


The Influence of Incubation Conditions and Sex on Growth and Dispersal in Hatchling Lizards

Matthew E. Gifford* , Christopher D. Robinson* & Timothy A. Clay†

* Department of Biology, University of Central Arkansas, Conway, AR, USA

† Department of Biological Science, University of Tulsa, Tulsa, OK, USA

Correspondence

Matthew E. Gifford, Department of Biology,
University of Central Arkansas, 201
Donaghey Ave., Conway, AR 72035, USA.
E-mail: megifford@uca.edu

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Abstract

Dispersal is a critical process that has profound influence on ecological and evolutionary processes. Many proximate factors influence natal dispersal, but it is currently unclear whether the conditions experienced during incubation play an important role. We manipulated incubation temperature and used mark–recapture of released hatchlings to test this hypothesis. We tested this hypothesis on the prairie lizard (*Sceloporus consobrinus*) using two experimental islands in a local reservoir. Incubation conditions influenced some aspects of hatchling morphology, but had little influence on the probability of dispersal. As generally predicted for a polygynous species, males were more likely to disperse than females; however, the growth rate of dispersing vs. resident individuals varied depending on sex. Dispersive male lizards did not grow faster than resident males, whereas female dispersers grew significantly slower than resident females. Although our study was not specifically designed to test for differential costs of dispersal for males and females, this pattern is consistent with recent research demonstrating sex-specific fitness costs of dispersal.

Introduction

Dispersal is a key life history trait that has important influence on ecological and evolutionary processes (Clobert et al. 2001). The multi-causal nature of dispersal suggests that disentangling the proximate and ultimate factors driving the evolution of dispersal can be difficult (Bowler & Benton 2005; Clobert et al. 2012). However, the processes that drive the evolution of dispersal are generally thought to include the avoidance of inbreeding and competition (e.g., for both resources and reproduction; Pfenninger et al. 1996; Le Galliard et al. 2003, 2005; Boinski et al. 2005; Cote & Clobert 2010). Indeed, some studies have demonstrated a significant relationship between variation in dispersal and fitness (Bonte & Lens 2007; Calsbeek 2009; Lowe 2010; Calsbeek et al. 2014). In addition to these ultimate drivers of dispersal, variation in dispersal is often also influenced by a host of factors intrinsic and extrinsic to the organism. For

example, dispersal from a natal site is influenced by intrinsic factors like genetic or developmental variation in dispersal ability (Doligez et al. 2009; Massot & Clobert 2000; Sinervo et al. 2006), innate behavioral variation, or morphology (Clobert et al. 2009; Cote et al. 2010, 2013); and extrinsic factors like habitat structure/quality or population density (Imbert & Ronce 2001; Matthysen 2005; Mathieu et al. 2010; Cocala et al. 2014).

Environmental conditions experienced during development (particularly in ectotherms) often influence the morphology and physiology of offspring (e.g., Andrews et al. 2000; Gorman & Nager 2004). In addition, conditions experienced during these early life stages can have important impacts on the probability of dispersal at later life stages (Massot & Clobert 2000; Benard & McCauley 2008; Bonte et al. 2008; Bestion et al. 2015). Because the pre-natal environment (e.g., temperature) often varies substantially, spatially and temporally, different dispersal patterns

could arise in offspring depending on where and when they were produced, potentially influencing population-level processes such as regional persistence of metapopulations (Benard & McCauley 2008). Indeed, several studies have demonstrated that dispersal is highly context-dependent. For example, maternally derived hormones have been shown to influence the dispersal behavior of juvenile lizards, although in a complex manner associated with the sex ratio of the clutch (Vercken et al. 2007). In addition, maternal condition had a significant effect on offspring dispersal, but other pre-natal environmental effects (including gestation temperature) had minimal influence (Massot & Clobert 2000). Finally, pre-natal temperature exposure can interact with post-natal environmental conditions to cause variation in dispersal. Interestingly, some evidence suggests that environmental effects on offspring can be sex-specific (Sorci et al. 1994; Uller et al. 2009). Although it is clear that juvenile dispersal can be strongly influenced by pre-natal maternal effects, very few studies have examined the influence of variation in developmental temperature on dispersal (but see Massot et al. 2002).

