

## Stage-based models of Jesus Christ lizards don't walk on water

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**Abstract:** Basilisk lizards (*Basiliscus basiliscus*) are common residents of riparian areas in Pacific lowland forests of Central America. We censused basilisk populations on three streams in Parque Nacional Corcovado, Costa Rica, adding a sixth year of data to a long term study begun in 1998. We found that all three populations have remained relatively stable since the 1998-1999 population crash. Previous studies have projected future population sizes of these lizards with a Lefkovich Stage-based model, despite uncertainty in transition values and incomplete life history information. We identified five alternate model structures, all consistent with data from the literature and from this long-term study. In general, the alternative models generated projections broadly similar to the original model. However, none of the models performed particularly well, even when tests were limited to one-year projections based on data from the previous two years. Our understanding of Corcovado basilisk populations is limited by basic demographic information.

**Key Words:** *Basiliscus basiliscus*, extinction, temporal variability

## INTRODUCTION

The Jesus Christ lizard (*Basiliscus basiliscus*) is one of the most common large lizards in Costa Rica (Savage 2002). It occupies riparian habitats in lowland Pacific forest and is named for its ability to run up to 20 m across water to avoid predation (Van Devender 1983). Over the past five years, basilisk populations have been monitored on the Rio Claro and two smaller streams in Parque Nacional Corcovado, Costa Rica (Berg et al. 1998; Babineau and Paine 1999; Aucoin et al. 2000; Braden et al. 2001; Kinney et al. 2002). Between 1998 and 1999, a basilisk population crash was reported (Babineau and Paine 1999) and researchers suggested that the Jesus Christ lizard might be at risk of extinction (Aucoin et al. 2000). This conclusion follows in part from using a Lefkovich stage-based model to project future population sizes (see Berg et al. 1998). However, this model relies upon very limited demographic information (Van Devender 1983) and a number of critical assumptions (Berg et al. 1998; Babineau and Paine 1999).

In addition to continuing the long-term study, we explored a number of alternate, but plausible basilisk population structures. First we wanted to examine how different reproductive strategies might

influence model projections. For example, when large males are in low densities, mating systems may shift due to a breakdown in dominance hierarchy (Van Devender 1983). Second, we questioned how sexual dimorphism might influence the size-age assumption of Berg et al. (1998). Their original model assumes that only the largest individuals (Stage 3) are reproductive, but Kinney et al. (2002) suggested that the Stage 3 size class is occupied solely by large males. If this is true, then all reproduction would have to be accomplished by Stage 2 females. In fact, Savage (2002) states that female basilisks reach sexual maturity at 20 months or 13.5 cm (snout to vent length), which could include all Stage 2 females. Clearly, we need to reevaluate assumptions regarding the demographic structure of Corcovado basilisk populations. The main objective of our study was to determine whether alternative model structures founded on different demographic assumptions more accurately project population numbers of the Jesus Christ lizards over one year.

## METHODS

**Continuation of long-term population monitoring:** On 4 and 5 February 2003, we censused basilisk lizard populations



along the Rio Claro and two smaller streams near the Estación Biológica Sirena, Parque Nacional Corcovado, Costa Rica. Stream 1 and Stream 2 were located 3.3 km and 1.1 km from the station, respectively, crossing the Sendero Pavo. For consistency, we followed the sampling and size classification procedures of Babineau and Paine (1999). Briefly, we counted all lizards seen along twelve 100 m transects on the Rio Claro above the estuary. We also sampled along five 100 m transects on Stream 1 and six 100 m transects on Stream 2. We categorized lizards < 20 cm (total estimated length) into Stage 1, 20 – 40 cm into Stage 2 and > 40 cm into Stage 3, using visual estimates from the minimum possible distance, before lizards took flight.

We then calculated the temporal variability (stability) of basilisk populations following the 1998–1999 population crash as the coefficient of variation (CV) over time, where  $CV = SD / \text{mean population size}$ .

