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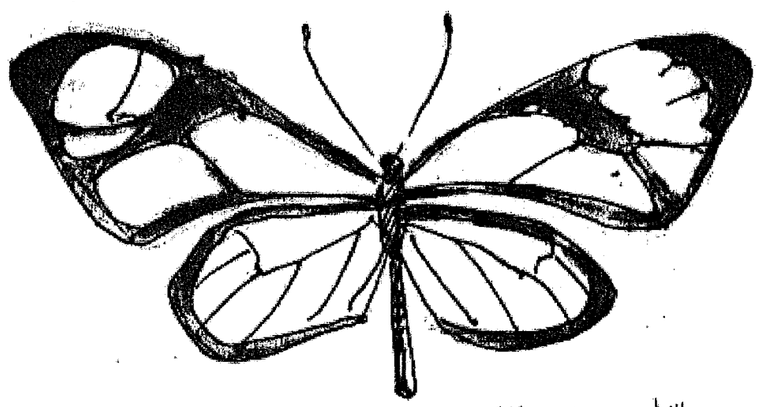

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Jesus lives: age-specific microhabitats and population dynamics in *Basiliscus basiliscus*

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Abstract: Basilisk lizards can be found in and around streams and small rivers in Pacific lowland forests. For the past five years, basilisk populations have been censused in three streams in Corcovado National Park, Costa Rica. Past studies have proposed several explanations for year to year variation in abundance and age structure. We considered how lizard size and age structure might interact with environmental conditions and affect mortality and natality. We tested the relationship between lizard size (which corresponds to age) and microhabitat location. We hypothesized that a size-structured dominance hierarchy would determine which individuals occupy the predator-free spaces. As predicted, smaller lizards tended to occur more frequently in open spaces on the Rio Claro. However, lizard size and microhabitat were unrelated on the two smaller streams. From 2001 to 2002, populations on the Rio Claro did not change, while the populations in the two smaller streams increased 2 - 3-fold, and immigration should be included in the population models. The five-year time series from 1998 to 2002 indicated negative density dependence in all three streams.

Key Words: basilisk lizard, Corcovado, immigration, Jesus Christ lizard, meta-population, negative density-dependence

Introduction

The lizard *Basiliscus basiliscus* is one of the more conspicuous vertebrates of Pacific lowland forests in Central America. Local populations tend to be centered around streams and small rivers where they are able to exploit their ability to elude predators by running across water. Five years of standardized abundance estimates have been collected on basilisk populations inhabiting each of three streams in Corcovado National Park, Costa Rica. These data have revealed high spatial and temporal variation in abundance and age structure, predation (Berg et al. 1998, Aucoin et al. 2000), egg mortality associated with high rainfall such as the La Niña in 1998 (Van Devender 1983, Babineau and Paine 1999) or differences in canopy cover and stream width (Braden et al. 2001).

Thus far, there has not been much consideration of how size and age structure might interact with environmental conditions in ways that influence mortality and natality. It is likely that basilisk populations exhibit a size-structured dominance hierarchy in which individuals compete for resources, such as suitable space along the river. We hypothesized that intraspecific competition would determine which individuals occupy the predator-free spaces. We predicted that larger, more dominant individuals would tend to occur in covered areas that offer more protection from predators. This trend should be more pronounced in the Rio Claro than the two smaller streams (Streams 1 and 2) due to greater predation on the Rio Claro (Aucoin et al. 2000), especially by avian predators (Berg et al. 1998).

As part of our research, we continued the annual census, estimated survival and reproduction parameters for a stage-based population model, and analyzed demographic patterns over the past 5 years. We also evaluated the sensitivity of lizard censuses to time of sampling.

Methods

Surveys of basilisk populations

On 2 and 3 February 2002, we sampled the Rio Claro and two smaller streams originally sampled by Berg et al. (1998) near the Estación Sirena, Corcovado National Park,

Costa Rica. Our protocol matched that of Braden et al. (2001). Stream 2 is a large stream located on the Pavo trail 1.1 km from the station. Stream 1 was ~1.2 km on the Pavo trail beyond Stream 2.

Once in the morning (08:00) and once in the afternoon (13:00), we slowly walked upstream along the banks of the rivers and counted all the basilisks observed over 500, 600, and 1200 m continuous stretches (Stream 1, Stream 2 and Rio Claro, respectively). Lizard observations were separated for each 50 m section along the way. At the Rio Claro, 2 observers walked in the water, ~5 m from the bank. At the other two streams, one of us walked in the water in the center of the stream. During the census, we visually categorized each lizard into one of three size classes following Babineau and Paine (1999): size class 1 (< 20 cm), size class 2 (20 – 40 cm) and size class 3 (> 40 cm). We assumed size class 1 to be young of the year, size class 2 to be 1 – 2 year olds and size class 3 to be older than 2 years (Braden et al. 2001). We tested for differences in the distribution of individuals with stage class across the three streams.