We designed our study to evaluate the influence of incubation temperature on dispersal in free-ranging hatchling lizards. Because incubation temperature can influence the morphology and growth rate of hatchlings, we also tested whether dispersal was associated with these traits. This design allowed us to examine the individual and interactive effects of developmental plasticity and sex on dispersal. Finally, we also tested for evidence of sex-biased dispersal and whether any relationship between dispersal and other traits differed between the sexes.

Methods

Study Species

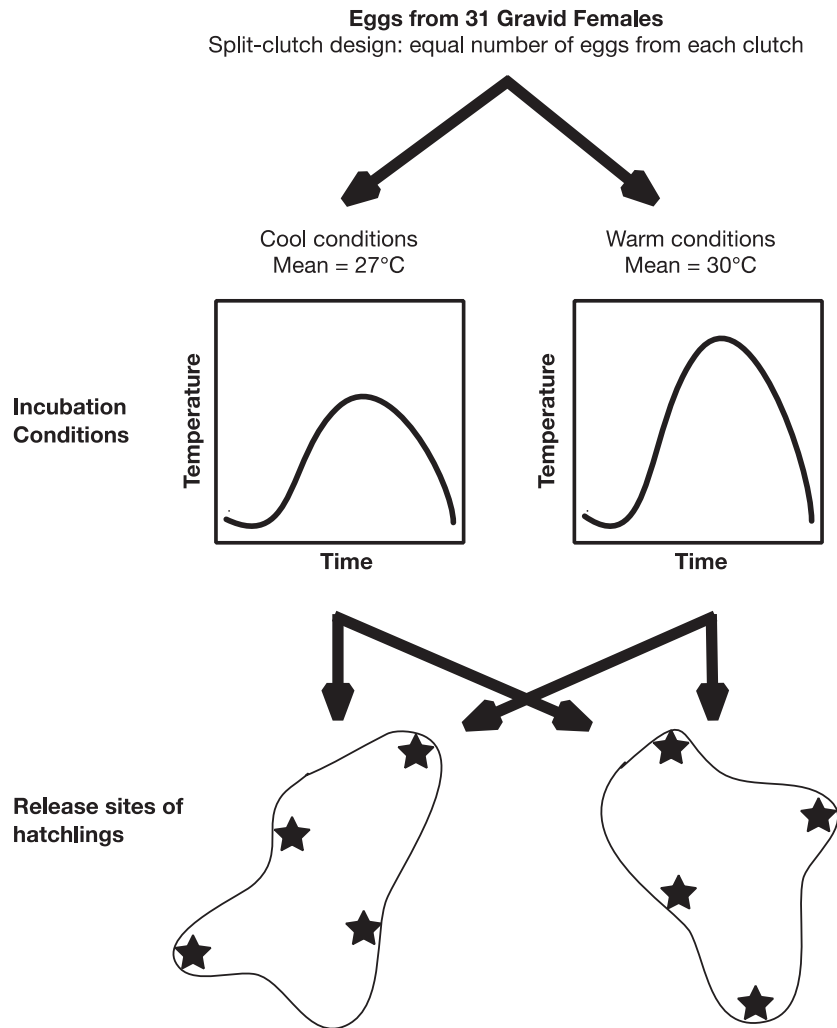
The prairie lizard (*Sceloporus consobrinus*) is a medium-sized lizard [up to approximately 73 mm in snout-vent length (SVL)] that is common to a variety of habitats in the south-central portion of the USA (Powell et al. 2016). This species and its closely related congener (*S. undulatus*) have served as important models for the study of lizard ecology and life history (see Niewiarowski et al. 2004). In southern portions of its range, females typically produce two clutches of eggs (seven to sixteen eggs per clutch in our population, pers. obs.) during a given reproductive season (Niewiarowski et al. 2004). Despite the popularity of these species in ecological research, dispersal has been rarely examined (Massot et al. 2003).

