ing waves. At the highest tide waterline, the lagoon bed at the margins has a more cobbled substrate (pers. observation) which may cause surface turbulence that interferes with echolocation of small fish by bats.

Our study was limited to comparisons between low and high tides. To more fully assess the effect of lagoon bed morphology and fish abundance on *N. leporinus* foraging behavior, a continuous temporal study across tides should be considered. For instance, as the waterline drops below the high tide flat, bat foraging activity should substantially decrease due to the sudden change in lagoon bed slope. Additionally, confounding factors such as moonlight intensity, changing lagoon bed characteristics over time, and the effect of waves and turbulence also are likely to influence *N. leporinus* foraging behavior, and warrant further attention.

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"I'm not dead yet": *Basiliscus basiliscus* population change, habitat characteristics, and putative migration in three riparian habitats

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Abstract: Since an initial census in 1998, annual counts have yielded decreasing numbers of *Basiliscus basiliscus* along three streams near Estación Sirena in Corcovado National Park, Costa Rica. We continued this long-term study on the population demographics of the basilisk lizard and investigated possible mechanisms for its annual population fluctuations, including predator abundance, microhabitat, canopy cover, rainfall and stream width. We predicted that older, more dominant individuals would be found in more sheltered habitats, leaving many younger individuals with less sheltered habitat. The total number of basilisks found in the Rio Claro increased from 2000 to 2001, whereas populations along two smaller streams decreased. Stage distributions, survivorship, and fecundity rates differed significantly from those in 2000. Given the available data there does not appear to be a direct correlation between rainfall, canopy cover, or predator abundance and basilisk population size over the past four years. When the three subpopulations were treated as one metapopulation, the total number of basilisks increased from 2000 to 2001 (118 to 123) and the population growth rate was nearly stable (λ=1.04). We propose that the three populations may be part of a larger metapopulation composed of sinks and sources, possibly connected by migration.

Key Words: basilisk lizard, jesus christ lizard, metapopulation, microhabitat

Introduction

Since an initial census in 1998 (Berg et al. 1998), annual counts have yielded decreasing numbers of basilisk lizards along three streams near Estación Sirena in Corcovado National Park, Costa Rica. Suggested mechanisms for basilisk population decline have included increased avian predation (Berg et al. 1998) and/or increased egg mortality associated with high rainfall (Van Devender 1983). In addition to continuing the annual census, estimating survival and reproduction parameters for a stage-based population model, we obtained rainfall data and measured stream characteristics (canopy cover, stream width) that may lead to increased avian predation. Previous studies have treated these streams as isolated populations. However, since populations are often connected by dispersal and migration, we present model predictions for metapopulation and individual subpopulation longevity for basilisks at Corcovado.

The risk to basilisks from avian predators may be strongly influenced by the degree of refuge that their microhabitats provide. Aucoin et al. (2000) showed that basilisks prefer sheltered habitat. Because many basilisk populations show age-class dominance (Van Devender 1983), we predicted that within a single stream site, older and presumably more dominant individuals would be found in the more sheltered habitats, leaving younger individuals in less sheltered habitats. Such a pattern would imply that habitat selection and size dominance might explain differences in population age structure between large and small streams in our study system.

Methods

Surveys of basilisk populations and stream characteristics

On 3-5 February 2001, we censused basilisk populations along the one river and two streams first sampled by Berg et al. (1998) near Estación Sirena, Corcovado National Park, Costa Rica. In contiguous 50 m transects we sampled 1200 m of the Rio Claro (beginning 200 m upstream from the mouth), 500 m

