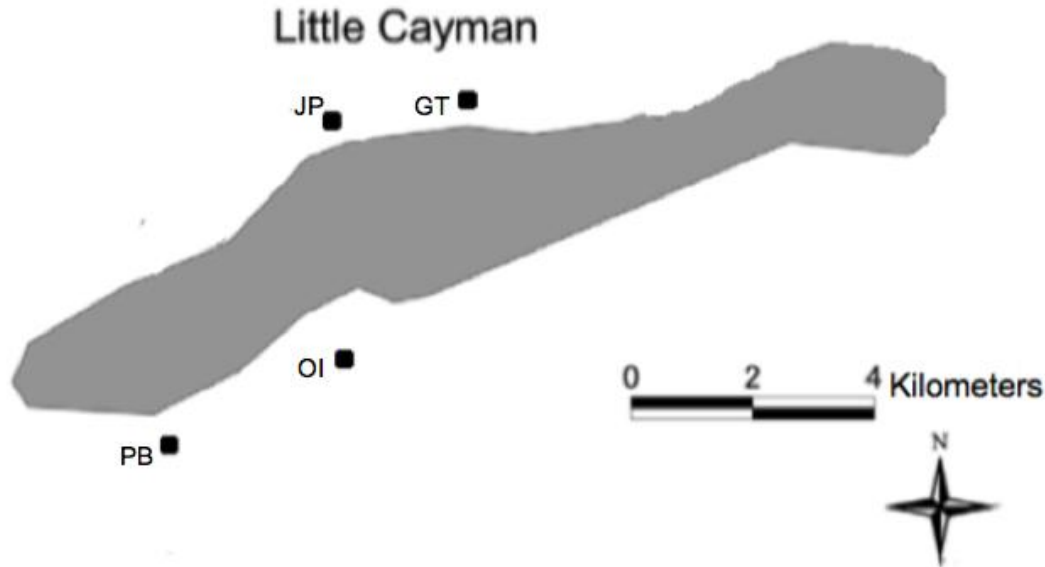


FIG. 1. Map of Little Cayman Island with study sites labeled (JP = Jackson's Point, GT = Grape Tree Bay, PB = Preston Bay, OI = Owen Island). JP and PB are within marine protected areas and GT and OI are outside the marine protected areas.

each site and calculated fish species dominance and species richness for each site using EcoSim version 7 (Gotelli and Entsminger 2009). We performed a Spearman's correlation analysis across all sites for coral species richness and fish species richness by transect. We used 95% confidence intervals to assess significant difference between sites.

RESULTS

Species richness of reef fish was 7.7% greater in Jackson's Point than in Preston Bay and Grape Tree Bay (Fig. 2).

Fish species dominance was not significantly different in Preston Bay and Grape Tree Bay, but both Preston Bay and Grape Tree Bay had 29% greater fish dominance than Jackson's Point (Fig. 3).

Proportional abundance of parrotfish was significantly higher in Jackson's Point and Grape Tree Bay than in Preston Bay ($F_{2,19} = 23.70$, $P < 0.0001$) This difference in abundance was driven by the difference in total abundance of parrotfish between the sites because they had similar total abundances of fish. The proportional abundance of bar jacks did not differ between sites.

Coral species richness was positively correlated with fish species richness across all three sites (Spearman's rank correlation $r_s = 0.742$, $P < 0.0001$) (Fig. 4).

DISCUSSION

Fish richness and dominance did not vary significantly between protected and unprotected areas. Previous studies in the Pacific-

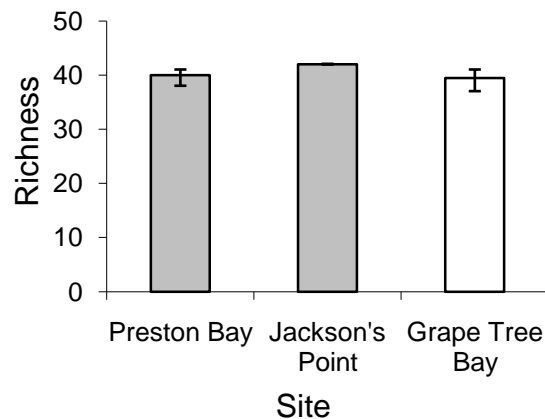


FIG. 2. Reef fish species richness at three different sites at Little Cayman on 6-8 March 2010. Jackson's Point has significantly greater richness than Preston Bay and Grape Tree Bay (data were rarified to the Jackson's Point site). Shaded bars are in marine protected areas. Error bars represent 95% confidence intervals.