Microhabitat assessment

To test the relationship between basilisk stage class and microhabitat we recorded the amount of vegetative cover (including dead and living stems with and without foliage) around each resting lizard. Microhabitat was categorized as open (no vegetation within 2 m), shade (vegetation 1 – 2 m from lizard) and cover (vegetation within 1 m). We used a chi-square test to determine whether stage class was independent of microhabitat (excluding stage class 3, which was too infrequent for analysis).

Mortality and natality

We calculated the population growth rate ($\lambda = Nt/Nt\text{-}1$) and proportion of individuals in each stage class for the three streams. We tested for density-dependence in basilisk population fluctuations over the past 5 years using a linear regression of population growth rate on Nt-1.

We constructed a Lefkovitch stage-based model to summarize population attributes and to help estimate stage-specific survivorships and fecundities for 2002. Fecundity of stage 3 and survivorship of stage 1 to 2 were estimated as $N1_t/N3_{t-1} + N2_t/N1_{t-1}$, respectively, where N1, N2 and N3 are number of individuals in stage classes 1 – 3, and t represents the current year. The survivorship from either stage 2 - 3 or stage 3 - 3 cannot be estimated directly from the demographic data (since both pools contribute to stage 3 in the next year), so we used Van Devender's estimate of 40% (1983) for stage 3 survivorship and solved for survivorship from stage 2 to stage 3. Streams 1 and 2 had more individuals of stage 2 in 2002 than there were individuals in stage 1 in 2001, which is impossible without immigration. Therefore, we extended the stage-based model to allow for immigration into stage 2. To estimate immigration, we used 2001 data for survivorship from stage 1 to 2, 2002 data for fecundity of stage 3 to 1, and iterated the model to calculate the amount of immigration that was needed to achieve the observed population growth rate.

TABLE 1. Proportion of individuals in three stage classes of basilisk populations in three riparian habitats over five 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	2002	1998	1999	2000	2001	2002	199-8	1999	2000	2001	2002
Stage 1	0.66	0.55	0.76	0.47	0.49	0.56	0.49	0.28	0.10	0.25	0.58	0.56	0.58	0.18	0.42
Stage 2	0.22	0.34	0.20	0.46	0.44	0.30	0.41	0.52	0.50	0.55	0.28	0.36	0.21	0.45	0.50
Stage 3	0.12	0.11	0.04	0.07	0.07	0.13	0.11	0.20	0.40	0.20	0.14	0.08	0.21	0.36	0.08
Total	343	92	74	102	102	105	37	25	10	20	50	25	19	11	36

Results

Abundance, growth rate and age distribution

Estimates of the Rio Claro population size were the same in 2002 as in 2001 (102 basilisks), while Streams 1 and Stream 2 increased (Table 1): population growth rates (λ) = 1.00, 2.00 and 3.27, respectively. The basilisk populations in all three streams had declined sharply between 1998 - 1999 and remained low in 2000 (Fig. 1). The Rio Claro population began to rebound in 2001. The 2002 census showed the first population increase in Streams 1 and 2 since 1998 (Fig. 1). All three populations showed negative density dependence across the 5 years (Fig. 2). Unlike some previous years, the relative abundance of different stage classes did not differ between the Rio Claro and the two streams ($\chi^2 = 3.20$, df = 2, P = 0.20; Table 1).

There was no relationship between basilisk abundance and distance upstream in any of the three streams (P > 0.20 for all 3 correlations between distance and basilisks/50 m, n = 10 – 12 – 24 sections per stream). On the Rio Claro, but not either stream, more basilisks were observed in the morning than in the afternoon (140 vs. 102). Censuses of Streams 1 and 2 produced quite similar numbers in morning and afternoons (18 vs. 20, 27 vs. 36, respectively).

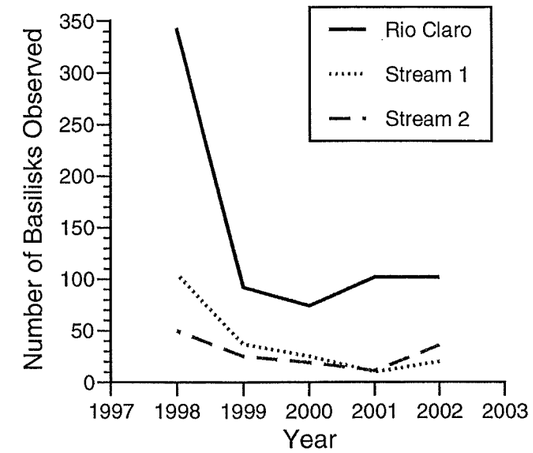

FIG. 1. Basilisk population size in three study sites from 1998 - 2002.