Experimental Design

In April 2015, we captured gravid female *S. consobrinus* (N = 31) by hand or with a noose from a forested location in Pulaski County, Arkansas (34.855, -92.199) and returned the lizards to the laboratory at the University of Central Arkansas (Fig. 1). In the laboratory, female lizards were housed individually in terraria (45 cm × 20 cm × 25 cm, L × W × H). Each terrarium contained a sand substrate (~2 cm depth), a piece of egg carton for a hide, and a rock as a perch site directly underneath a suspended 40W incandescent bulb (creating a thermal gradient). The incandescent bulbs and room lights were set on a 13L:11D photoperiod, similar to natural conditions at the capture site during April. We fed lizards vitamin-dusted crickets (*Acheta domestica*) three times per week and misted each enclosure with water twice each day. We monitored lizards frequently and gauged progression of gestation by gently palpating each lizard's abdomen. Once oviposition seemed imminent (females refused food and appeared lethargic), we induced egg laying using an intracoelomic injection of 0.1–0.3 ml of oxytocin (2–6 USP units; VetOne, MWI, Meridian, ID).

After injection, each female was placed individually in a ventilated plastic container containing a moist sand substrate and the oviposition container was placed into a dark incubator at 30°C (VL-36, Percival Scientific, Perry IA). We checked each female every hour post-injection to collect eggs. All females began laying eggs within 5 h of injection. Females were left undisturbed for 24 h after they finished laying eggs. All females fully recovered from this procedure and were released back at the capture location. Eggs were weighed (to the nearest 0.1 mg) and placed individually into a sealed plastic cup (59 ml) filled with a mixture of 35 g fine silica sand and 3.5 g of distilled water. This combination results in a water potential of approximately -10 kPa (Oufiero & Angilletta 2006).

Using a split-clutch design, an approximately equal number of eggs from each clutch were randomly assigned to one of two fluctuating incubation treatments. Incubation conditions were chosen to represent contemporary conditions in natural nests (Warner & Andrews 2002), and conditions embryos might potentially be exposed to as climate warms. We attempted to incorporate this latter effect by modifying both the mean and variance of incubation temperature (see below). The first incubation treatment approximated average natural incubation conditions with a mean temperature of 27°C (Warner & Andrews 2002), a minimum nighttime temperature of 23°C,



Hatchlings released at four locations on each island, 50:50 sex ratio, randomly with respect to clutch, and equal representation of incubation conditions.

Fig. 1: Experimental protocol used in this study. See text for further details.

and a maximum daytime temperature of 32°C. The second incubation treatment was warmer with a mean temperature of 30°C, a minimum nighttime temperature of 23°C, and a maximum daytime temperature of 38°C. Incubation conditions were maintained in two programmable incubators (Percival 36-VL, Percival Scientific, Perry, IA) that provided smooth transitions between temperatures, not step changes. Individual egg containers were arranged into larger trays that were placed into incubators. We rotated egg containers and trays every 2 wk to avoid positional effects within each incubator. At the time, we rotated eggs we checked the moisture content of each egg container and added distilled water as needed to maintain moisture level.