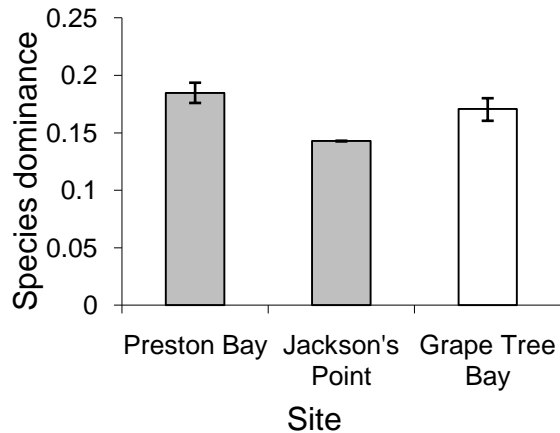


FIG. 3. Reef fish species dominance at three different sites at Little Cayman on 6-8 March 2010. Preston Bay and Grape Tree Bay had significantly greater dominance than Jackson's Point (data were rarified to the Jackson's Point site). Shaded bars are in marine protected areas. Error bars represent 95% confidence intervals.

ic Ocean have found large differences between marine protected and unprotected areas (McClanahan 1999). Our findings may be a result of low human impact across all of Little Cayman, as Little Cayman is under far less fishing and development pressures than neighboring islands and has never had a large scale commercial fishing operation (Cheek and Gu 2008, Pattengill-Semmens and Semmens 2002, Creary et al. 2008). The largest pressure on fish populations appears to be overfishing of the Nassau grouper spawning aggregation, which is now under government protection (Cheek and Gu 2008).

The data revealed a difference in parrotfish proportional abundances that may be affected by location on the island rather than protection status, as parrotfish were more abundant at the two northern sites (Jackson's Point and Grape Tree Bay) than at Preston Bay. This may be due to wind and weather conditions, a higher abundance of parrotfish predators, or another trophic-level effect on one side of the island that we did not measure (Mumby et al. 2006). We did not find a difference in bar jack proportional abundance across any sites, which could be due to the low proportional abundance of bar jacks across all sites. Future studies may benefit from including sites on deeper portions of the

reef, as more large piscivorous fish and other predators live in those pelagic zones, and fishing pressure is higher there.

We found a correlation between fish and coral species richness, which is consistent with previous findings that fish declines are driven by dependence on declining coral (Jones 2004). While marine protected areas restrict fishing in the area, they cannot protect coral reefs against large-scale threats to coral health, such as hurricanes, global warming, disease and pollution, which can lead to declines in fish populations.

However, the marine protected areas in Little Cayman are protecting relatively unimpacted areas, as island residents fished the surrounding waters sustainably prior to the establishment of marine protected areas (Cheek and Gu 2008). Therefore, these areas may be an example of protected areas being created prior to shifting baselines, as the marine protected areas in the Cayman Islands were established in 1986, and there has been

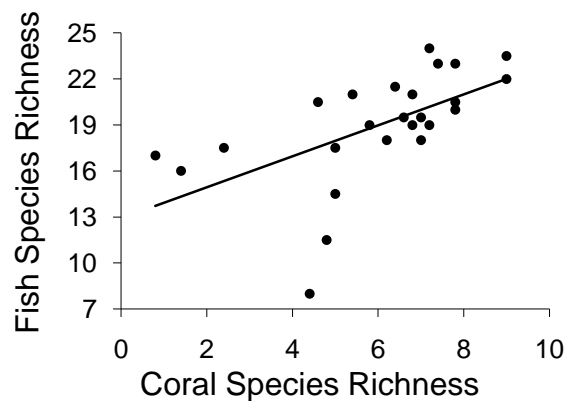


FIG. 4. Spearman's correlation between reef fish and coral species richness at four sites at Little Cayman Island on 6-8 March 2010.

