
Population dynamics and demographics of a tropical lizard (*Basiliscus basiliscus*) in Corcovado National Park, Costa Rica

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Abstract

In populations with size-structured dominance hierarchies, such as basilisk lizards, intraspecific competition may force smaller individuals into less preferred habitats where they experience greater predation. The size of the basilisk population at Corcovado National Park was nearly halved from 1998 to 1999, which created an opportunity to test a hypothesis that relates microhabitat use, size-structured dominance hierarchies, and population dynamics. We surveyed the basilisk and avian predator populations along a river (Rio Claro) and two smaller streams. Our data, combined with data from two previous censuses, were used to estimate the age structures of each population and test whether size classes differed in their recovery from the population decline. Basilisks in all three populations used sheltered microhabitats more than expected based on availability, with the strongest preference occurring in the Rio Claro population, which also had the highest number of avian predators. We found a greater proportion of smaller individuals along the Rio Claro, but similar population structures along Streams 1 and 2, compared to 1999 surveys. This indicates that avian predation pressure exerts a stronger influence on the Rio Claro population. All populations declined from 1999 to 2000, and sensitivity analyses indicate that these populations will continue to decline unless the proportion of large individuals increases dramatically in the next few years.

INTRODUCTION

Predation pressure and intraspecific competition are forces that exert constant pressure on animal populations. These forces have particularly complex influences on populations with a size-structured dominance hierarchy that affects the distribution of resources, such as space or food, among individuals. In particular, competition for predator-free space may force smaller, competitively inferior individuals into less preferred habitats, and the resulting increases in mortality on small size classes can have ramifications for the age structure and growth rate of the population as a whole.

The basilisk lizards (*Basiliscus basiliscus*) of Corcovado National Park, Costa Rica, are an ideal species in which to examine the demographic consequence of intraspecific competition for protection from predation. Because reproduction is seasonal rather than continuous, the age structure of the population can be inferred from the relative abundance of three distinct size classes that are recognizable based on body length. A population decline of more than 50 % in three populations of *B. basiliscus* occurred between 1998 and 1999 (Babineau & Paine, 1999), and presented an opportunity to test for relationships between age structure, dominance hierarchies, and population dynamics in local populations that occupy different habitat types.

Susceptibility to avian predation is likely to vary among populations of basilisks in the Sirena area that inhabit different sized streams and are exposed to different levels of avian predation (Berg et al., 1998). One population inhabiting the relatively large and open Rio Claro is exposed to many more avian predators than two smaller streams east of the Sirena Biological Station (Berg et al., 1998). We hypothesized that because of the avian predators, the Rio Claro causes the larger lizards to choose the most sheltered microhabitats such as vegetation, roots and branches, live trees, and fallen logs. The dramatic reduction in population size in 1998, which affected larger basilisks in particular, may have allowed smaller lizards to move into these optimal microhabitats previously occupied by the larger lizards. We hypothesized that the demographic response to the 1998 population decline would differ among size classes and different populations. We predicted that there would be a larger proportion of younger individuals in the Rio Claro population this year compared to previous years because of higher predation pressure on the Rio Claro compared to the smaller streams. We also predicted that in the two small stream populations, where fewer avian predators decreases the need for sheltered habitats, the populations would remain at a stable stage distribution, because survivorship of young individuals would not disproportionately increase in comparison to older individuals.

Habitat Type	Rio Claro		Stream 1		Stream 2	
	Available	Used	Available	Used	Available	Used
Sheltered	0.35	0.74	0.68	0.84	0.69	0.70
Exposed	0.65	0.26	0.32	0.16	0.31	0.21

Table 1. Proportion of sheltered and exposed microhabitat availability and use by basilisks in each of three focal populations