**Original model structure:** To construct a three-stage Lefkovich model, we estimated survival and fecundity from 2002 and 2003 census data. Stage 1 and Stage 2 survivorship, fecundity and growth rate ( $\lambda$ ) were estimated as in previous years. We estimated annual survivorship from Stage 1 to Stage 2 as  $N_{2,t} / N_{1,t-1}$ , where  $N_1$ ,  $N_2$  and  $N_3$  are the number of individuals in Stages 1, 2, and 3, respectively. We assumed  $N_{3,t-1} \rightarrow N_{3,t}$  survivorship was 0.4, based on estimates of adult survivorship for basilisks in Guanacaste, Costa Rica (Van Devender 1983). Survivorship from Stage 2 to Stage 3 was estimated as  $[N_{3,t} - (N_{3,t-1} \times 0.4)] / N_{2,t-1}$ . Thus, this estimate is dependent on the assumption that adult survivorship (Stage 3  $\rightarrow$  Stage 3) is fixed at 0.4. We estimated fecundity as  $N_{1,t} / N_{3,t-1}$ . We estimated population growth rate ( $\lambda$ ) as the total population divided by the total population of the previous year.

**Alternative model structures:** To explore the consequences of the original

model's assumptions, we proposed five alternative models for the basilisk population in Rio Claro (Fig. 1). Data from Stream 1 and Stream 2 were not included, because basilisk population densities were so low there ( $n = 57$  and  $22$ , respectively). Models 2, 4, and 6 relax the assumption that Stage 2 represents 2 year-old basilisks. In these models, we allowed 0.5 of the surviving Stage 2 individuals to remain in Stage 2. Models 3 – 6 assumed that within this class of models, Stage 2 females reproduce. Models 5 and 6 examined the consequences of alternative assumptions about sexual dimorphism in body size. Here, we assumed that Stage 3 individuals were actually all male and that Stage 2 females were responsible for all reproduction.

We examined the consequences of assumptions in all six models by comparing their projections to actual basilisk census data. We ran the models using transition probabilities estimated from 1999 and 2000 population data and compared one-year projections to actual 2001 data. We then ran all models again using 2001 and 2002 data for transition probability estimates and compared one-year projections to 2003 census data. We do not present models using transition probabilities from 1998 and 1999 census data; they projected almost immediate basilisk extinction.

We also did not estimate transition probabilities using population changes from 2000 to 2001, because estimated Stage 3  $\rightarrow$  Stage 3 survivorship was lower than our assumed survivorship of 0.4, even if survivorship from Stage 2 to Stage 3 was assumed to be zero. While there are ways one could attempt to work with these data, they would require jettisoning the value of adult survivorship obtained from the literature (Van Devender, 1983). This assumption (based on data from Guanacaste) has been consistent for all past modeling of Corcovado basilisk populations. It could be informative to explore the effects of varying