of Stream 1 (beginning at its intersection with the Pavo Trail, 3.3 km from Estación Sirena), and 600 m of Stream 2 (beginning at its intersection with the Pavo Trail, 1.1 km from Estación Sirena). At each study site, surveyors walked upstream along each bank (two surveyors per bank in the Rio Claro; one per bank in Streams 1 and 2) and counted all basilisks seen. We did not census areas beyond the riverbanks, since transects running perpendicular to the riverbank by Berg et al. (1998) and Aucoin et al. (2000) yielded no basilisks. We censused the Rio Claro and Stream 2 twice and Stream 1 once; the larger population size of the two replicates was used in the analysis (102 vs. 96 for Rio Claro; 10 vs. 3 for Stream 2). We made the population censuses in the afternoon in Rio Claro, in the mid-morning in Stream 1 and in the late morning in Stream 2. We surveyed each transect for approximately 8 min. During the census, we visually categorized body length (tail included) into the size classes established by Babineau and Paine (1999): size class 1: <20 cm; size class 2: 20 - 40 cm; and size class 3: >40 cm. As in 1999 and 2000, size class 1 was assumed to be the young of the year, size class 2 to be 1-2 year olds, and size class 3 to be ages > 2 years (reproductive adults).

We also recorded the number of potential predators observed (herons, falcons, and squirrel monkeys) along each transect during sampling, and calculated the number of predators per observation hour for each stream. At the beginning of each 50 m transect, we measured stream width with a tape measure and canopy cover at the edge of the riverbank with a spherical densiometer. We obtained rainfall data for 1998, 1999, and 2000 from records kept at Estación Sirena.

Microhabitat assessment

Basilisk microhabitat was assessed for all three stage classes along the Rio Claro. Microhabitat components were classified as "sheltered," which included dead wood, roots and riparian vegetation, or "not sheltered," which included dirt, leaves, flat rock, pebbles and sand. We estimated the percent cover of sheltered components within a 2 m^2 area surrounding the site where each stage 3 basilisk was first observed, and for the microhabitats of an equivalent number of randomly selected stage 1 and stage 2 basilisks.

Population demographics and modeling

We treated each stream as a distinct

Table 1. Comparison of stream characteristics measured in 1998 and 2001.

	Stream width[1] (m) (mean ± SD)		Canopy cover[1] (%) (mean ± SD)		Predators per observation hour[2]	
Stream	1998	2001	1998	2001	1998	2001
Rio Claro	18.1 ± 6.1	29.6 ± 20.3	65.7 ± 8.5	67.9 ± 16.0	6.0	2.3
Stream 1	2.8 ± 0.7	2.0 ± 0.7	90.4 ± 2.3	89.3 ± 5.4	0.4	0.0
Stream 2	2.8 ± 1.0	3.3 ± 1.0	90.6 ± 2.4	87.9 ± 4.4	0.5	1.0

[1] n = 24, 10, and 12 for Rio Claro, Stream 1 and Stream 2, respectively.

[2] hours of observation time = 3, 2, and 1 for Rio Claro, Stream 1 and Stream 2, respectively.

Table 2. Proportion of individuals in three stage classes for basilisk populations along three riparian habitats over four years in Corcovado National Park, Costa Rica. The total number of individuals censused in each year at each site is indicated in the bottom row.

	Rio Claro				Stream 1				Stream 2			
	1998	1999	2000	2001	1998	1999	2000	2001	1998	1999	2000	2001
Stage 1	0.66	0.55	0.76	0.47	0.56	0.49	0.28	0.10	0.58	0.56	0.57	0.18
Stage 2	0.22	0.34	0.20	0.46	0.31	0.40	0.52	0.50	0.28	0.36	0.21	0.46
Stage 3	0.12	0.11	0.04	0.07	0.13	0.11	0.20	0.40	0.14	0.08	0.21	0.36
#Indiv.	343	92	74	102	105	37	25	10	50	25	19	11

subpopulation in a metapopulation, calculating the proportion of individuals in each stage class for each subpopulation separately and for the metapopulation as a whole. Similarly, the discrete population growth rate, $\lambda = N_{t+1}/N_t$, was calculated for each subpopulation and for the metapopulation. We used Chi-square analyses to test for differences in proportional size class distributions between the subpopulations and metapopulations in 2000 and 2001, and among subpopulations in 2001.