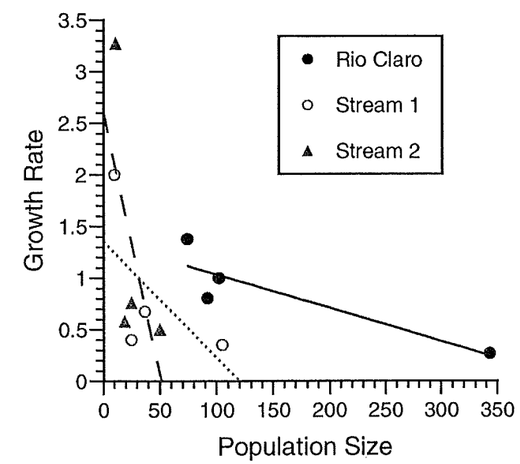

FIG. 2. Density dependence of *B. basiliscus* population growth rates at Rio Claro (solid line), Stream 1 (dotted line) and Stream 2 (dashed line): y = 1.36 - 0.003 (x), r^2 = 0.79; y = 1.36 - 0.01 (x), r^2 = 0.35; y = 2.61 - 0.05 (x), r^2 = 0.41, respectively. Replacement growth rate is λ = 1.

Microhabitat assessment

The occurrence of stage classes was related to cover type in the Rio Claro (Table 2; $\chi^2 = 13.89$, df = 2, P < 0.001; in particular). Stage class 1 individuals were over-represented in the open while stage 2 were over-represented in shade microhabitats (obs. vs. exp. = 35 vs 26 and 18 vs. 12.0, respectively). In Streams 1 and 2 (combined due to small samples), stage class was independent of cover type ($\chi^2 = 2.28$, df = 2, P = 0.32).

TABLE 2. Number of basilisks, by stage class, occurring in microhabitats classified as open, shade or cover on the Rio Claro or Streams 1 and 2.

	Rio Claro			Streams 1 & 2		
	open	shade	cover	open	shade	cover
Stage 1	35	7	8	14	4	0
Stage 2	13	18	14	14	9	3
Stage 3	1	2	4	5	4	2

Mortality and natality

In the Rio Claro, apparent survivorship from stage 1 - 2 increased between 2000 and 2001, while estimates of survivorship from stage 2 - 3 and fecundity (stage 3 - 1) declined from 2001 (Fig. 2). In streams 1 and 2, apparent fecundity increased from the previous year but remained very low (<20%) relative to populations on the Rio Claro (Fig. 3). We estimated immigration rates of stage 2 individuals into these streams as 2.2 and 2.6 respectively (per individual of stage 2 at t – 1; Fig. 3).

Discussion

Over the past 5 years, basilisk populations in the Rio Claro, Stream 1 and Stream 2 have been declining. In 2000 – 2001, Braden et al. (2001) recorded the first increase in a basilisk population on the Rio Claro. This year, we recorded the first population increases in Streams 1 and 2. This makes the extinction scenario of Braden et al (2001) seem less probable.

In Streams 1 and 2, there were more stage 2 individuals this year than stage 1 individuals last year, providing strong evidence for immigration. This is consistent with Braden et al.'s (2001) verbal characterization of Corcovado basilisks as a system of populations connected by migration. Fig. 3 represents one way to incorporate immigration into the stage-based model. We propose however that only Streams 1 and 2 exchange demographically meaningful numbers of immigrants. The large distance separating the Rio Claro from the other streams, along with rough topography, make lizard dispersal between the two seem unlikely. Future studies could investigate other possible demographic links by looking at tributaries of the Rio Claro.

Demographic patterns in space and time could be a result of interactions between dominance hierarchies and predation risk. We found that the smallest lizards occupied the most open habitats on the Rio Claro, implying that they should be most sensitive to predation, especially when larger stage classes are abundant. Conversely, the largest lizards on the Rio Claro may preferentially occupy cover habitats where they are less likely to be detected by predators (Aucoin et al. 2000). However, large size might create increased predation risk under some circumstances. For example, large lizards require more food and could be forced to move away from rivers in search of food during the dry years, presumably making themselves a more desirable prey item for ocelots. Age specific microhabitat preferences and patterns in predation risk (Berg et al. 1998) probably vary between streams. On Streams 1 and 2 there was no relationship between stage class and cover type.