METHODS

Surveys of basilisk and avian predators

On 4 - 6 February 2000, we observed three basilisk populations near Sirena Biological Station, Corcovado, Costa Rica. We sampled 1200 m of the Rio Claro (beginning 200 m upstream from the mouth), 500 m of Stream 1 (located 3.3 km from station on the Pavo trail), and 600 m of Stream 2 (located 1.1 km from station on the Pavo trail). We censused each stream twice, which demonstrated that our counts had high repeatability, so we used the larger of the two censuses for each population in the analysis (69 vs. 74, 23 vs. 25, 16 vs. 19 for Rio Claro, Stream 1, and Stream 2, respectively). During censuses, we recorded the number and size of lizards observed along both sides of the riverbank. We visually estimated lizard size and age following the methods of Babineau and Paine (1999): size class 1: < 20 cm total body length (young of year); size class 2: 20 – 40 cm (2 years old); and size class 3: ≥ 40 cm (reproductive

adults). All four researchers censused the Rio Claro, two on each bank, and two researchers censused Streams 1 and 2, one per bank, with each researcher walking upstream and visually scanning a 3 m corridor along the edge of the riverbank. Berg et al. (1998) found that basilisks do not occur at distances greater than 5 m perpendicular to the riverbank, and we confirmed this observation by haphazardly resampling four 10-m transects perpendicular to the riverbank. We also recorded the number of avian predators (raptors and herons) observed during censusing efforts and calculated number of predators observed per observation hour for each stream.

Habitat assessment

To test our assumption that the availability of sheltered microhabitat influences basilisk mortality, we recorded the microhabitat of each observed lizard as either sheltered or exposed. Sheltered microhabitats, defined by their three-dimensional structural complexity, included vegetation, live trees, fallen logs, and roots or branch-

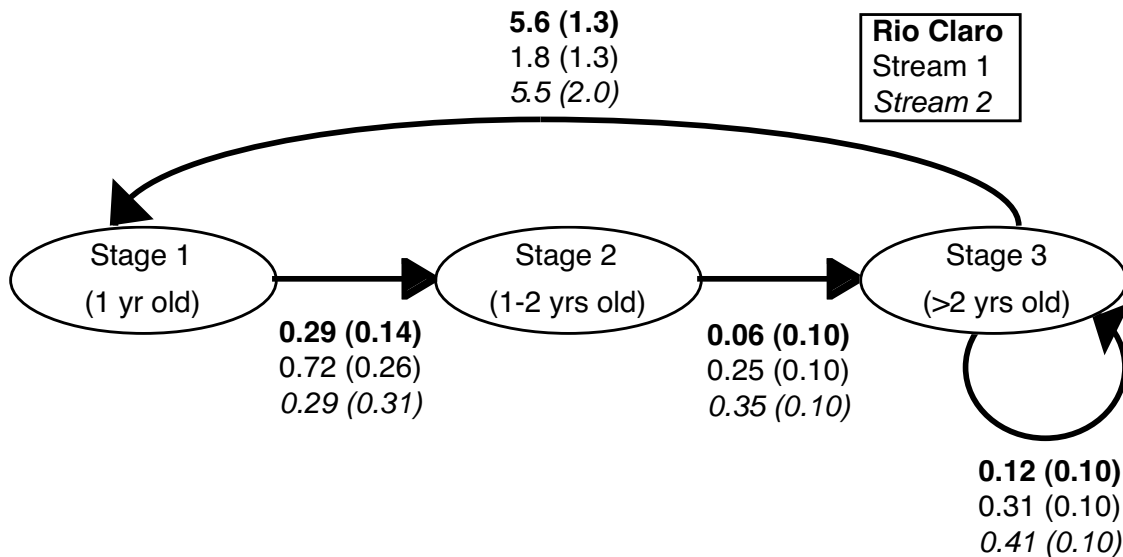


Figure 1. Schematic life cycle diagram for three basilisk populations in Corcovado National Park, Costa Rica. Arrows represent flows from one stage class to the next and numbers indicate survivorship probabilities (1999 values in parenthesis). Stage 1 to Stage 2 survivorship and Stage 3 to Stage 1 fecundity derived from empirical data. Stage 2 and Stage 3 survivorship estimated with a Lefkovich matrix assuming a linear increase in survival function between Stage 2 and Stage 3 (see text).

es. Exposed microhabitats included sand/mud bank, rock face (incline > 45°), rock (incline < 45° or gravel bed), and leaf litter. The exposed microhabitats are more susceptible to avian predators than the sheltered microhabitats. We recorded the microhabitat for each censused individual, estimated the proportion of each microhabitat class along the entire sampled streambank, and compared microhabitat use with microhabitat availability for each stream using chi-square analysis.