little development on Little Cayman compared to neighboring islands since then (Pattengill-Semmens and Semmens 2002, Creary 2008). Grand Cayman is much more developed than Little Cayman and has very different reef composition with fewer grouper, parrotfish, and snapper and lower richness of fish species than Little Cayman (Pattengill-

Semmens and Semmens 2002). With increased development possible on Little Cayman in coming years, human impacts may increase. Therefore, baseline studies such as this one are essential for assessing the impacts of future anthropogenic influences.

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HORIZONTAL DISTRIBUTION OF SETTLING POST-LARVAL REEF FISH AT JACKSON'S POINT, LITTLE CAYMAN

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Faculty Editor: Brad W. Taylor

Abstract: While much research has been done on the juvenile stage of coral reef fish, little is known about the post-larval and pre-settlement stages. Many factors may influence the distribution of post-larval fish and we chose to test the effect of increasing water depth, sea grass cover, and zooplankton abundance (prey) on the distribution of settling post-larval fish at Jackson's Point, Little Cayman. We predicted that with increasing depth, post-larval fish abundance would also increase because a larger water column can hold more fish, but this effect would diminish closer to the reef where predation may decrease the abundance. We collected samples of zooplankton and post-larval fish abundance along five transects during the night and estimated percent sea grass cover during the day. A linear regression model with a quadratic term provided the best fit to post-larval fish abundance as a function of distance from shore, supporting our prediction that post-larval fish abundance increases with increasing depth but then decreases, possibly due to predation near the reef. We did not find a relationship between post-larval fish abundance and zooplankton abundance or percent sea grass cover. Since post-larval fish abundances seem mostly unaffected by environmental factors, post-larval fish numbers may not determine juvenile abundance on the local scale of this study. Hence, fish abundance could be more dependent on the habitats available for post-larval fish to develop into juveniles.

Keywords: community structure, coral reef, distribution, Little Cayman, settling fish, zooplankton

INTRODUCTION

Settling post-larval fish recruitment rates are likely important factors in shaping reef fish community structure but much about the early life of fish remains unknown. Pulses of post-larval recruits are related to lunar phases and spawning events but are affected by highly variable meteorological, hydrological, and biological processes in the pelagic zone that render them largely unpredictable (DeLoach 1999). Several factors may drive the distribution of settling post-larval fish; we investigated the hypotheses that distribution depends upon depth, prey distribution, substrate, and predation risk. If distribution were dependent upon depth, fish number would increase with increasing depth (approximated by distance from shore) due to greater available space in the water column. If distribution were dependent on prey, we would expect to see more fish with greater amounts of zooplankton. If settling post-larval fish were distributed based upon substrate, we would expect fish number to increase with greater sea grass cover (Worthington 1991). If distribu-

tion depended upon predation risk, we would predict that there would be fewer settling post-larval fish near reef assemblages due to the concentration of predators that forage on or near the reef (Shulman 1985). We predicted that post-larval fish numbers would increase with increasing depth until the reef where predation pressure would drive the numbers back down resulting in a hump-shaped distribution.

METHODS

On the nights of 7 - 8 March 2010 at Jackson's Point, Little Cayman, we estimated zooplankton and settling post-larval fish abundance along five 50 m transects parallel to the shoreline at distances of 30 m, 45 m, 60 m, 75 m, and 90m from the shore. The first transect at 30 m was roughly in the middle of the sea grass bed and the final transect was near the reef crest. Every 10 m we towed a 30-cm-diameter plankton net three meters through the water to collect zooplankton from 0.21 m^3 of water. On the first night, we sampled zooplankton at one half of each transect and fish

abundance at the other, then switched transect sides on the second night. In the lab, we counted the total number of zooplankton in each sample and sorted them into size groups of <1 mm, 1-2 mm, and >2 mm.