After 40 d for the 30°C treatment and 50 d for the 27°C treatment, we began checking eggs daily for

hatching lizards. Each hatchling was immediately measured for snout-vent length (SVL, to the nearest 0.5 mm), body mass (to the nearest 0.1 mg), and hindlimb span (the distance between the tips of the longest toes on each hindlimb when legs were extended perpendicular to the body axis, to the nearest 0.5 mm) and placed into enclosures (configured identically to those used for females). We housed five hatchlings per enclosure and fed them small vitamin-dusted crickets daily. Hatchlings were maintained in the lab for a maximum of 7 d prior to release on experimental islands (see below). Prior to release, we determined sex of each lizard by checking for the presence of enlarged post-anal scales (present in males), measured and weighed them a second time, and clipped three toes in a unique combination for identification. We never clipped more than a single

toe from any limb and never removed the longest toe on each hindlimb. We assigned hatchlings to experimental islands at approximately equal sex ratio (~50:50), randomly with respect to maternal ID, and maintaining an equal representation of each incubation treatment on each island.

Field Procedures

Hatchlings were released onto two islands in Lake Ouachita, a reservoir located in Garland and Montgomery Counties in Arkansas. The two islands were similar in structure but differed in size and did not have lizards inhabiting them at the time of release. The large island (hereafter referred to as Big Island) has a vegetated area of 3800 m²; the smaller island (hereafter referred to as Bone Island) has a vegetated area of 1900 m². Both islands are vegetated with a mix of deciduous trees (oak, hickory, maple, persimmon, and winged elm) and coniferous trees (red cedar and shortleaf pine). Dense undergrowth (brier) and open understory (short grass and bare rock) were present on each island, and their proportions were similar between islands. Surrounding each island, there was an expanse of bare rock between the water and the vegetated area that varied in size depending on lake level. We measured potential prey availability on each island using sticky traps. Prior to releasing lizards, we deployed sticky traps at a similar density on each island in a variety of habitats to capture the breadth of prey items available to lizards. Sticky traps measured 10 cm × 10 cm. At approximately 0800 h, we placed 15 traps on Bone Island and 30 traps on Big Island. We collected traps after ten hours and identified captured arthropods to order. *Sceloporus* prey on a wide variety of arthropods including hymenopterans (ants), coleopterans, arachnids (spiders), orthopterans, and hemipterans (Lemos-Espinal et al. 2003). Therefore, we focused our prey censuses on these taxa. We quantified prey availability on each island as the number of insects per trap.

We released hatchlings in two groups, the first on June 29, 2015 (30°C treatment) and the second on July 16, 2015 (27°C treatment). Each time we released hatchlings in groups at four specific locations on each island. Specific release locations on each island were chosen to maximize the longitudinal and latitudinal distance between sites. We did not quantify specific habitat characteristics at each release location as our focus in this study was on potential influence of incubation conditions on dispersal. Groups of lizards were chosen randomly with respect to clutch of origin, and we attempted to maintain an

equal sex ratio on each island (Big Island sex ratio = 51% M:49% F; Bone Island sex ratio = 55% M:45% F). On Big Island, we released 160 hatchlings (40 at each location), resulting in a density of 0.042 lizards m⁻². On Bone Island, we released 84 hatchlings (21 at each location), resulting in a density of 0.044 lizards m⁻².

We recaptured surviving hatchlings in late August and late September. Release and recapture locations were recorded in UTM coordinates using a Trimble Juno 3B GPS unit (Trimble Navigation Limited, Sunnyvale, CA). Dispersal distance was calculated as the linear displacement between the release and recapture locations. For those lizards recaptured more than once (N = 27), we only used location data from the final recapture location to calculate dispersal distance. We measured all recaptured lizards for SVL and body mass. Similarly, for those lizards recaptured twice, we used values at final recapture to calculate growth rates, which were used in analyses (outlined below). Growth rate was calculated as the difference in lizard body size between captures divided by the time (days) elapsed between captures.