We constructed a Lefkovitch stage-based matrix model to describe the short-term dynamics of each subpopulation and the metapopulation. We used 2000 census data as the basis for calculating annual survival rate of stage 1 individuals and the fecundity of stage 3 individuals. We estimated stage 2 survival rate algebraically using Van Devender's (1983) estimate of 40% survivorship for stage 3 individuals and census data from 2000 and 2001. Stage 3 was assumed to be the only stage capable of reproduction (Van Devender 1983). We conducted sensitivity analyses for each subpopulation and for the metapopulation to assess the relative impact of each stage on λ at stable stage distribution (SSD) by increasing survivorship of each stage, one at a time, by 10%.

Results

Stream characteristics

Compared with 1998, the Rio Claro and Stream 2 were wider in 2001, while Stream 1 was narrower (Table 1). There was no change in canopy cover on any of the three sites, and predator abundance remained low on Streams 1 and 2, and decreased on the Rio Claro (Table 1). Annual rainfall totals for 1998, 1999, and 2000 were 4.85 m, 6.31 m, and 5.63 m respectively. Although data for 2001 are incomplete at the time of this writing, the season thus far was extremely dry compared to previous years (R.T. Holmes, pers. comm.), and no rain fell during our eight days in Corcovado.

Microhabitat

Larger basilisks occupied more sheltered locations than smaller basilisks in Rio Claro. Microhabitats occupied by both stage 3 and stage 2 basilisks contained a significantly higher percentage of sheltered habitat components than did those of stage 1 individuals (ANOVA, F = 13.04, df = 2, P = 0.0001; Fig. 1).

Population demographics

The Rio Claro basilisk population increased between 2000 and 2001 (74 to 102), whereas Stream 1 and Stream 2 populations decreased (25 to 10, 19 to 11). Population growth rates (λ) were estimated at 1.38, 0.44 and 0.52 for Rio Claro, Stream 1, and Stream 2 respectively (Fig. 2). The total numbers from all three streams combined, which we consider here as the metapopulation, increased from 2000 to 2001 (118 to 123, $\lambda = 1.04$; Fig. 2).

Stage structure differed between subpopulations in 2001. Rio Claro had a significantly greater proportion of stage 1 individuals than Streams 1 and 2, whereas Streams 1 and 2 had a significantly greater proportion of stage 3 individuals than Rio Claro (χ^2 = 15.16, df = 4, P = 0.004). Stage structure in 2001 differed from stage structure in 2000. On

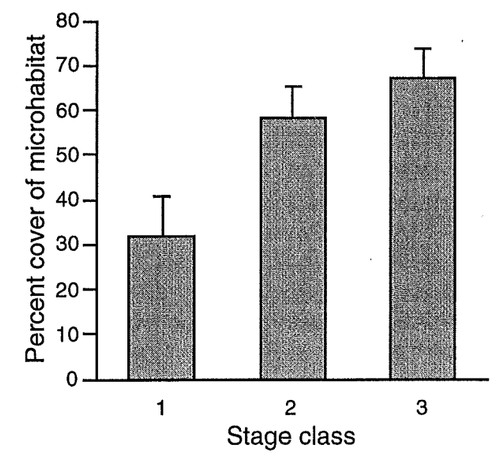

Fig. 1. Percent cover of sheltered habitat (± 1 SE) for three stage classes of *Basiliscus basiliscus* along the Rio Claro near Estacíon Sirena, Corcovado National Park, Costa Rica in 2001 (n = 9).

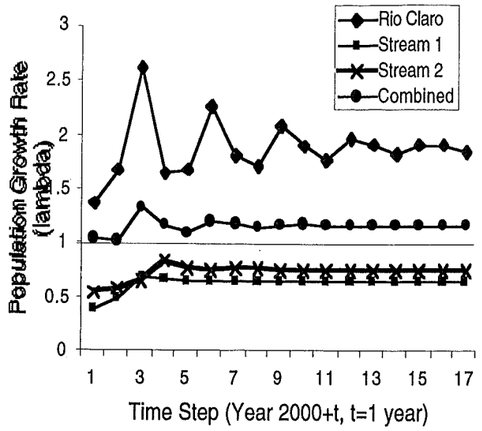

Fig 2. Projected population growth rate (lambda) of basilisk lizards found in three streams in Corcovado National Park, Costa Rica. Lambda was calculated by iteration in a Lefkovitch matrix. Series labeled Rio Claro, Stream 1, and Stream 2 represent the dynamics of individual subpopulations. The Combined category treats all three subpopulations as a metapopulation.

