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SURVIVORSHIP RATES OF ADULT *ANOLIS MARIARUM* (SQUAMATA: POLYCHROTIDAE) IN TWO POPULATIONS WITH DIFFERING MEAN AND ASYMPTOTIC BODY SIZES

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ABSTRACT

We compared adult survivorships in two populations of the lizard Anolis mariarum with different mean and asymptotic body sizes to examine one prediction of age-specific mortality theory; that populations that experience higher adult mortality should exhibit earlier maturation and smaller adult body sizes. We used a maximum likelihood approach to evaluate different survivorship models and model-averaging to estimate survivorship and capture probabilities for each site and sex. Relative tail length did not affect survivorship rates of adults in these two populations, but body size was related to survivorship, with the largest individuals at the time of first capture having lower survivorship rates, so body size was included as a covariate in some of the models examined. Analyses revealed that males at both sites had higher survivorships than females, but there were no differences among the sites in survivorship rates or capture probabilities for either sex. The differences in body sizes documented for these sites still could represent life history adaptations to differences among the sites in mortality rates in the egg or juvenile stages of the life cycle, or may represent a case of phenotypic plasticity to differing environmental conditions, but they appear not to be related to differences in adult survivorships. The estimates of annual survivorships (11.7% to 21.2%) were high for a small, mainland Anolis, and this is the first report of survivorships of male anoles exceeding those of females.

KEYWORDS: Survivorship; Body size; Sex differences.

INTRODUCTION

There is growing evidence that multilocus quantitative phenotypic traits show greater inter-population divergence than do neutral molecular markers (Merilä & Crnokrak, 2001; Reed & Frankham, 2001), implying not only that natural selection on phenotypic traits in

natural populations is pervasive, but also that it is directional (vs. stabilizing), leading each population to adapt to its own local conditions (*i.e.*, Baker, 1992; Waldmann & Andersson, 1998). Recently, Bock, *et al.* (2009) applied a different approach by comparing sites for many quantitative traits (instead of only the “trait of interest” vs. neutral molecular markers) in six populations of the

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Polychrotid lizard *Anolis mariarum* Barbour 1932 in the Cordillera Central of Colombia. They quantified the degree of micro-geographic divergence in body size, different orthogonal aspects of body shape variation, and lepidosis for both males and females. They argued that those traits that differed by comparable magnitudes but in differing patterns among sites likely represented cases of random divergence among isolated demes via genetic drift, while those traits that exhibited the greatest amounts of divergence and were correlated with environmental differences among sites were more likely to be aspects of the phenotype that have been influenced by divergent selection pressures yielding local adaptations to each site. Their study found that all traits differed significantly among the sites in both sexes, but attempts to correlate these differences with two environmental variables (mean annual temperature and mean annual precipitation) indicated that only body size was related to precipitation levels at each site, implying that body size had been the target of past natural selection (Bock, *et al.*, 2009).

However, differences among populations in mean and asymptotic body sizes could also be simply a phenotypic response to the different environmental conditions at each site. For example, sites that receive less rainfall might provide better thermoregulation opportunities to these high-elevation ectotherms, thereby improving their foraging and digestive efficiencies (Avery, 1994; Chen, *et al.*, 2003; Du, *et al.*, 2000; Ji, *et al.*, 1996; Van Damme, *et al.*, 1991; Zhang & Ji, 2004) and hence growth rates (Autumn & deNardo, 1995; Avery, 1984; Niewiarowski, 2001; Niewiarowski & Roosenburg, 1993). To inspect for this possibility, Bock *et al.*, (2009) conducted a capture-mark-recapture study of individually-marked lizards from their two most extreme sites (in terms of precipitation and body sizes), and also reared a small number of adult males from both sites in a common garden study in the laboratory. Despite the fact that the asymptotic body size of males at the wettest site was 7% less than at the driest site, growth rate data were equivocal, with males but not females growing faster at the driest site. When males from both populations were reared in the laboratory, growth rates for both populations increased, but did not differ significantly among groups. However, both groups attained the same asymptotic sizes in the laboratory as were documented for their populations in the field, reinforcing the conclusion that body size differences at these sites represent fixed, genetically-based local adaptations.