To record post-larval fish abundance at each site, we rotated around a fixed point near the surface of the water for 10 seconds shining a dive light to attract fish and counted the number of fish we observed in the light beam. We also recorded post-larval fish abundance at 15 additional sites along the transects where we did not collect zooplankton. During the day on 8 March, we took digital pictures of all 30 of our sample sites and estimated the percent sea grass cover.

We analyzed the effect of distance from shore (a proxy for depth), sea grass cover, and zooplankton abundance on post-larval fish abundance using a linear regression model with a linear and quadratic term. We tested for curvilinearity by estimating the significance of the quadratic term (Neter et al. 1996).

A significant quadratic term indicates a curvilinear model fits the data better than a linear model. Because the absolute numbers of zooplankton differed between the two sampling days and we did not sample the same sites for both zooplankton and fish abundance on the same day, we averaged the number of post-larval fish and zooplankton for each transect by day. We matched up mean zooplankton and fish abundance by day and transect, rather than by individual site. We pooled the averages across the two sampling days, which provided $n=10$ data points for our analysis.

RESULTS

Distance from shore explained the settling post-larval fish distribution with quadratic model (quadratic fit: $r^2_{29 \text{ adj}} = 0.47$, $P = 0.003$). In contrast, the spatial distribution of

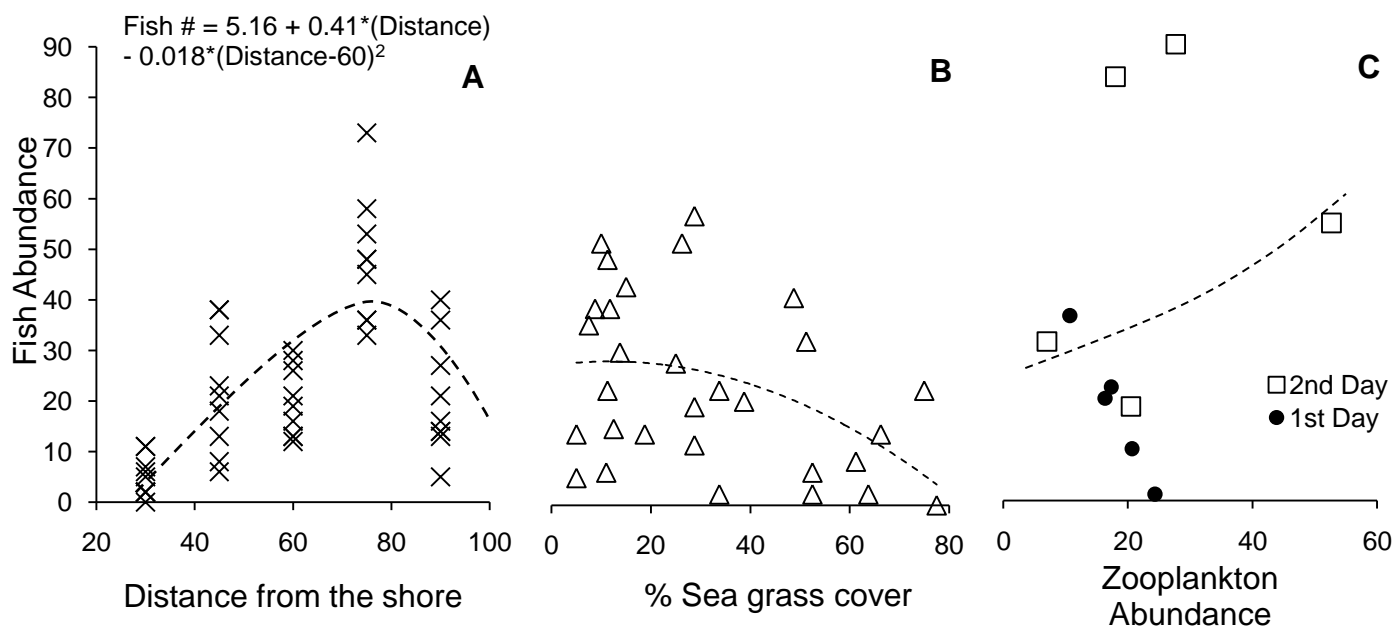


FIG. 1. Distance from shore (proxy for water depth), percent sea grass cover, and zooplankton abundance across two days as predictors of post-larval fish abundance at Jackson's Point, Little Cayman. Panel a) Settling post-larval fish distribution fit according to a quadratic term as distance from shore increased. Panel b) Settling post-larval fish distribution did not fit according to a quadratic term with increasing distance from shore. Panel c) Settling post-larval fish distribution did not fit according to a quadratic term with increasing distance from shore, across the two sampling dates.

TABLE 1. Wind speed, direction, temperature, and water current data during our sampling times. Source: NOAA's Integrated Coral Observing Network for Little Cayman Station (19.699° latitude, -80.06° longitude).

Date	Time	Wind speed (m/s)	Wind direction (azimuthal degrees)	Temp at 3 m deep (°C)	W-E current (m/s)	S-N current (m/s)
7-Mar	1900	10.41	49.29	25.59	0.02	-0.01
	2000	10.073	47.01	25.51	0.02	-0.01
	2100	10.22	45.37	25.52	0.01	-0.01
	2200	10.37	43.73	25.52	0.01	-0.01