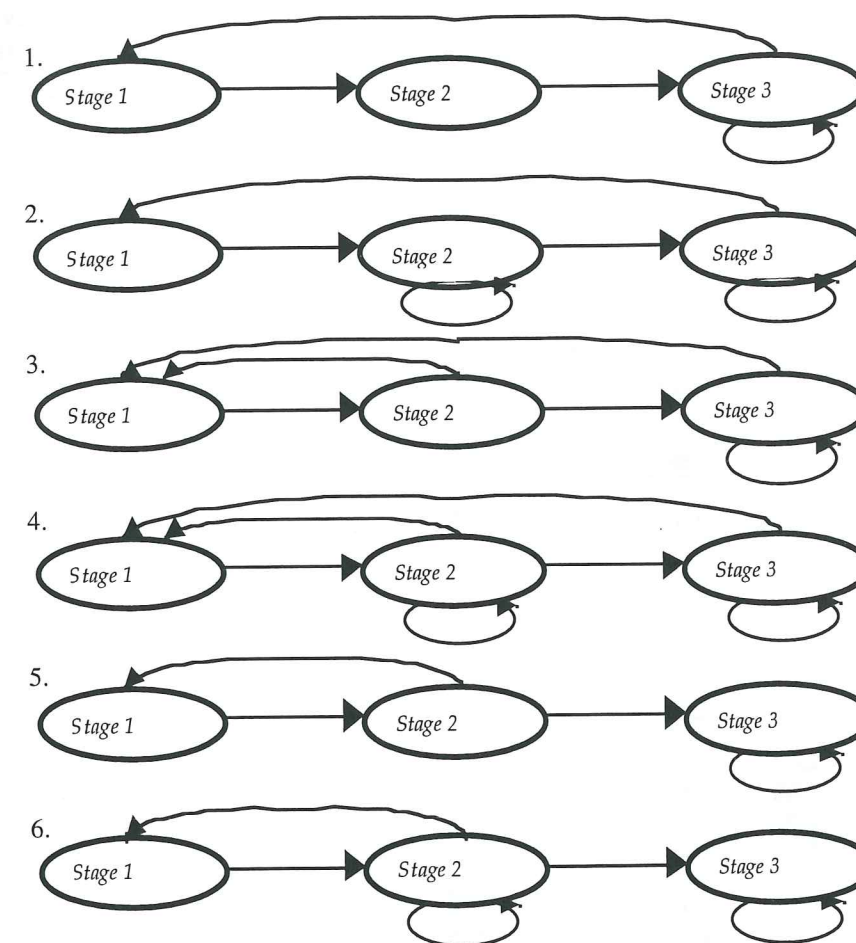


FIG. 1. Lefkovich stage-based models used to project basilisk populations. Model 1 is the original model (see Berg et al. 1998). Models 2, 4, and 6 allow for survivorship within Stage 2. Models 3, 4, 5 and 6 incorporate reproduction into Stage 2. Models 5 and 6 eliminate reproduction from Stage 3.

that value, especially since we expect basilisks may respond differently to the conditions at Corcovado than in Guanacaste. It is important to note, however, that this 0.4 value is the only parameter in our models that is based on actual demographic (dynamic) studies of basilisks. Such data are unavailable for Corcovado.

## RESULTS

**Continuation of long-term population monitoring:** The number of basilisks censused in the Rio Claro decreased from 102 to 85 between 2002 and 2003 resulting in a population growth rate ( $\lambda = N_t / N_{t-1}$ ) of 0.83 (Fig. 2). This decline was associated

with a 9% reduction in estimated Stage 1  $\rightarrow$  Stage 2 survivorship (Table 1). In Stream 1, basilisk densities were the highest recorded since the population crash of 1998–1999 (Table 1) and resulted in a population growth rate ( $\lambda = N_t / N_{t-1}$ ) of 2.85. This increase in basilisk densities was associated with an estimated 31% increase in Stage 1  $\rightarrow$  Stage 2 survivorship. In contrast, basilisk densities declined by 39% in Stream 2 ( $\lambda = 0.61$ ). This decline was associated with 33% drop in estimated annual fecundity (Table 1).

Since the basilisk decline in 1998–1999, populations in the Rio Claro have been relatively stable, as evidenced by low temporal variability ( $CV = 0.14$ ). In contrast,



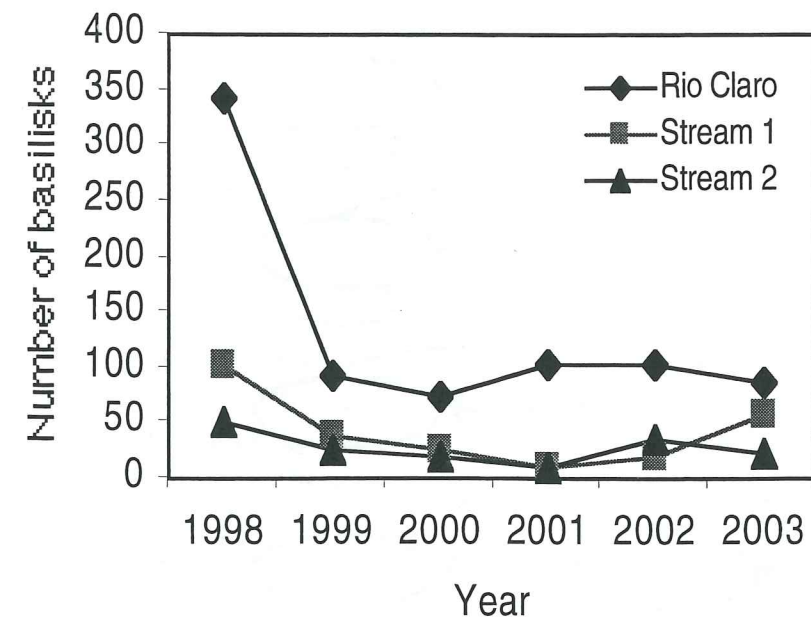


FIG. 2. Abundance of basilisk lizards (*Basiliscus basiliscus*) in three rivers in Parque Nacional Corcovado, Costa Rica.