Population demographics and modeling

We calculated the proportion of individuals in each stage class, and estimated population growth rate during the last year as $\lambda = N_t / N_{t-1}$ ($t = \text{year}$). We tested for differences in the size class distributions between 1999 and 2000, and among streams in 2000, using chi-square analyses. We used 1999 and 2000 demographic data to generate a Lefkovich stage-based matrix model to describe each population of lizards. Empirical data were used to calculate survivorship between size class 1 and size class 2, and to estimate fecundity between size class 3 and size class 1 (size class 3 was assumed to be the only class with reproductive females) (Van Devender, 1983). To estimate survivorship for size classes 2 and 3, we assumed that annual survival increased linearly between the two size classes (increasing survival with size is typical for organisms with indeterminate growth and a dominance hierarchy) (Begon et al., 1996). By iteration, we found that a 0.06 increase in survivorship between size class 2 and size class 3 generated the observed frequencies between 1999 and 2000 in all three populations. Finally, we conducted a sensitivity analysis in which we increased the survivorship of each size class by 0.25 to compare the relative importance of impacts on each size class for the population growth rate (λ) at a stable stage distribution (SSD).

Table 2. Proportion of individuals in each size class for the three basilisk populations over three years in Corcovado National Park, Costa Rica. There were significant differences between stage distributions in 1999 and 2000 in all populations.¹ Size class distributions differed significantly between populations in 2000.² The total number of individuals censused each year at each site is indicated at the bottom row.

	Rio Claro			Stream 1			Stream 2		
	1998	1999	2000	1998	1999	2000	1998	1999	2000
Stage 1	0.66	0.55	0.75	0.56	0.49	.028	0.58	0.56	0.57
Stage 2	0.22	0.34	0.20	0.31	0.40	0.52	0.28	0.36	0.21
Stage 3	0.12	0.11	0.04	0.13	0.11	0.20	0.14	0.08	0.21
# Individ.	343	92	74	105	37	25	50	25	19

¹ (Rio Claro $\chi^2 = 9.96$, $df = 2$, $p < 0.01$; Stream 1 $\chi^2 = 9.91$, $df = 2$, $p < 0.01$; Stream 2 $\chi^2 = 9.78$, $df = 2$, $p < 0.01$).
² ($\chi^2 = 54.57$, $df = 4$, $p < 0.001$)

RESULTS

Surveys of basilisks and avian predators

Our censuses revealed a total of 118 basilisks: 74 in the Rio Claro, 25 in Stream 1, and 19 in Stream 2. We observed three raptors and five herons along the Rio Claro. The number of avian predators per observation hour (4 in the Rio Claro, 0 in both Streams 1 and 2) did not differ from that reported in 1998 ($\chi^2 = 0.98$, $df = 2$, $p = 0.61$ (Berg et al., 1998)).

Habitat assessment

Basilisks in all populations preferentially occupied sheltered habitats (Table 1). This preference was strongest in the Rio Claro population: $\chi^2 = 53.78$, $df = 2$, $p < 0.001$ (testing the null hypothesis that preferences were the same among populations).

Population demographics

All three populations declined between 1999 and 2000. Growth rates ($\lambda = N_t / N_{t-1} - 1$) were 0.80, 0.68, and 0.76 for the Rio Claro, Stream 1, and Stream 2, respectively. Size structures differed among the populations and between 1999 and 2000 within each population. In the Rio Claro, the proportion of size class 1 increased from 1999 (Table 2), primarily due to reduced abundances in size classes 2 and 3. In Stream 1, the size distribution peaked in size class 2 (Table 2) due to a decrease in the number of size class 1 individuals from 1999 estimates. In Stream 2, the proportions of size class 3 increased and size class 2 decreased from 1999 estimates (Table 2) due to a decrease in the number of size class 2 individuals. Model projections indicated that none of the populations were at a stable stage distribution (SSD).

There was a general increase in survivor-

ship from 1999 estimates across all size classes, and the increase was two- to fourfold in size classes 2 and 3 in both Streams 1 and 2 (Figure 1). A sensitivity analysis of the parameters in the model indicated that survivorship of size class 2 had the largest impact on population growth rate (λ) at SSD (Figure 2). By systematically adjusting survivorship of the adult size classes in the model, we determined that populations will not converge on a positive growth rate unless the survival of size classes 2 and 3 exceed 0.37 and 0.42, respectively.