8-Mar	1900	8.20	57.48	25.74	0	-0.01
	2000	8.27	57.39	25.78	0	-0.01
	2100	8.34	57.31	25.82	0	-0.01
	2200	8.88	67.47	25.9	0	-0.01

fish was not associated with the spatial distribution of zooplankton (quadratic fit: $r^2_{27 \text{ adj}} = -0.037$, $P = 0.77$), or sea grass cover (quadratic fit: $r^2_{27 \text{ adj}} = 0.12$, $P = 0.25$). The distribution of fish peaked at 75 m away from the shore, which was the second closest transect to the reef crest. Zooplankton abundance was significantly higher on the second day ($F_{28} = 16.41$, $P = 0.0004$).

DISCUSSION

As predicted, post-larval fish abundance was positively related to distance from shore, but declined near the reef crest, possibly due to predation. The relationship between post-larval fish and distance from shore may be due to the increase in depth that occurs moving away from the shoreline. Since dense aggregations of post-larval fish experience greater mortality (Brunton and Booth 2003), post-larval fish may spread out and occupy the entire water column, resulting in higher abundances in deeper areas. Also, we attracted post-larval fish with a flashlight, so even if cubic density of post-larval fish was equal at all depths, there would be more fish that could be observed at greater depths if fish from throughout the water column were attracted to the light. Predation is a likely explanation for the decrease in abundance seen near the reef because piscivorous fish prey on post-larval fish most heavily near the reef, giving them a lower abundance despite having the deepest depth.

The hypothesis that post-larval fish abundance is related to zooplankton abundance, their preferred prey, was not supported by the data. However, differences in weather between sampling dates may have influenced this relationship. On the first sampling date, the northeasterly winds were very strong and we observed lower total zooplankton abundance than on the second sampling date, when the winds were calmer (Table 1). Although there was no relationship between zooplankton and post-larval fish abundances, there appeared to be a strong negative relationship based on data from the first sampling date. This relationship was based on limited data and disappeared when data from the second sampling date were added.

The hypothesis that sea grass cover is related to post-larval fish abundance in the water column was not supported by the data. Even though more post-larval fish settle in denser sea grass areas (Worthington 1991), the same pattern may not occur throughout the water column since post-larval fish may exhibit small-scale migration over the course of a night (Brunton and Booth 2003).

