WE FOUND JESUS CHRIST IN CORCOVADO: STREAM SIZE AND THE POPULATION STRUCTURE OF *BASILISCUS BASILISCUS*

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Abstract. We surveyed three populations of basilisk lizards on rivers of different sizes in Corcovado National Park. We hypothesized that the population structure of basilisks would reflect lower survivorship on the larger river due to higher predator abundance and decreased protection from visual predators. As predicted, estimated survival from age class 1 to age class 2 was markedly lower on the large river (0.33 vs 0.48 - 0.57 on the two smaller rivers). However, estimates of annual adult survival were higher on the large river (0.35 vs. 0.19 - 0.24), as were estimates of annual per capita reproductive rates (5.6 vs. 3.6 juveniles/adult). Higher adult survival on large rivers could be the result of more abundant large food items or a reversal in predation risks between large and small basilisks on large and small rivers. Basilisk populations seem to be adequately described by a simple 3-stage population model.

Keywords: Stage-based population model, basilisk lizard

INTRODUCTION

Basilisk lizards (*Basiliscus basiliscus*) are found at high densities in tropical riparian environments. Juveniles are almost entirely insectivorous while adults will consume a variety of insects, other invertebrates, small fish, fruit, and flowers. Predation, particularly from raptors and large aquatic birds such as herons, plays a central role in the high annual mortality rates that have been reported for basilisks (~ 85% for juveniles and ~60% for adults) (Van Devender 1983).

Basilisks occur both on large rivers with open canopies (e. g., Rio Claro) and on smaller rivers with closed canopies. We hypothesized that juvenile survivorship would be lower along the large river due to higher predator abundance and increased exposure to visual predators. Basilisk populations could also be influenced by differences in food availability between small and large rivers. We tested these hypotheses by comparing large and small rivers with respect to the age structure of the basilisks, abundance of predators, and food availability.

METHODS

We surveyed three populations of basilisk lizards in Corcovado National Park, Osa Peninsula, Costa Rica. We conducted 12 100 m transect surveys in a large river (the Rio Claro) and 11 100 m transect surveys in two small rivers west of the Sirena Field Station (6 in "Small 1" located ~ 3.5 km from Sirena on Pavo Trail, and 5 in "Small 2" - 3rd stream from Sirena on Pavo Trail). We recorded all basilisks we observed on both banks and categorized them by size into three stage classes (stage 1, stage 2, adult). Based on the distribution of sizes, stage 1 almost certainly corresponds to age 1, stage 2 to age 2, and adults to ages 3 and above. We recorded all basilisk predators (raptors, herons, squirrel monkeys) observed when surveys were being conducted and calculated predators observed / hour of observation for large versus small rivers. At 25 and 75 m in each transect we measured river width with a sonin electronic distance measure and canopy cover using a spherical densiometer; these values were averaged for each transect. We placed 8 sticky traps both on the Rio Claro and Small 1 and collected them ~24 hours later to obtain estimates of basilisk food abundance.

We also conducted three 100 m transect surveys perpendicular to each river to look for basilisk use of non - river habitat.

We used analyses of variance (ANOVAs) to test for differences in river width and canopy cover between the 3 rivers, and used a student's t-test to test for differences in insect abundance between the Rio Claro and Small 1. We tested for differences in predator abundance between the Rio Claro and the small rivers using Chi square analysis.

We also used Chi - square analyses to test for differences among rivers in the proportion of basilisk individuals within each stage class. We then used a stage-based population model (Lefkovich matrix) to identify possible values for the demographic parameters that could not be calculated directly from our survey data: survival from stage 2 to adult, annual survival of adults, and the adult contribution to stage 1 (fecundity x survival from egg to stage 1). By iteration, we identified the values for these three parameters that would produce a basilisk population of a stable size (Lambda = 1) and with a stable age distribution that matched our empirical estimates for the abundance of stage 1, stage 2, and adults. Estimates were calculated separately for each population.

RESULTS

We observed and classified a total of 498 basilisk lizards (Table 1). The proportion of individuals in stage 2 relative to stage 1 (an estimate of survival from stage 1 to 2, assuming a stable stage distribution) was significantly different among rivers ($X^2 = 7.44$, df = 1, $P < 0.01$): estimates = 0.33 for the Rio Claro versus 0.57 and 0.48 for the small rivers. We did not observe any basilisks in the three transects conducted perpendicular to each river.

The Rio Claro averaged ~18m wide compared to ~2.8m for the two small streams ($F_{2,20} = 60.72$, $P < 0.001$; Table 2), and the Rio Claro had a relatively open canopy (~66% canopy cover) compared to the closed canopy of the small rivers (~90% canopy cover); ($F_{2,20} = 52.23$, $P < 0.001$; Table 2). We saw > 10-fold more predators per observation hour on the Rio Claro compared to the small rivers ($X^2 = 15.97$, $P < 0.05$; Table 2). Our invertebrate traps collected similar numbers of small insects (< 2mm) on the Rio Claro and Small 1 ($F_{1,14} = 0.85$, $P = 0.37$; Table 2).

For all three populations our empirical demographic data (Table 1) were easily simulated with a simple stage-based population model (Fig. 1). Estimated survival probabilities from stage 2 to adult were very similar for all populations (0.35 - 0.39, Fig. 1). Estimated annual survival of adults was markedly higher on the big river than on the small rivers (0.35 vs. 0.19 - 0.24, Fig. 1). Statistical comparisons of adult survival were not possible, but the magnitude of difference was similar to that for the transition from stage 1 to stage 2, which was highly significant. Estimates of annual reproductive contributions (fecundity x probability of survival to our census time) were ~56% higher for the big river compared to the two small rivers. The two small rivers yielded very similar demographic estimates for all life stage transitions. The demographic estimates we present appear to be the only biologically possible mathematical solutions that could match our demographic data under a stable population size and a stable stage distribution. (We were unable to calculate the analytical solutions, but we evaluated hundreds of trial and error estimates for the three unknown parameters.)