In the present study, we used the same capture-mark-recapture data sets collected by Bock, *et al.* (2009) to examine another potentially explanatory variable, by estimating adult survivorships in each population. On a

proximate level, if survivorships are lower for some reason at the wet site, mean body size would be expected to be smaller, and fewer (or no) individuals would be expected to attain the maximum body size for the species (although this would not explain the maintenance of a low asymptotic body size of individuals from this population when reared in the laboratory). In addition, on an ultimate level, life history theory predicts that selection would favor an earlier age/size at sexual maturity in populations that experience higher adult mortality rates (Abrams & Rowe, 1996; Gadgil & Bossert, 1970; Law, 1979; Reznick, 1982; Charnov & Berrigan, 1990; Reznick, *et al.*, 1990), and that the trade-off between investing in reproduction vs. growth also should produce smaller adults at sites with lower adult survivorships (Shine, 1980; Niewiarowski & Dunham, 1994). To examine these predictions, we report here estimates of survivorships obtained from maximum likelihood analyses of the capture-mark-recapture data sets for each site.

MATERIAL AND METHODS

Anolis mariarum occupies low vegetation in open (usually human disturbed) grasslands in the Cordillera Central of northern Colombia, from 1,300 to 2,700 m elevation (Páez, *et al.*, 2002; Palacio-B, *et al.*, 2006). The two populations examined in this study were from the Caldas (6°01'54"N, 75°36'02"W; 2,500 mm annual precipitation) and Santa Elena municipalities (6°17'22"N, 75°30'57"W; 1,600 mm annual precipitation) in the Antioquia Department (Figure 1). Bock, *et al.*, (2009) individually marked lizards at these two sites from 12 October 2004 until 1 April 2005, and a subset of their data, corresponding to seven visits to each site, were analyzed and are presented here. There were comparable time intervals between successive visits, with three visits during the wet season and four visits during the dry season for each site.

Individuals with snout-vent lengths (SVL) of 36 mm or less were classified as juveniles because it was impossible to reliably sex them based on external morphology. Of the 27 juveniles captured, 22 were not recaptured again and one was recaptured a second time while still in the juvenile size class. These individuals were eliminated from further analyses, and the remaining four juveniles that were later recaptured as sexable adults were retained. In total, the data sets analyzed in this study contained 99 individuals from Caldas (57 males and 42 females) and 100 individuals from Santa Elena (72 males and 28 females).

We used the Cormack-Jolly-Seber capture-mark-recapture model (Lebreton, *et al.*, 1992) to estimate

survivorships using Program MARK (White & Burnham, 1999). This software employs a maximum likelihood approach and decomposes the observed return rates of marked individuals into estimates of the two components of this parameter; survival probability (Φ) and capture probability (p ; symbols follow Lebreton, *et al.*, 1992). Factors thought to affect Φ and p were used to formulate alternative models. MARK uses information-theoretic methods to estimate the likelihood of each model (Anderson, *et al.*, 2000) and permits the use of a multi-model approach, in which Akaike weights are used to compute weighted overall estimates for Φ and p (Burnham & Anderson, 1998). This model-averaging approach permits evaluation of various models simultaneously, giving models with the larger Akaike weights greater influence on the overall model-averaged estimates.

Model averaging is appropriate only when the models adequately fit the data, and a common cause of lack of fit is violation of the assumption that Φ is homogeneous within groups included in the models (here, sites and/or sexes). Body size has been shown to influence return rates in other lizard species (Turner, 1977), so as a preliminary step, we ran pilot analyses on each of the four subsets of data (males and females from Caldas and Santa Elena), using SVL as an individual co-variate. In each analysis, we compared a linear model (to inspect for evidence that Φ was lower for either smaller, or for

larger, individuals), a non-linear model (to inspect for evidence that Φ was lower for both the smallest and largest individuals), and a reduced model that ignored the covariate SVL.