Our study suggests that abundance of the free-swimming settling stage of post-larval fish may not correlate strongly with adult fish recruitment. Fish at this stage seem to be very abundant and not greatly limited by food resources or predation. Post-larval fish abundance may not be as important in determining the number of juveniles as is the availability of high quality habitats that allow

post-larval fish to mature into juveniles. Input from the ocean may keep post-larval fish numbers relatively constant; the limiting factor may be the ability to find a settling place to survive to a juvenile. Although our study did not indicate the ecological significance of the post-larval fish life stage, little is known about post-larval fish, and this lack of knowledge in itself warrants further study.

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“OH HELL!” ANALYSIS OF DEALERSHIP AND RISKY BIDDING

DAEWOONG LEE AND CHASE R. RAINES

Abstract: “Oh Hell!” is a card game that has generated considerable interest among the Dartmouth Biology FSP 2010 group, and many questions regarding its strategy remain virtually untouched. This study tested the hypotheses that dealership reduces “Oh Hell!” fitness, and that consistent and safe bidding outperforms riskier bidding. Our findings suggest that dealer fitness is lowered, but we were not able to fully explore the consistent-bidding hypothesis.

Key Words: Bidding, blackout, bust and up, dealer, dealing, elevator, nomination whist, oh shit, riskiness.

INTRODUCTION

“Oh Hell!” is a card game ideal both for adults and children, and requires sound reasoning power combined with a touch of luck to be able to survive in each round. Playable with three to seven persons, the game consists of placing bids and winning the exact number of tricks in order to acquire points (Rigal and Sharif 2005). Each game consists of thirteen rounds. The number of cards dealt in each of the thirteen rounds to each player is 7, 6, 5, 4, 3, 2, 1, 2, 3, 4, 5, 6, and 7, respectively. In this game, the responsibility to deal rotates counterclockwise through all players, and invariably one or two players deal more or less frequently than others. Bidding begins to the left of the dealer, and thus the dealer is the last to bid. Rules prohibit the number of bids to equal the number of tricks played in each round, so at least one player in each round will not be able to win the number of tricks he or she bid, causing the person to exclaim, “Oh HELL!” Considering that the dealer is not always free to declare desired bids, because he is always the last to bid, the question of whether dealing reduces “Oh Hell!” fitness has aroused wide interest among the Dartmouth Biology FSP 2010 community. We tested the hypothesis that, in agreement with the general feeling of the “Oh Hell!” community, dealing indeed reduces the fitness. Alternatively, the game may be entirely fair, but certain low-fitness individuals in the population use the “dealer gets screwed” hypothesis as a convenient cover for their lack of ability. We used the final score after each game as a proxy for “Oh Hell!” fitness, and first predicted that the number of rounds that an individual dealt during a given game would be inversely correlated with the individual’s final score and probability of making successful bids. Our second prediction was that the placement of players would have non-random effects on final scores, as a player’s performance

may be influenced by the relative location of the dealership, which is unevenly distributed among players. We also tested whether certain individuals were more subject to the potential dealership handicap in the official “Oh Hell!” ranking by ChocolateDream™.

Secondly, certain players tended to play safe by declaring lower and more achievable bids, while others favored declaring higher, riskier bids. No literature has tested these competing theoretical models, and here we also attempt to test which method best correlates with “Oh Hell!” fitness, as represented by final scores and the number of wins. The consistent bidding model predicts that consistent bidders have a higher chance of winning each round and thus higher final scores. On the other hand, the risky bidding model predicts that earning a greater score in each round overcompensates the lower bidding success rate and leads to higher final scores.

METHODS

From January to March, 2010 in various locations in Costa Rica and in Little Cayman Island, we collected data from 22 “Oh Hell!” games, which in total consisted of 286 rounds. We followed 14 players and recorded the number of players present in each game, whether they met their bid, whether they acted as a dealer, their score in each round, winner of each game, and final scores after each game.

Based on the official ranking of players by ChocolateDream™ (as of March 8, 2010 report. See Appendix A), we tested to see if there was a correlation between ranking and dealership ability, as defined by the difference in average score per round as a dealer and as a non-dealer.