We assumed basilisk length corresponded to age, but this relationship may not be exact due to sexual dimorphism (males larger than females). It is possible that we underestimated survivorship from stage class 2 to 3 by as much as half if stage class 3 females were so small that they were all counted as stage class 2. At present, we know of no way to sex basilisks in the field. It may be

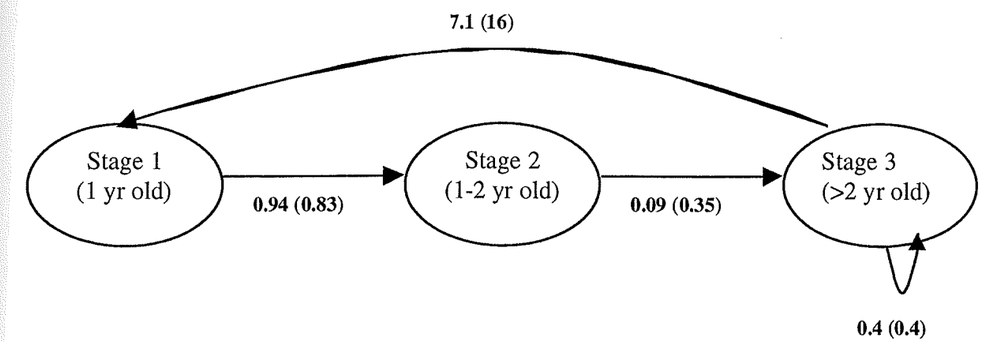

FIG. 3. Schematic life cycle diagram of survivorship and fecundity for the Rio Claro basilisk population in Corcovado National Park, Costa Rica. Arrows represent per capita flow rates (ind • ind^{-1} • year^{-1}) from one stage class to the next: survivorship from stage 1 to 2, from stage 2 to 3 and for those surviving within stage 3. The arrow from stage 3 to 1 represents fecundity. Values are estimates for 2002 with estimates for 2001 in parentheses.

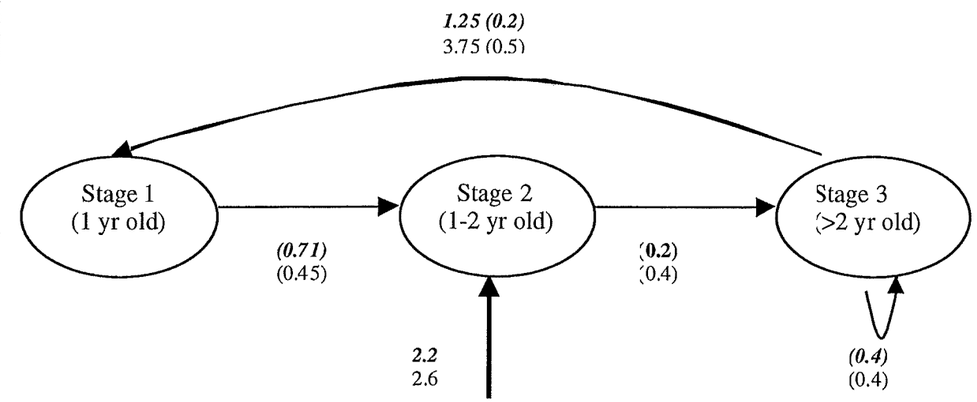

FIG. 4. Schematic life cycle diagram of survivorship and fecundity for the Stream 1 and Stream 2 basilisk populations in Corcovado National Park, Costa Rica. Arrows represent per capita flow rates (ind • ind^{-1} • year^{-1}) from one stage class to the next: survivorship from stage 1 to 2, from stage 2 to 3 and for those surviving within stage 3. The arrow from stage 3 to 1 represents fecundity. Values are estimates for 2002 with estimates for 2001 in parentheses.

that sexual dimorphism is minor until individuals reach reproductive age (stage class 3), in which case this is not a problem for sampling. Patterns of sexual dimorphism could be evaluated by capturing, sexing, and measuring a subset of basilisks.

We found evidence for negative density dependence in all three streams. Obviously this pattern was strongly influenced by the large population decline from 1998 to 1999. Since we do not have demographic data from before 1998, we cannot judge where the recent decline fits into greater trends in the population. Continued long-term data should clarify which factors influence which life stages of basilisk populations from year to year, and allow for the continued refinement of populations models that will help us understand how multiple demographic processes interact to produce vertebrate population dynamics in nature.

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