Another aspect of body size potentially related to survivorship in lizards is relative tail length (Downs & Shine, 2001; Fox & McCoy, 2000; Wilson, 1992). At both sites in this study, 38% of the individuals had experienced tail autotomy and were either in the process of regenerating or had already completely regenerated their tails. We therefore conducted an analysis to obtain an index of relative tail length at the time of first capture for each individual at each site to be used as a covariate in a second pilot survivorship analysis. We first conducted a two-way ANOVA of body size (SVL), with site and sex as main factors, and reconfirmed previous results (Bock, *et al.*, 2009) of significant body size variation among the sites ($F = 15.25$, $P \leq 0.001$), but failed to show evidence of sexual size dimorphism at either site ($F = 2.72$, $P > 0.10$). We therefore pooled data for both sexes at each site and regressed tail length on SVL, using data only from individuals with intact tails. Intact tail length was significantly correlated with SVL at both sites (Caldas, $R^2 = 0.63$, $P < 0.001$; Santa Elena, $R^2 = 0.85$, $P < 0.001$), so we used the regression equation for each site (Caldas, Tail length = $-0.9491 + 2.16395 \cdot \text{SVL}$; Santa Elena, Tail length = $-10.45 + 2.34854 \cdot \text{SVL}$) to calculate the residuals from this regression line not only for the individuals with intact tails in each population, but also for individuals with regenerating or regenerated tails. These residuals thus provided a continuous measure of the relative total tail length (intact tail, or tail base plus regenerated portion) for all individuals at each site. This linear covariate was used in models that compared estimated survivorships for each sex and site versus estimates of survivorship that ignored relative tail length at the time of first capture.

These analyses (*see* Results below) failed to show any effect of relative tail length on Φ , so subsequent analyses did not include this covariate. However, the analyses of the effects of body size on Φ showed that larger individuals had lower estimates of Φ , so SVL was retained as a covariate in some models of the main analysis.

In the main analysis, the pooled data set was used to inspect for the importance of three main effects; Site, Sex, and Time (differences in Φ or p among the seven sampling periods). We implemented 14 competing models that differed in whether survivorship and capture probabilities varied, or not, among the sites, sexes, and time intervals, and also in terms of whether SVL was included as a covariate (Table 1). Time effects in the models assumed that Φ and p were either constant across all sampling periods, variable across all sampling periods,

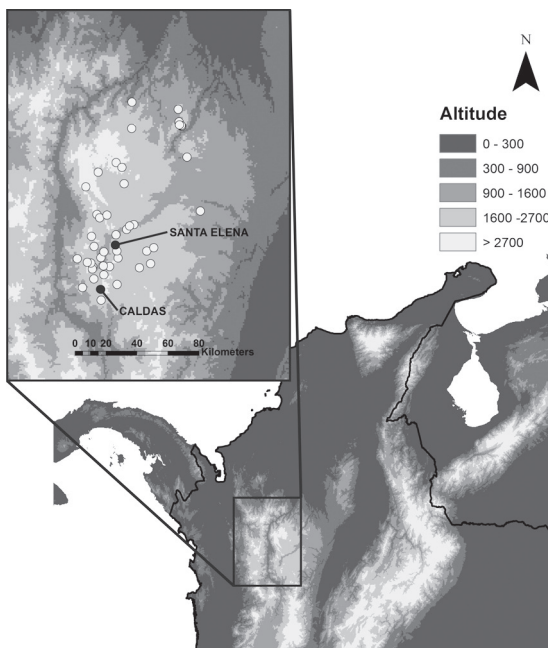


FIGURE 1: Documented distribution of *Anolis mariarum* in northern Colombia, with the location of the Caldas and Santa Elena study sites indicated by the filled circles.

TABLE 1: List of the 14 competing models analyzed in Program Mark for the pooled data set (males and females from both sites). The explanation defines each model in terms of the effects of time and body size (SVL) on survivorship (Φ) and capture probability (p).