RESULTS

Average score per round was 8.23 points as a dealer and 9.06 points as a non-dealer (Fig. 1, paired- $t_{127} = -1.76$, $P = 0.08$). Winning of games showed no relationship with the number of deals ($\chi^2_2 = 0.59$, $P = 0.75$). The number of deals had a marginally significant effect on the final score, with increasing number of deals reducing the final score (ANOVA, $F_{2,125} = 2.76$, $P = 0.068$). However, the number of deals did not have any significant effect on the bidding success rate (ANOVA, $F_{12,102} = 2.25$, $P = 0.11$). In addition, placement of player with respect to the dealer and geographical location of the game had no effect on each player's final score, regardless of the number of players participating in a game (ANOVA for 5-player game: $F_{4,20} = 0.52$, $P = 0.73$; for 6-player game: $F_{5,30} = 0.54$, $P = 0.74$; for 7-player game: $F_{6,70} = 1.37$, $P = 0.24$).

Successful bidding rate did not correlate with the average score per round when bids were successful. The success rate of making bids had significant effect on the final score (ANOVA, $F_{1,126} = 29.72$, $P < 0.0001$). The average score when bids were successful also had significant impact on the final score (ANOVA, $F_{1,126} = 29.72$, $P < 0.0001$).

The difference in average score between rounds when a player did and did not deal was correlated with the ChocolateDream™ ranking index ($r^2 = 0.42$, $F = 6.60$, $df = 1,9$, $P = 0.03$).

DISCUSSION

Our study has answered the popular question regarding dealing; in rounds when players deal, they are more likely to experience reduced overall “Oh Hell!” fitness. The number of deals was inversely correlated to final scores (Fig. 1). This is especially meaningful considering that games with a lower number of players force each player to deal more frequently, but players should have higher scores since the number of tricks available is the same regardless of the number of players. However, placement of players with respect to the dealer showed non-significant result, suggesting that in general the disadvantage of dealing is evenly distributed among all players throughout each game.

On the other hand, our data did not clearly differentiate among the risky bidding hypotheses. The proxies used for risky bidding, namely bidding success rate and average score for successful bids, did not correlate with each other, suggesting

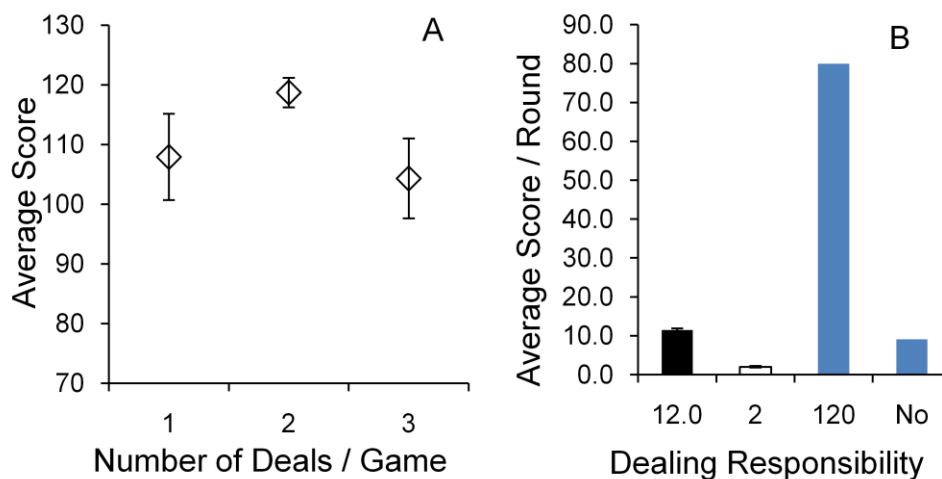


FIG. 1. The number of deals and dealing responsibility negatively affected the final score. Data collected from 22 “Oh Hell!” games, observed from January to March, 2010 in Costa Rica and in Little Cayman Island.