TABLE 1. Proportion of basilisks in each stage class.

	Proportions			
River	Stage 1	Stage 2	Adult	Total
Rio Claro	0.66	0.22	0.12	343
Small 1	0.55	0.31	0.13	105
Small 2	0.58	0.28	0.14	50

TABLE 2. Stream characteristics.

		Predation Measurements		
River	River width (m) (mean ± SD)	Canopy cover (%) (mean ± SD)	Predators per observation hour[a]	Insects per trap (mean ± SE)
Rio Claro	18.07 ± 6.13	65.7 ± 8.5	6	11.4 ± 2.7
Small 1	2.73 ± 0.70	90.4 ± 2.3	.4	8.5 ± 1.6
Small 2	2.88 ± 0.95	90.6 ± 2.4	.5	

[a] Hours of observation = 3, 2.5, 2 for Rio Claro, Small 1, and Small 2.

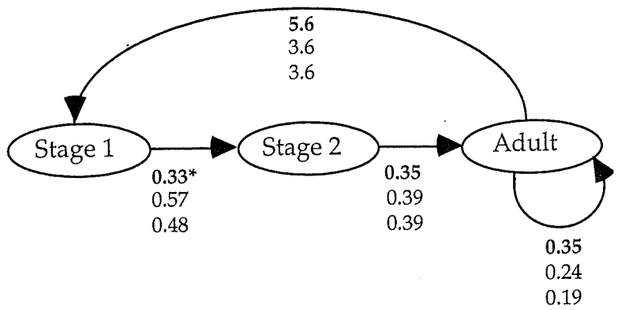

FIG. 1. Survival rate for each stage. Stage 1 to stage 2 are observed values all other values were produced by model. Bold values represent large river.
* P < 0.01

DISCUSSION

The proportion of stage 2 basilisks relative to stage 1 basilisks was much lower on the larger river. Assuming that production of stage 1 individuals is similar between years or that the populations approximate a stable stage distribution, this can only be explained by increased mortality or emigration. The most probable explanation for reduced survival is higher predation of small basilisks on the large river. The large river had many more potential predators and had less canopy cover, which presumably made it easier for raptors to find and capture basilisks from the air. Basilisks often sleep in overhanging branches and drop into the water when disturbed to avoid predation (Van Devender 1983). The low canopy cover and relatively open banks on the larger river would provide fewer habitats that facilitate this predator avoidance behavior.

In contrast to the case for small basilisks, large basilisks appeared to have greater survival on large rivers than on small ones. We hypothesize that this difference is a result of differences in food availability. Juveniles are almost entirely insectivorous while larger basilisks expand their diet to include a variety of small vertebrates, fruit, and even flowers (Van Devender 1983), which might be more available on large rivers. An alternative explanation is that predation risks are greater for adults on the smaller rivers than on the large rivers. Potential predators for adult basilisks could include jaguars, ocelots and other cat species. Although basilisks on the large river suffer from higher juvenile predation (stage 1 - stage 2), it may provide a better habitat for adults.

Estimates of adult reproductive contributions were mathematically and biologically possible, but are the furthest removed from our empirical data and may be the least reliable. Nonetheless, they appear to be biologically sensible. Survival probabilities suggest more larger lizards on the big river (adults greater than 4 years old), which would tend to have higher reproductive contributions. Fecundity estimates for adults are 10 to 144 eggs, suggesting survival probabilities of 1.5 - 21.6 (Van Devender 1983) from the time of hatching to our census data in February. Basilisks breed during the dry season at Corcovado (Van Devender 1983) explaining the discrete, non-overlapping stages that we observed.

At Corcovado, basilisks seem to depend almost exclusively on rivers as their habitat. Our perpendicular transects revealed no basilisks > 5 m away from the river, and the collective observations of 18 people over 8 days revealed < 4 basilisks more than 5 m from a river.

To our knowledge, this is the first study to estimate basilisk population structure and demographic transitions. Our demographic estimates describe populations that match the basilisk lizards in all ways that we can evaluate. For example, Van Devender (1983) reported that no basilisk has been known to live beyond 7 years in the wild and our estimates predict that only 14 per 1000 basilisk on the large river would be > 5 years old (9 per 1000 on the small rivers). Our demographic estimates depend critically on the assumption that these

populations approximate a stable age distribution and a stable population size (Lambda ~ 1). We know of no information that challenges these assumptions. Our demographic data could have falsified the assumptions (e.g., if the abundance of stage 2 exceeded stage 1) but did not. Basilisks appear to have been about equally abundant at this site for 3 of the last 6 years (Ayres, pers. comm.).

If the assumptions of a stable age distribution and stable population size are valid, similar demographic surveys in another year should reveal similar proportions of stage classes and overall abundance. Measurements of adult food resources are also necessary to further understand adult survival.

*Note to future investigators: One of us (BWW) was nearly bitten by a fer de lance while conducting transects on the Rio Claro. This site corresponds to that described by Colwell (1985) as the site of his memorable bite. Peccary researchers at the Sirena station who have logged thousands of hours of fieldwork in the area told us that most of their fer de lance sightings are within 15 m of rivers. We advise that you be watchful and wear boots whenever in these habitats.

LITERATURE CITED

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