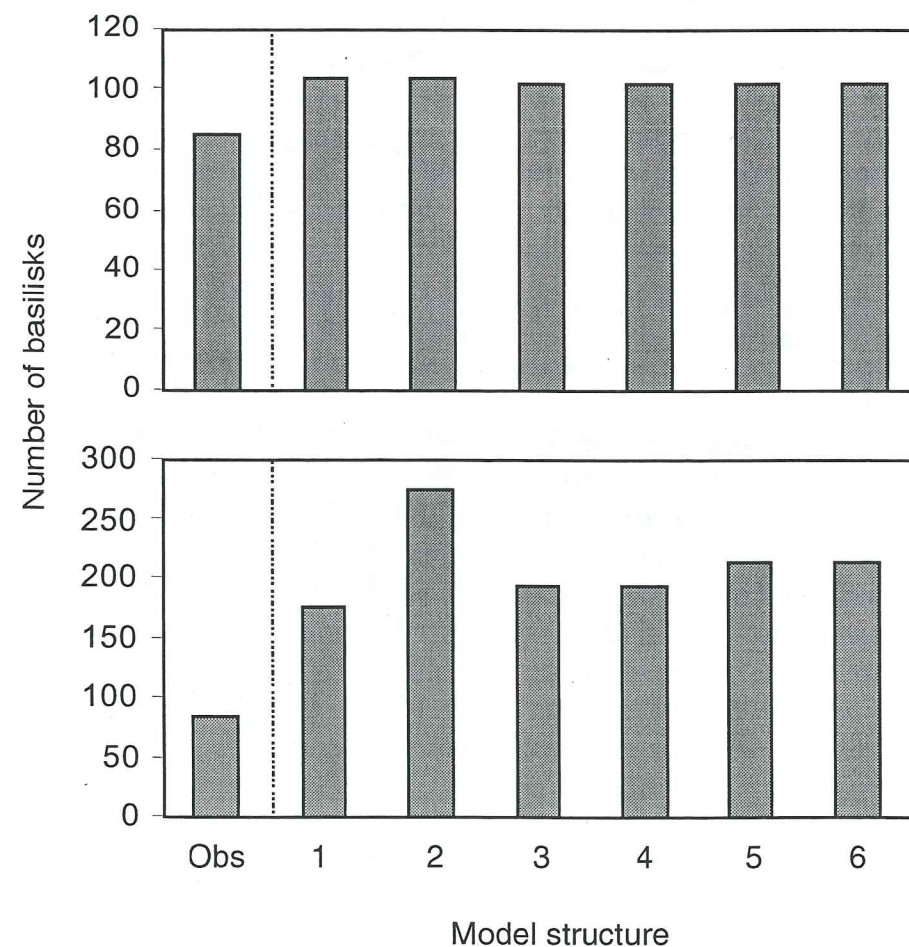


FIG. 3. Projected and observed (Obs) numbers of basilisk lizards (*Basiliscus basiliscus*) on the Rio Claro, Parque Nacional Corcovado, Costa Rica for six different stage-based population structures (see text for details). We used Lefkovich models to project 2001 numbers from 1999–2000 census data (upper panel) and 2003 numbers from 2001–2002 census data (lower panel). Model structures are illustrated in FIG. 1.

TABLE 1. Number (#) and proportion (%) of individuals in three stage classes of basilisk populations in three rivers over six years in Parque Nacional Corcovado, Costa Rica. Data are from censuses with visual estimates of total length. Size classes are: Stage 1 (< 20 cm), Stage 2 (20–40 cm), Stage 3 (> 40 cm).

River	Stage	1998		1999		2000		2001		2002		2003	
		#	%	#	%	#	%	#	%	#	%	#	%
Rio Claro	1	226	0.66	51	0.55	56	0.76	48	0.47	50	0.49	47	0.55
	2	75	0.22	31	0.34	15	0.20	47	0.46	45	0.44	30	0.35
	3	41	0.12	10	0.11	3	0.04	7	0.07	7	0.07	8	0.09
Total #		343		92		74		102		102		85	
Stream 1	1	59	0.56	18	0.49	7	0.28	1	0.10	5	0.25	3	0.05
	2	32	0.30	15	0.41	13	0.52	5	0.50	11	0.55	46	0.81
	3	14	0.13	4	0.11	5	0.20	4	0.40	4	0.20	8	0.14
Total #		104		37		25		10		20		57	
Stream 2	1	29	0.58	14	0.56	11	0.58	2	0.18	15	0.42	2	0.09
	2	14	0.28	9	0.36	4	0.21	5	0.45	18	0.50	18	0.82
	3	7	0.14	2	0.08	4	0.21	4	0.36	3	0.08	2	0.09
Total #		50		25		19		11		36		22	

basilisk populations in Stream 1 and Stream 2 were more dynamic ( $CV = 0.61$  and  $0.41$ , respectively).