Model	Explanation
$\Phi(\cdot)p(\cdot)$	Survivorship and capture probability were constant throughout the study
$\Phi(\text{Site})p(\cdot)$	Survivorship differed at the sites but capture probability was constant
$\Phi(\text{Site-SVL})p(\cdot)$	Survivorship differed at the sites (after adjusting for SVL) but capture probability was constant
$\Phi(\cdot)p(\text{Site})$	Survivorship was constant but capture probability differed at the sites
$\Phi(\text{Site})p(\text{Site})$	Both survivorship and capture probability differed at the sites
$\Phi(\text{Sex})p(\cdot)$	Survivorship of males and females differed but capture probability was constant
$\Phi(\text{Sex-SVL})p(\cdot)$	Survivorship of males and females differed (after adjusting for SVL) but capture probability was constant
$\Phi(\cdot)p(\text{Sex})$	Survivorship was constant but capture probability of males and females differed
$\Phi(\text{Sex})p(\text{Sex})$	Both survivorship and capture probability of males and females differed
$\Phi(\text{Site-Sex})p(\text{Site-Sex})$	Both survivorship and capture probability for each sex and site differed
$\Phi(\text{WetDry})p(\cdot)$	Survivorship differed in the wet vs. dry season, but capture probability was constant
$\Phi(\cdot)p(\text{WetDry})$	Survivorship was constant, but capture probability differed in the wet vs. dry season
$\Phi(\text{WetDry})p(\text{WetDry})$	Both survivorship and capture probability differed in the wet vs. dry season
$\Phi(t)p(t)$	Survivorship varied over all six time intervals and capture probability varied for all six recapture events (Full Cormack-Jolly-Seber model)

or different between sampling periods in the wet season (first three visits) and dry season (last four visits). Model fit in the analyses was evaluated using AIC scores as described in Johnson & Omland (2004), with the lowest score indicating the best fitting model and a $\Delta\text{AIC} > 2$ indicating substantial support for a real difference between models. After running all 14 models, weighted estimates of Φ and p for males and females at both sites were calculated.

RESULTS

Of the 199 adult *A. mariarum* captured in this study, 70 were recaptured one or more times (with a maximum of four recaptures), providing data for estimation of Φ and p for both sexes at each site. In the pilot analyses of the effect of relative tail length on survivorship rates, the model with the lowest AIC score was the least parameterized model (constant Φ and constant p , with no relative tail length covariate included) for all data sets (males and females at both sites), and only one of the eight models that included this covariate produced a $\Delta\text{AIC} < 2$, so we did not include relative tail length at the time of first capture as a covariate in the main analysis.

In the pilot analyses of the effect of body size on survivorship rates, the lowest scoring model for each sex/site was the least parameterized model (constant Φ and constant p , with no body size covariate included), but the four models that included SVL as a covariate of Φ also had relatively low AIC scores (2.2 for Caldas males, 2.1 for Santa Elena males, 1.4 for Santa Elena

females, and 0.5 for Caldas females), indicating that individuals that were large upon first capture exhibit lower survivorship rates. Thus, SVL was included in some models in the main analyses that compared survivorships of males and females at the two sites.

Four models in the main analyses had AIC values of less than 2 and that were lower than the least parameterized model (Table 2). All four of these models included Sex effects, while none included Site effects or differences in Φ or p as a function of Time or season. The model with the third lowest AIC score included SVL as a covariate of Φ . Consistent with these results, the model-averaged estimates of Φ and p (Table 3) indicated that these parameters differed among the sexes, but not the sites.

DISCUSSION

Contrary to our prediction, we found no evidence that adult survivorships were lower at the Caldas site, where mean and asymptotic body sizes were smaller. However, age-specific mortality theory also predicts that populations may differ in adult body sizes when juvenile mortality rates differ, with a life history shift towards delayed maturity, longer adult lifespan, and larger body sizes in sites where juvenile mortality rates are higher (Abrams & Rowe, 1996; Gadgil & Bossert, 1970; Law, 1979; Reznick, 1982; Charnov & Berrigan, 1990; Reznick, *et al.*, 1990). Unfortunately, it is difficult to examine this possibility in *A. mariarum*, given that it is extremely rare to encounter eggs or recapture marked juveniles.

TABLE 2: Selection table for fits of the 14 competing models of the capture-mark-recapture data (model explanations from Table 1).