the Rio Claro, a significantly smaller proportion of stage 1 individuals and significantly greater proportion of stage 2 and 3 individuals were found in 2001 than in 2000 ($\chi^2 = 16.67$, df = 2, P = 0.0002). On Stream 1, there were significantly greater proportions of individuals in stage class 1 and 2 ($\chi^2 = 11.80$, df = 2, P = 0.003) in 2001. There was no significant difference between the proportions of individuals in any stage class on Stream 2 in 2000 and 2001 ($\chi^2 = 4.81$, df = 2, P = 0.09). When considered as a metapopulation, 2001 had a significantly smaller proportion of stage 1 individuals, but a greater proportion of stage 2 and 3 individuals than 2000 ($\chi^2 = 11.80$, df = 2, P = 0.003). There was an increase from 2000 estimates in Rio Claro survivorship across all stage classes, and the fecundity approximately tripled (Fig. 3). Streams 1 and 2 had similar survival rates in both years, but fecundities decreased (Fig. 3).

Model Projections

The Lefkovitch stage-based matrix models indicate that none of the populations had a stable stage distribution (SSD). If there is no dispersal between subpopulations, the model predicted extinction in the Stream 1 population by 2004 and in the Stream 2 population by 2007. If subpopulations are connected by dispersal, our prediction shows that the metapopulation will not go extinct. The sensitivity analysis indicated that survivorship of stage class 1 in Rio Claro, stage class 3 in Stream 1 and stage class 2 in Stream 2 had the largest impacts on subpopulation growth rates. Survival of stage class 1 had the greatest impact on metapopulation growth rate.

Discussion

After four years of study, changes in

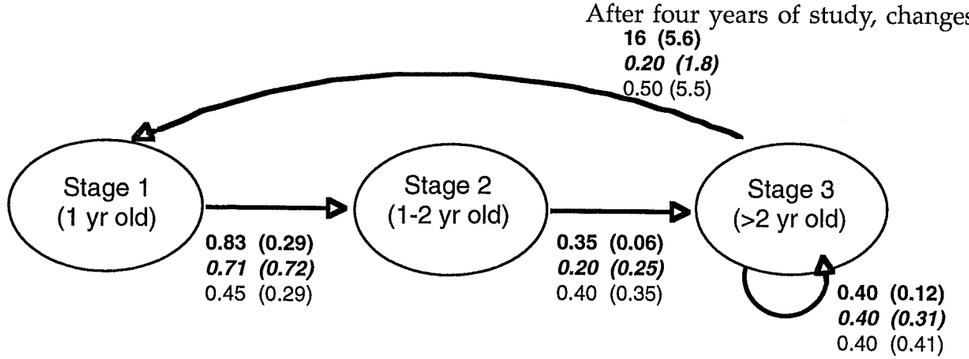

Fig. 3. Schematic life cycle diagram of survivorship and fecudnity for three basilisk subpopulations in Corcovado National Park, Costa Rica. Arrows represent flows from one stage class to the next: survivorship from stage 1 to 2, from stage 2 to 3, and for those surviving within stage 2; and fecundity from stage 3 to 1. Numbers represent estimate for 2001 parameters, while those for 2000 are shown in parentheses. Bold type represents Rio Claro, bold italics represents Stream 1, and plain text represents Stream 2.

