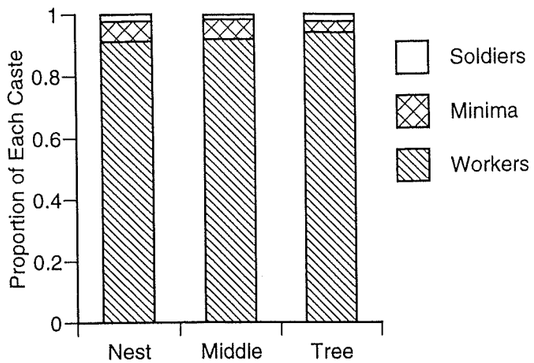

Fig. 1. Proportion of each caste at three positions along the foraging trail. There is no significant difference in the proportions of each caste.

minima) is evenly distributed along the trails. Alternatively, there may be plasticity in the behavior of each class. For example, we observed soldiers clearing trails and carrying leaves, which means that they would patrol the entire length of the trail. Dickinson et al. (1998) also found no difference in the dispersion of soldiers along foraging trails. It is also plausible that there is no mechanism (e.g., caste-specific pheromones) by which *A. colombica* colonies generate single caste aggregations. If this is the case, a constant proportion of castes would be expected along the trail. Minima, however, may be more concentrated in the nest for colony maintenance.

Literature Cited

Dickinson, S. W., A.M. Eaken, D. L. Poulin, and K. E. Weir. 1998. *Atta colombica* caste distribution along foraging trails. Pp. 60-61 *in* E. S. Berg and R. F. Douzinas, editors. Dartmouth Studies in Tropical Ecology. Hanover, New Hampshire, USA.

Stevens, G. C. 1983. *Atta cephalotes*. Pp. 688-691 *in* D.H. Janzen, editor. Costa Rican Natural History. Chicago: University of Chicago Press.

Wetterer, J. K. 1994. Forager polymorphism, size matching, and load delivery in the leaf-cutting ant, *Atta cephalotes*. Ecological Entomology. **19**, 57-64.

Population declines and changes in demographic structure of basilisk lizards (*Basiliscus basiliscus*) along three tropical streams

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Abstract: In 1998, three populations of the riparian basilisk lizard (*Basiliscus basiliscus*) were censused to estimate the demographic parameters of stage-specific survivorship and fecundity. We resurveyed these populations one year later, in 1999, and found a large (>50%) decline in abundance. The simultaneous decline in all three spatially separated populations suggests exogenous forces, though the specific causal mechanisms for the decline were not tested. Additionally, the 1998 study made two main assumptions: (a) population growth rates (λ) are at replacement, and (b) the populations have a stable stage distribution (SSD). Our data show that the assumption that the populations had an SSD may be valid, but the assumption that λ=1 is not.

Key Words: Jesus Christ lizards, population model, endogenous forces, exogenous forces

Introduction

Basilisk lizards (*Basiliscus basiliscus*) are common iguanids on riverbanks in the lowland forests of Central America. They are large (males up to 1 m in length), active lizards with the ability to run on water for up to 20 m (Van Devender 1983). They can live at very high densities (up to 400 individuals per hectare), which makes them an ideal organism for population studies.

Berg et al. (1998) surveyed basilisk populations along three separate streams in Corcovado National Park, Costa Rica in February 1998. We resurveyed these populations one year later in order to measure the population growth rates and to empirically refine the estimates of stage-specific survivorship and fecundity that the previous investigators had derived from a stage-based model. Development of their model relied on two main assumptions. The first was that the population was neither growing nor declining (λ=1). The second was that the proportion of individuals in each stage class was constant from year to year; in other words, the populations were considered to have a stable stage distribution (SSD). With two years of data, we could test their assumptions that λ=1 and that the populations were at SSD.

Methods

On the afternoons of 5-7 February 1999, we censused the populations of basilisk lizards living on three rivers near the Sirena Biological Station, Corcovado National Park, Costa Rica. We censused the Río Claro from 200 m inland from the mouth to 1400 m upstream. We censused this river twice to ensure that our census results were repeatable. The first census yielded 68 individuals, the second 96. For analysis, we used the survey with the larger estimate, because we knew at least 96 individuals existed in the population. In addition, we censused 500 m upstream from the intersection of Stream 1 with the Pavo trail (3.1 km north of Sirena). On Stream 2, (1.1 km north of Sirena), we censused 600 m upstream of its intersection with the Pavo trail. These were the same stream segments sampled by Berg et al. (1998).