DISCUSSION

Predation pressure and habitat use

The observed preferential use of sheltered microhabitats supports the hypothesis that more intense avian predation on the Rio Claro has produced marked differences in microhabitat preferences. Despite the higher levels of avian predation pressure on the Rio Claro, basilisks in all three populations preferred similar habitats. Although avian predation may be a crucial determinant of basilisk habitat choice, other pressures such as terrestrial predators (snakes, ocelots, and opossums), food distribution, or thermoregulatory needs may influence microhabitat selection.

Population demographics

The observed size class distribution of basilisks in the Rio Claro supported our prediction that after a large reduction in population size, the proportion of younger individuals would increase relative to larger individuals. Younger individuals may have increased accessibility to sheltered habitats due to a decrease in dominant individuals, thereby increasing the survival and abundance of these younger individuals. Although this hypothesis accurately predicted the shift in the size distribution of the Rio Claro population, the smaller streams did not remain at a stable stage distribution (SSD). Our prediction assumed (1) that avian predation was the primary factor influencing microhabitat use, and (2) that populations in smaller streams were subject to less avian predation pressure than the Rio Claro. Because we observed different size distributions in each of the three populations, it appears that a single mechanism cannot adequately explain the dynamics of these populations.

Contrary to our assumptions, survivorship appeared to decrease with age in these basilisk populations. This runs counter to the usual pattern that organisms with indeterminate growth and

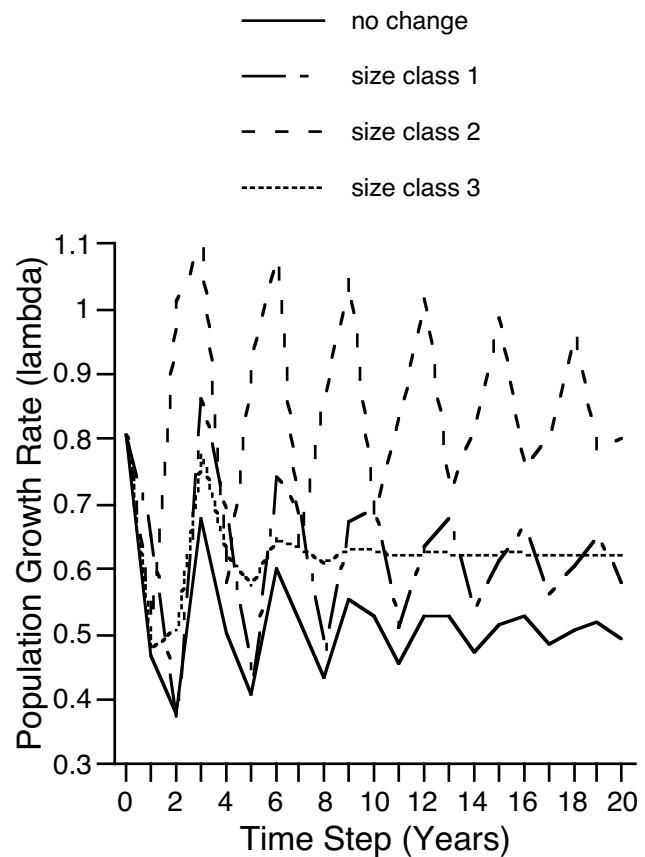


Figure 2. Results from a sensitivity analysis on the impact of survivorship to projected population growth rate for a *B. basiliscus* population in the Rio Claro, Concovado national park, Costa Rica. In each scenario, survivorship was increased by 0.25 for the indicated size class. By the end of the projection, all populations were at SSD.

dominance hierarchies tend to experience higher survivorship at older ages (Begon et al., 1996). It may be that larger individuals are actually more susceptible to predation. Larger basilisks may be more visible and less capable of running across bodies of water to escape capture (Van Devender, 1983). Some large predators may also prefer large basilisks. Another possible explanation for the apparently low survival of larger individuals is that they are more likely to escape detection during the census (Babineau & Paine, 1999). If so, this would have reduced our estimates of survivorship for larger lizards and inflated fecundity estimates.

Summary

Our census indicates that all three *B. basiliscus* populations are still declining, and that the decline continues because of low survivorship of larger basilisks. We observed higher abundance of avian predators along the Rio Claro, coinciding with the predicted increase in the proportion of smaller individuals. However, the size

class distributions in Stream 1 and 2 suggest that non-avian predators may also influence population structure. Populations will continue to decline if survivorship of the larger size classes does not increase.

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