[Fig. 3 - schematic of life cycle]

stream characteristics and predator abundance show no long-term patterns that could explain the observed changes in demographic characteristics and population fluctuations of basilisk lizard populations at these study sites in Corcovado. For example, while the populations have declined, estimates of predator abundance also have declined and canopy cover has not changed. There is also no clear relationship between population changes, rainfall and stream width with the available data. While more data on these extrinsic factors, along with quantification of other site-specific factors such as insect (food) abundance, could provide the means to assess basilisk population changes, we propose an additional explanation. It has previously been assumed that basilisk migration is rare and that the three riparian habitats could therefore be considered isolated populations (Berg et al. 1998, Babineau et al. 1999, Aucoin et al. 2000). We propose that these three populations in fact may be part of a larger metapopulation, linked by migration. If this were the case, the high fecundity in Rio Claro may allow it to serve as a source of dispersing basilisks to Streams 1 and 2, which in turn function as sinks (Pulliam 1988). In addition to the low fecundity rates, the basilisk populations of Streams 1 and 2 also have low growth rates. Model projections predict extinction for these streams within six years. The Rio Claro, meanwhile, has a very high population growth rate, which, given the current demographic traits we measured, leads to a projected population in the thousands within six years. Such rapid growth may lead to density-dependent constraints such as food and habitat limitations, leading to a population crash. Dispersal could alleviate this situation. When considered as a metapopulation, the population appears to be growing at a lower, more stable rate. A population growing at such a rate is predicted to achieve a stable stage distribution, have less chance of encountering density-dependent constraints, and therefore have greater longevity than a population growing at a rate as high as on the Rio Claro.

Basilisks may disperse both along and between water-ways. Despite the findings of Berg et al. (1998), we observed several basilisks away from water sources, some farther than 100 m. If basilisk migration occurs, it may be driven by habitat availability. We found that older basilisks were more common in sheltered habitat and that proportionally more stage 3 individuals were found near Streams 1 and 2. Sheltered habitat may be of greater importance to older basilisks than young basilisks because their ability to run across water is limited and their size makes them a more obvious, as well as a more desirable target for potential predators. As shown by Aucoin et al. (2000), Streams 1 and 2 have more sheltered habitat than the Rio Claro. We propose that dispersing subdominant stage 3 males may settle in small streams due to habitat quality and the low density of resident adults. As evidenced by the low number of stage 1 or 2 individuals in these populations, however, these older individuals may not be reproducing well on these smaller streams; i.e., they may be sinks.

Since 1999, basilisk lengths have been classified in stages according to a range of body lengths, with 0 - 20 cm corresponding to young of the year, 20 – 40 cm to ages between 1 and 2, and > 40 cm to ages 2 and older (Babineau and Paine 1999, Aucoin et al 2000, this study). However, an exact relationship between basilisk size and age has yet to be established. We therefore cannot be certain that the size-based classification system we used accurately reflects age. Further knowledge of the basilisk size/age relationship would help ensure that stage class categorization is consistent and biologically accurate in this long term study.

As a further caveat, we note that the number of basilisks encountered appeared to vary with time of day and amount of search time. Thus differences in basilisk counts due to differences in the hour of sampling and search time could be interpreted as changes

in the population if methods are not standardized from year to year. Continuation of this annual monitoring of basilisk populations should adopt explicit, standardized methods for both time of day and search time. Observations during our sampling suggested that search times greater than 10 min per transect yielded little change in the number of basilisks observed; we therefore recommend 10 min as a standard search time for transects (with one researcher observing each riverbank on smaller streams and two per riverbank on the larger Rio Claro). From our two censuses of Stream 2 and general observations, basilisks seemed to be less active in the mornings, especially before mid-morning, when the temperature becomes hot. We suggest that sites be identified and 50-m transects flagged in the morning. Non-intrusive measures (such as stream width, percent cover) can be taken at this time. Basilisks are skittish; many of our basilisk sightings were made as they fled from us. Censusing should be done in the afternoon (as it was in 1999 and 2000), when basilisks are fully active and a couple hours have passed to allow them to return to their streamside perches after the disturbance of the morning flagging.

A final note: the Rio Claro and riverbanks in general in Corcovado have been reported to be sites of rather high snake abundance, including the fer de lance, *Bothrops asper* (Berg et al 1998). While we saw no snakes, we did come within meters of a couple crocodilians (one small, one not so small) ~ 300 m up the Rio Claro. In all areas, vigilance is recommended.

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