To census these populations, we replicated as closely as possible the methods of Berg et al. (1998). In each river, we sampled 50 m transects, counting and assigning size classes to each basilisk visible from the water's edge. We did not census further inland from the river, because Berg et al. (1998) did not find any basilisks further than 5 m from the river edge. On the Rio Claro, each bank was individually scanned by one person walking upstream at the edge of the river. For the other two smaller streams, one person scanned both banks while walking up the middle of the stream. Size class 1 individuals were estimated visually to be those < 20 cm long (including tail), and were assumed to be young of the year; size class 2 individuals were between 20 and 40 cm and considered to be juveniles(1-2 yrs old); and size class 3 individuals were > 40 cm in length, and assumed to be reproductive adults.

Using our census data and the 1998 data from Berg et al., we constructed a Lefkovitch (stage-based) matrix to better understand the changes in stage-specific survivorship and fecundity of the populations between 1998 and 1999. We had empirical estimates of: (a)

survivorship of yearlings to juveniles (stage 1 in 1998 to stage 2 in 1999); (b) the number of yearlings produced by each reproductive (stage 1 in 1999 from stage 3 in 1998); and (c) the change in population size over the past year (N_{1999}/N_{1998}). We used this model to better estimate the survivorship of adults (stage 3 in 1998 to stage 3 in 1999) and juveniles (stage 2 in 1998 to stage 3 in 1999).

Results

We found that all three populations of *B. basiliscus* had declined sharply since 1998 (Fig. 1). Using the differences in abundance between years, population growth rates were calculated to be much less than 1 (Rio Claro = 0.28, Stream 1 = 0.35 and Stream 2 = 0.50). The relative proportions of individuals in each stage class in 1999 changed slightly from 1998 estimates (Table 1). However, these differences were not significant (G-Test, X^2= 3.06, df=2, P=0.22), suggesting that the populations may be at SSD.

Vital rates were dramatically reduced in 1999, compared to 1998. For all three populations, survivorship from stage class 1 to stage class 2 declined to about one half of 1998 estimates (Fig. 2). Survivorship probabilities for stage class 2 to stage class 3 and stage class 3 to stage class 3 were approximately 30 percent of the 1998 estimates (Fig. 2). Similarly, our estimate of fecundity (stage class 3 to stage class 1) declined to about one third of the estimates of 1998 (Fig. 2).

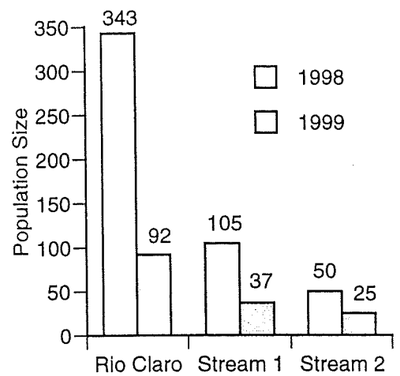

Fig. 1. 1998 and 1999 abundances for 3 populations of *Basiliscus basiliscus* at Parque Nacional Corcovado, Costa Rica. 1998 data from Berg et al. (1998).

Table 1. Size class distributions for three populations of *Basiliscus basiliscus* in Corcovado National Park, Costa Rica in 1998 (from Berg et al. 1998) and in 1999. There was no significant difference in stage distributions between years (see text).

	Rio Claro		Stream 1		Stream 2	
	1998	1999	1998	1999	1998	1999
Stage 1 (1 yr old	0.66	0.55	0.56	0.49	0.58	0.56
Stage 2 (2 yrs old)	0.22	0.34	0.31	0.40	0.28	0.36
Stage 3 (> 2 yrs old)	0.12	0.11	0.13	0.11	0.14	0.08