Classifying dispersers from philopatric individuals (i.e., non-dispersers) is operationally difficult because common movements for routine purposes (e.g., foraging) can be mistakenly interpreted as dispersal (Gaines & McClenaghan 1980). For example, using the straight-line dispersal distance can be problematic because the distance an individual lizard moves can be influenced by the local habitat characteristics it experiences so these movements could be a response to factors unrelated to dispersal per se (Massot et al. 2003). As an alternative, one can use the distribution of individual dispersal distances to classify individuals as dispersers vs. residents using a threshold value of movement distance. Most dispersal kernels are leptokurtic and highly right-skewed, so determining this threshold value can be difficult. Frequently, studies use thresholds determined by home range size of the study animal, defining dispersing individuals as those that moved a distance greater than one home range diameter and residents as those moving a distance less than this value (Clobert et al. 1994; Massot & Clobert 2000). Mean home range diameter for adult prairie lizards in another population is 39 m for males and 26 m for females, and the mean home range diameter across both sexes is 35 m (Gifford, unpubl. data). Given these data, we defined resident males as those who moved a distance <35 m and dispersers as those that moved >35 m. We defined resident females as those that moved <25 m and dispersive females as those that moved >25 m. The threshold

values used here are similar to those used in other studies of lizard dispersal (e.g., Clobert et al. 1994; Massot & Clobert 2000). Only 1 lizard out of 25 (4%) that were recaptured during both August and September censuses moved away from the release location and returned to a location closer to the release point. Therefore, we feel confident in our categorization of lizards as dispersers and residents.

Statistical Analyses

All statistical analyses were performed using R (version 3.1.1). Statistical significance was determined at $p < 0.05$. We tested the influence of incubation conditions on hatchling morphology with mixed effects models in the *lme4* package (Bates et al. 2014). For mixed models, incubation treatment and hatchling sex were treated as a fixed effects and maternal ID (clutch) was treated as a random effect. We also included the interaction between sex and treatment to test whether male and female morphology differed in response to incubation temperature. Hatchling SVL also was included as a covariate in models testing for differences in hindlimb length and tail length due to the allometric relationship between body length and these traits in lizards. Statistical significance of fixed effects was tested using the Kenward-Roger approximation for denominator degrees of freedom (Kenward & Roger 1997) in *lmerTest* (Kuznetsova et al. 2014). We tested for differences in prey availability using a Wilcoxon rank sum test.

Because some individuals were recaptured in one census but not the other, we incorporated imperfect recapture success in our estimates of dispersal using multistate capture–mark–recapture (CMR) models in the R package *marked* (Laake et al. 2013). Multistate CMR models take into account the spatial location of each individual at each capture session. A capture history was developed for each individual where an A was assigned to an individual that was recaptured at a location within the cut-off distance for residents (sex-specific, see above), and a B assigned for individuals captured at a location exceeding the cut-off threshold. Because lizards were unable to disperse off of each island, the estimated ‘emigration’ probability from the multistate CMR models represents a dispersal probability. Multistate CMR models estimate the following parameters: survival (S), recapture probability (p), and emigration probability (ψ = transition probability from one location to another [i.e., disperse or not]). All parameters can vary as a function of fixed covariates. We tested the fixed covariates of island (i = Big vs. Bone Island), time (t = recapture session), incubation

conditions (inc = 27°C vs. 30°C treatment), and sex (male vs. female) on each parameter.

We fitted a Cormack–Jolly–Seber (CJS) model to the CMR data using hidden Markov models (model = ‘hmmMSCJS’ in *marked*). Because of the limited number of recapture episodes over a relatively short period of time (~3 mo), we did not include time (t) as a factor when estimating survival probability (S) or emigration probability (ψ). However, t was included in modeling of recapture probability (p). Thus, we started from model $\{S(i*inc*sex)p(i*inc*sex*t)\psi(i*inc*sex)\}$ that included interaction terms between island, incubation conditions, sex on S and ψ , and all interaction terms on p . We had no prior information about the optimal model structure; we tested all models by simplifying factors for each parameter. We compared competing models using AICc values (Burnham and Anderson 2004). When multiple competing models had AICc values lower than 2, we tested the statistical significance of specific effects using likelihood ratio tests (LRT).