Model	AIC	Δ AIC	AIC weight	Parameters
$\Phi(.)$ $p(\text{Sex})$	579.76	0.00	0.250	3
$\Phi(\text{Sex})$ $p(.)$	580.85	1.10	0.145	3
$\Phi(\text{Sex-SVL})$ $p(.)$	581.36	1.60	0.112	4
$\Phi(\text{Sex})$ $p(\text{Sex})$	581.68	1.93	0.096	4
$\Phi(.)$ $p(.)$	581.93	2.17	0.084	2
$\Phi(\text{WetDry})$ $p(.)$	582.36	2.61	0.068	3
$\Phi(.)$ $p(\text{WetDry})$	583.06	3.30	0.043	3
$\Phi(\text{Site})$ $p(.)$	583.42	3.70	0.040	3
$\Phi(\text{Site-Sex})$ $p(\text{Site-Sex})$	583.51	3.76	0.038	6
$\Phi(.)$ $p(\text{Site})$	583.88	4.13	0.032	3
$\Phi(\text{Site})$ $p(\text{Site})$	584.13	4.38	0.028	4
$\Phi(\text{WetDry})$ $p(\text{WetDry})$	584.36	4.60	0.025	4
$\Phi(\text{Site-SVL})$ $p(.)$	584.65	4.89	0.022	4
$\Phi(t)$ $p(t)$	585.94	6.18	0.011	11

An alternative possibility is that the differences in adult body sizes in these two populations do not represent an adaptive shift in life history strategies, but rather result from phenotypic plasticity under differing environmental conditions. In many species of ectotherms, cooler environmental temperatures have been shown to produce slower growth rates but also larger body sizes at maturity, and both adaptive and non-adaptive explanations have been offered to explain this phenomenon (Angilletta, *et al.*, 2004; Atkinson & Sibley, 1997). In this study, the Santa Elena site that exhibited larger body sizes was a cooler site, being 600 m higher in elevation than the Caldas site. However, Bock, *et al.* (2009) found no evidence of differing growth rates in these two sites for adult females, and some evidence that adult males actually grew faster at the cooler site, contrary to the expected pattern. Their study also examined other high elevation sites (where precipitation levels were high) and found lizards there had smaller body sizes that were more comparable to those at the wet Caldas site. Thus, it seems more likely that variation in precipitation levels among the sites is what has influenced in some

TABLE 3: Model-averaged estimates of annual survivorship rates and capture probabilities of males and females from the Caldas and Santa Elena populations.

Population	Φ		p	
	Males	Females	Males	Females
Caldas	19.2%	11.8%	0.22	0.17
Santa Elena	21.2%	13.0%	0.22	0.16

way the growth trajectories and asymptotic body sizes in these populations. However, to distinguish among the adaptive life history shift vs. phenotypic plasticity hypotheses, reciprocal transplant studies with long-term monitoring or multi-generational common garden rearing experiments (Cox, *et al.*, 2006; Ferguson & Talent, 1993; Iraeta, *et al.*, 2006; Niewiarowski & Roosenburg, 1993; Thorpe, *et al.*, 2005) will be required.

Our annual survivorship estimates for *A. mariarum* were high compared to those published for other small mainland anoles (Andrews, 1979; Fitch, 1973; Lister, 1981; Schoener & Schoener, 1982), and were more comparable to those reported for *Anolis* populations in the Caribbean (Rubial & Philibosian, 1974; Schoener & Schoener, 1978, 1982). However, another small, high elevation anole in Costa Rica also has been reported to exhibit apparently high survivorships (Fitch, 1972). Unfortunately, most early studies of *Anolis* demography only obtained estimates of annual turnover, information on maximum life spans, or conducted analyses of return rates, without decomposing this parameter into its two constituent components (Φ and p), so direct comparison of our results with these studies are inappropriate. However, Andrews & Nichols (1990) rigorously estimated Φ and p for *A. limifrons*, a lowland rainforest species similar in body size to *A. mariarum*, and found much lower values of Φ (1.3% to 5.5% annual survivorships) and much higher values of p (from 0.45 to 0.81), with no evidence of differences among males and females for either parameter.

We have monitored several *A. mariarum* populations located near the Caldas site for almost ten years and have recaptured some individuals almost two years after their having been first marked as juveniles. This contrasts with many estimates of an almost complete annual turnover in many small mainland *Anolis* species (Fleming & Hooker, 1975; Andrews, 1979; Andrews & Nichols, 1990; Irschick, *et al.*, 2006), and is consistent with our conclusion that Φ in *A. mariarum* is high. Estimates of p from the monitoring project also were similar to those obtained in this study, both in magnitude and in terms of males

having slightly higher capture probabilities than females, perhaps because males tend to perch more conspicuously than females while performing social displays.