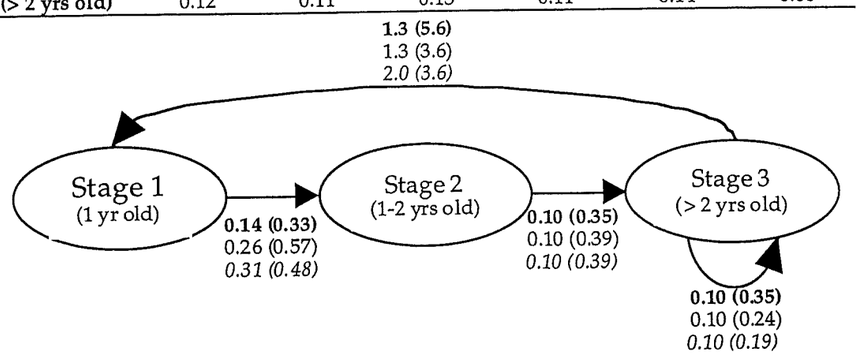

Fig. 2. Life cycle diagram for three populations of *Basiliscus basiliscus* a t Corcovado National Park, Costa Rica (**Río Claro**, Stream 1, *Stream 2*; 1998 rates in parentheses). Survivorship from Stage 1 to Stage 2 and fecundity of Stage 3 to Stage 1 derived from 1998 and 1999 census data. Survivorship from Stage 2 to Stage 3 and Stage 3 to Stage 3 estimated with a Lefkovitch matrix (see text).

Discussion

In the one year since the 1998 census, all three *B. basiliscus* populations had dramatically decreased by 50 to 72%. It seems implausible that the three populations independently experienced declines due to endogenous forces. Migration, the only mechanism able to demographically link the three populations, is probably a rare event in this species, as Berg et al. (1998) found no basilisks further than 5 m from any river edge. It also seems unlikely that basilisks would move downstream and along coastal beaches to another stream.

We therefore propose that some exogenous force was probably responsible for the decline of the *B. basiliscus* populations. Increased precipitation is one environmental factor that could cause substantial declines in *B. basiliscus* populations, as flooding can be a major source of egg mortality (Van Devender, 1983). The frequency of flooding may have been higher in 1998, a particularly wet La Niña year. This mechanism is consistent with the decrease in fecundity (stage class 3 to stage class 1 transition) we observed, which was between 33 - 50% that of the 1998 estimates. However, survivorship for all stages also decreased to about one third of the 1998 estimates, indicating that mortality of juveniles and adults, and not only reproduction, contributed to the observed declines.

Because we had two years of data, we did not need to make the same assumptions in our study that Berg et al. did in 1998. Our data show that Berg et al.'s assumption that the populations had an SSD may be valid, but since these populations have greatly declined since 1998, the assumption that λ=1 is not. Both studies made several additional assumptions that will require further testing: (a) stage 1 corresponds to age 1, and all surviving individuals in stage 1 move to stage 2 in the next year; (b) stage 2 corresponds to age 2, and all surviving individuals in stage 2 move to stage 3 in the next year; and (c) only individuals in stage class 3 reproduce. This last assumption is tenuous, since Van Devender (1983) reports that male sexual maturity in this species may occur by year 1 and males may sneak matings before they achieve dominance.

In both 1998 and 1999, survivorship probabilties did not differ drastically between age classes. In an organism with indeterminate growth, like the basilisk lizard, it is uncommon to have equal mortality on all size classes: it is more common to out-grow predators, and therefore have increased survivorship in larger stage classes (Begon et al. 1990). Given our observations to the contrary, we suspect the probability of detecting the size class 3 individuals was less than that of the smaller size classes. This may have introduced a systematic bias into our estimates of survivorship and fecundity. Such a bias, however, does not affect our finding that the three *B. basiliscus* populations declined between 1998 and 1999.

If the frequency of such population declines has been relatively high historically, then *B. basiliscus* may have evolved certain life history traits to allow a quick rebound to pre-disturbance abundances. In contrast, if these declines have been relatively infrequent, then the population may not have evolved such mechansims for rapid population growth, and successive rapid disturbances could cause localized extinction. The frequency of population fluctuations and the population's resilience after disturbance need to be studied further, as they have important implications for both the population dynamics and life history strategies of *B. basiliscus*.

Literature Cited

Begon, M, Harper, J. L. and Townsend, C. R., Ecology. Pp. 474-475. Cambridge, MA, USA.

Berg, E. S., S. C. Braman, B. W. Wright and M. P. Ayres. We Found Jesus Christ in Corcovado: Stream Size and the Population Structure of *Basiliscus basiliscus*. Pp. 82-85 *in* E. S. Berg and R. F. Douzinas, eds. Dartmouth Studies in Tropical Ecology. Hanover, NH, U. S. A.

Van Devender, R. W., *Basiliscus basiliscus* (Chisbala, Garrobo, Basilisk, Jesus Christ Lizard). Pp. 379-380 *in* D. H. Janzen, ed. Costa Rican Natural History. University of Chicago Press. Chicago, IL, U. S. A.