We used generalized linear mixed effects models to test for the influence of lizard characteristics on juvenile dispersal because previous studies have revealed that dispersal behavior is often similar among siblings (Massot et al. 1994). Therefore, in this analysis maternal ID (clutch) was included as a random effect. In this analysis, juvenile dispersal was coded as a binary variable (1 for dispersers and 0 for residents); therefore, we modeled the error variance using a binomial distribution. We included incubation treatment, hatchling sex, and island as fixed effects in this analysis and hatchling body mass and body condition at release as additional covariates.

We tested whether dispersive and resident individuals differed in field growth rate. For this analysis, growth rate (g/day) was the response variable and dispersal category (dispersed vs. resident), island, treatment, and sex were included as fixed effects. We also included the dispersal category by sex interaction to test whether the pattern of variation in growth rate between dispersive and resident individuals differed between the sexes. Maternal ID was also included as a random effect in this analysis.

Results

Effect of Incubation Conditions and Sex on Hatching Morphology

We obtained 324 eggs from 31 females, of which 270 successfully hatched (overall hatching success = 83.3%). Hatching success did not differ

significantly between incubation treatments (27°C treatment = 83.4%, 30°C treatment = 83.2%; $\chi^2 < 0.01$, $p = 0.99$). Incubation conditions did not significantly influence hatchling body size (SVL, $F_{1,218.55} = 0.158$, $p = 0.691$; mass, $F_{1,218.82} = 0.009$, $p = 0.926$), but did significantly affect hatchling hindlimb span ($F_{1,216.98} = 25.373$, $p < 0.001$) and tail length ($F_{1,217.80} = 70.156$, $p < 0.001$). Hatchlings from the 30°C treatment had both longer hindlimbs and longer tails than hatchlings from the 27°C treatment (hindlimb span, 30°C = 38.27 ± 1.66 mm, 27°C = 37.63 ± 1.41 mm; tail length, 30°C = 30.02 ± 2.01 mm, 27°C = 28.68 ± 1.67 mm, mean \pm SD). Body size did not differ at hatching between the sexes (SVL, $F_{1,229.04} = 0.113$, $p = 0.737$; mass, $F_{1,224.73} = 3.473$, $p = 0.064$) nor did the sexes respond differently to incubation conditions (interactions; SVL, $F_{1,225.11} = 0.276$, $p = 0.600$; mass, $F_{1,222.66} = 0.132$, $p = 0.716$). Both hindlimb span and tail length at hatching differed between the sexes (hindlimb span, $F_{1,230.66} = 6.003$, $p = 0.015$; tail length, $F_{1,239.08} = 5.816$, $p = 0.017$). In neither case was interaction between incubation treatment and sex significant (hindlimb span, $F_{1,225.40} = 0.057$, $p = 0.812$; tail length, $F_{1,231.79} = 1.241$, $p = 0.267$). Male hatchlings had slightly longer hindlimb spans and tail lengths than females (hindlimb span, males = 38.21 ± 1.57 mm, females = 37.67 ± 1.52 mm; tail length, males = 29.63 ± 1.68 mm, females = 29.05 ± 2.13 mm, mean \pm SD).

Lizard Growth and Dispersal in the Field

Prey availability did not differ significantly between islands (number of insects collected trap⁻¹, Wilcoxon rank sum test: $W = 194.5$, $p = 0.309$). We recaptured 73 of the 244 lizards released on the two islands (29.9%). The percentage of lizards recaptured differed between the two islands and was 2.18 times higher on Bone Island (46.4%) than on Big Island (21.3%). On each island, we recaptured a similar percentage of each sex (Bone Island, males = 48.6%, females = 44.7%; Big Island, males = 19.5%, females = 23.1%).