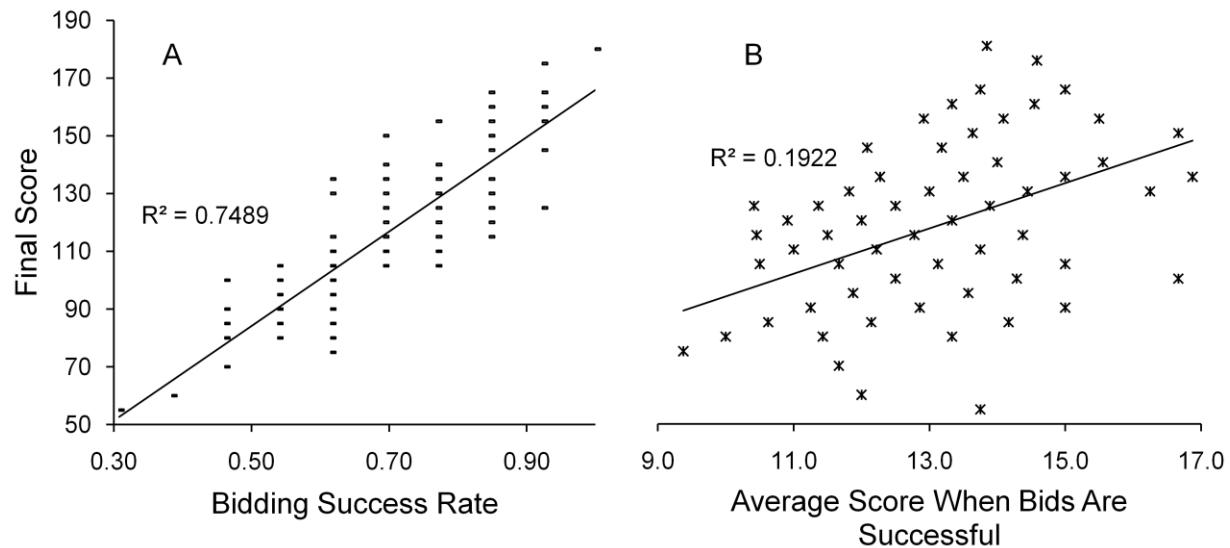


FIG. 2. Final scores were significantly correlated with the bidding success rate (Panel A) and with average score for successful bids (Panel B). However, the bidding success rate and the average score for successful bids were not correlated ($r^2 = 0.004$, $F_{1, 126} = 0.55$, $P = 0.46$).

that risky bidding does not necessarily result in low bidding success rate. Other factors, such as the reasoning and observational ability of players with respect to the strength of each hand may have confounding influences. Further study is needed to incorporate the bidding data and quantify the strength of a player's hand to more fully explore the hypothesis.

The official "Oh Hell!" ranking index is maintained by ChocolateDream™, and it is known to emphasize the ability of players to win, consistency in scoring higher than the average final score, and depth of experiences. Our analysis showed that the performance of a player when dealing is strongly correlated with the ranking, indicating that the ability to overcome the dealership handicap is crucial in competing for higher ranking.

This study is among the first to address the challenges of "Oh Hell!" card game, and we hope that this groundbreaking effort will be followed by greater interest in this ecologically important game. Perhaps paralleled only by Euchre and Newton's Laws in its importance, "Oh Hell!" holds the key to understanding the current global climate change, and thus further studies regarding the subject will better prepare mankind to face the uncertain future.

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APPENDIX A – THE OFFICIAL CHOCOLATEDREAM™ "OH HELL!" RANKING

Player	Ranking*
Chase	1
Erin	2
Sam	3
Duckles	4
Dillon	5
JingJing	6
Amy	7
Molly	8
Jen	9
Emily	10
Nikki	11
Jess	12
David	13
Sarah	14

*The ranking index incorporates the following parameters: Aw = Average win per round, W = Number of wins, F = Z-score of average final score, S = Average score per round, C = Number of games above average final score, and G = Number of games participated.

$$\text{Ranking Index} = 60*Aw + 10*W + 10*F + 3*S + 6*C + G$$

(Source: ChocolateDream™ “Oh Hell!” March 8, 2010 Ranking Report)

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