The high proportion of individuals with broken tails in this study might suggest that predation rates in these populations are high, contradicting our conclusion that survivorships were high. However, it has been argued that tail-break frequency in lizards is a better index of predator inefficiency than of actual predation rates (Schoener, 1979). For example, tail break frequencies in *Anolis sagrei* were shown to be higher in populations with higher survivorships (Schoener, 1979; Schoener & Schoener, 1980). Perhaps the current predator community present in *A. mariarum* habitat is depauperate as a consequence of the high levels of human disturbance this area has experienced.

More surprising was the failure to demonstrate an effect of tail autotomy on survivorship in this study, given that tail loss has been shown to affect locomotor abilities in other lizard species (Ballinger, et al., 1979; Brown, et al., 1995; Chapple, et al., 2004; Martin & Avery, 1998; Punzo, 1982) and has recently been shown to affect jumping performance in *Anolis carolinensis* (Gillis, et al., 2009). Tail loss also has been shown to directly reduce survivorships in certain lizard species (Fox & McCoy, 2000; Wilson, 1992) or increase vulnerability to predators in staged encounters (Congdon, et al., 1974; Dial & Fitzpatrick, 1981; Downs & Shine, 2001; Vitt & Cooper, 1986). Again, the lack of an effect of relative tail length on survivorship in this study is consistent with our conclusion that survivorship in these populations are high, perhaps because predators are few and/or inefficient.

CONCLUSION

The main conclusion of this study was that models that included the variable Sex in either the Φ or p terms provided the best fits to the data. Previous studies have shown that male and female anoles have comparable survivorship rates (Andrews & Nichols, 1990; Schoener & Schoener, 1982), or, in highly polygynous species, that males may have lower survivorships (Schoener & Schoener, 1982). Our study is the first to document lower survivorships in female anoles. Perhaps the costs to females of egg production under thermal stress in this high-elevation species exceed the costs to males of increased conspicuousness to predators while displaying.

RESUMEN

Comparamos las sobrevivencias de los adultos en dos poblaciones de la lagartija Anolis mariarum con distintos promedio y asíntotas de sus tamaños corporales, para examinar una predicción de la teoría de mortalidad específica de edad; que las poblaciones que experimentan mayor mortalidad de los adultos deben exhibir maduración sexual más temprana y menores tamaños corporales en los adultos. Utilizamos la técnica de máxima verosimilitud para evaluar diferentes modelos de sobrevivencia y una técnica de modelo-promediado para estimar sobrevivencia y probabilidades de recaptura para cada sexo y sitio. La longitud relativa de la cola no afectó las tasas de sobrevivencia de los adultos en estas poblaciones, pero el tamaño corporal estuvo relacionado con la sobrevivencia, siendo los individuos más grandes en el momento de la primera captura los que presentaron las tasas de sobrevivencia más bajas; por lo tanto, el tamaño corporal fue incluido como una covariable en algunos de los modelos examinados. Los análisis revelaron que los machos de ambos sitios presentan mayores sobrevivencias que las hembras, pero no encontramos diferencias entre los sitios entre las tasas de sobrevivencia o las probabilidades de captura para cada sexo. Aún así, las diferencias documentadas en los tamaños corporales entre estos sitios pueden representar adaptaciones en las historias de vida ante diferentes tasas de mortalidad en las clases de edad tempranas como huevos o juveniles en cada sitio, o por otra parte puede representar un caso de plasticidad fenotípica ante diferentes condiciones ambientales, las cuales no parecen estar relacionadas con diferencias en las sobrevivencias de los adultos. Los estimativos de sobrevivencia anual (11.7% a 21.2%) fueron altos para este Anolis continental de pequeño tamaño. Este es el primer reporte para el género en que la sobrevivencia de los machos excede a la de las hembras.

PALABRAS-CLAVES: Supervivencia; Tamaño corporal; Diferencias sexuales.

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