**Alternative model structures:** In general, we found that the six model structures were ineffective at predicting population densities of basilisk lizards, even when forecasts were limited to one year (Fig. 3). Using the 2001–2002 data, all six models consistently overestimated 2003 population densities. Similarly, using 1999–2000 data, all models overestimated 2001 basilisk numbers by at least 100% and in one case by more than 200% (model 2). Variation in model structure did not dramatically affect projections of basilisk population numbers.

## DISCUSSION

**Continuation of long-term population monitoring:** From 1998–1999, the abundance of basilisk lizards decreased markedly in the Rio Claro, Stream 1, and Stream 2 (Babineau and Paine 1999). This led to the suggestion that basilisks may be

declining with potential risk of extinction (Babineau and Paine 1999, Braden et al. 2001). We suggest that the trends since 1999 indicate there is no immediate risk of local extinction. Since the 1998–1999 crash, populations have oscillated between positive and negative population growth. Populations of basilisks have been relatively stable over the past five years. Stream 1 and Stream 2 may potentially be at greater risk because they have smaller numbers and have been more variable over time. But, it is difficult to draw definitive conclusions about population dynamics by examining only six years of census data, especially with no independent estimates of survival or reproduction.

**Alternative model structures:** Our results illustrate the limitations of the Lefkovich stage-based model, based on annual census data, to project future populations of the Jesus Christ lizard. This is due in part to the reliance of the model on several key assumptions that we cannot test with available data. The assumptions of  $\lambda = 1$  and stable stage distribution (required to estimate transition rates from stage structure



data) are clearly violated, as can be readily seen in the census data (Babineau and Paine 1999; Aucoin et al. 2000; Table 1).

Assumptions regarding survivorship are critical. Specifically, this long-term study has been relying on an adult survivorship value of 0.4 (Van Devender 1983), which is clearly inconsistent with some years of our census data. For example, for 1998–1999 and 2000–2001,  $N_{3_t}/N_{3_{t-1}}$  was  $< 0.4$ . Because  $N_{3_t}$  includes both survivors from  $N_{3_{t-1}}$  and advancement from  $N_{2_{t-1}}$ , we cannot estimate  $N_{2_{t-1}}$  without a plausible estimate of adult survivorship. This problem was recognized by Braden et al. (2000), but they reconciled the issue by incorporating an immigration term into the model — even though there is strong evidence indicating that basilisks do not venture far from their local stream habitats (Berg et al. 1998). We have no direct estimates of immigration rates. It is clear that modeling efforts are limited by basic knowledge regarding the demography of basilisk lizards at Corcovado.

In addition to our uncertainty about actual survivorship, we also lack data on development rates and maturation. The original Lefkovich model (Berg et al. 1998) assumed that basilisks spend one year as Stage 2 individuals and then advance to reproductive maturity in Stage 3. While this may have been appropriate for an exploratory model at that time, it would be imprudent to base continued modeling effects on assumptions for which we have no empirical support. We found that alternate model structures (incorporating different assumptions regarding maturation rates) sometimes generated different outcomes. Nevertheless, all of the Lefkovich models were generally ineffective at projecting basilisk populations (Fig. 3). More complex (but perhaps more realistic) models would incorporate density dependence and environmental

stochasticity. However, models of density dependence, in particular, are even more demanding in terms of empirical estimates. Finally, Lefkovich modeling to date has used only two years of prior data, and thus does not take full advantage of our long-term census data. We found that projections were particularly sensitive to which pairs of consecutive years were used to estimate transition rates.

We suggest that future investigators exercise caution when interpreting Lefkovich model output. Actual data on individual survivorship and fecundity of basilisks would make the interaction between modeling and empirical research more productive and rewarding. It would be useful to explore possibilities for mark-recapture estimates of survivorship and techniques for sexing individual lizards.

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