The ten best models based on AICc values are shown in Table 1. Because all four top models were identical with respect to effects on survival and recapture probability, we used likelihood ratio tests of the four top models (i.e., those with AICc values <2) to identify the best model overall (Table 2). This model included survival (S) as a function of island, recapture probability (p) dependent on time, island, and incubation conditions, and emigration probability (psi) as a function of lizard sex alone (Table 2). Models that

included an effect of island or incubation conditions did not significantly improve model fit over the model that included sex effects alone on emigration probability. No models that included sex by incubation condition interactive effects on emigration probability scored AICc values <2, suggesting that these interactions are not significant. Based on model #1, male hatchlings were significantly more likely to disperse from their release site than female hatchlings (males = 0.454 ± 0.074 , females = 0.194 ± 0.051 , Fig. 2a).

We used generalized linear mixed effects models to test whether morphological characteristics were associated with dispersal probability. Based on CMR modeling, these analyses did not include effects of island or incubation conditions. Hatchling dispersal was not significantly influenced by incubation treatment, body mass, body condition (residuals from the regression of body mass on SVL), or hindlimb length at release (Table 3). However, consistent with CMR modeling results, male hatchlings were significantly more likely to disperse than female hatchlings (Table 3). Indeed, 65% of all recaptured males dispersed, whereas 30% of recaptured females did. Considering all recaptured individuals, incubation conditions did not have a significant effect on field growth rates ($F_{1,65.72} = 1.767$, $p = 0.188$). Hatchling growth rate did not differ significantly among islands,

Table 1: Model selection for survival (S), recapture probability (p), and emigration (i.e., dispersal) probability (psi). Model #1 appears in bold because it was determined to be the best model based on likelihood ratio tests of significant effects (Table 2)

#	Model	K	AICc	Δ AICc	AICc weights	-lnLik
1	{S(i)p(t+i+inc) psi(sex)}	10	562.660	0.00	0.228	271.330
2	{S(i)p(t+i+inc)psi (i+sex+inc)}	12	562.778	0.118	0.214	269.389
3	{S(i)p(t+i+inc) psi(i+sex)}	11	562.936	0.276	0.198	270.486
4	{S(i)p(t+i+inc)psi (sex+inc)}	11	563.158	0.498	0.177	270.579
5	{S(i)p(t+i+inc)psi (i+sex*inc)}	13	564.767	2.107	0.079	269.385
6	{S(i)p(t+i+inc)psi (sex*inc)}	12	565.118	2.458	0.066	270.559
7	{S(i)p(t+i+inc)psi(.)}	9	568.476	5.816	0.012	275.238
8	{S(i)p(t+i+inc)psi(i)}	10	568.783	6.213	0.011	274.392
9	{S(i)p(t+i+inc) psi(i+inc)}	11	569.148	6.487	0.009	273.574
10	{S(i)p(t+i+inc) psi(inc)}	10	569.438	6.778	0.008	274.719

nor between dispersers and residents (Island, $F_{1,65.248} = 0.312$, $p = 0.578$; dispersal category, $F_{1,65.992} = 3.357$, $p = 0.071$), but did differ between sexes ($F_{1,65.935} = 5.638$, $p = 0.020$). In addition, the growth rate of dispersers and resident individuals differed depending on sex (i.e., a significant dispersal by sex interaction, $F_{1,62.085} = 8.417$, $p = 0.005$). Specifically, in males, growth rate of dispersers and residents did not differ significantly ($F_{1,30} = 1.153$, $p = 0.292$); but in females, dispersers grew significantly slower than residents ($F_{1,27} = 9.186$, $p = 0.005$; Fig. 2b).

Discussion

Incubation temperature had a significant influence on some aspects of hatchling lizard morphology. Specifically, hatchlings from eggs incubated under warmer, more widely fluctuating conditions, had longer

hindlimbs and longer tails than hatchlings from cooler, less variable, conditions. Although there was a statistical difference in hindlimb length of hatchlings incubated under different conditions, the magnitude of this difference was relatively small (1.7%, 0.64 mm). These patterns of variation in response to incubation temperature are generally similar to those observed for the closely related species *S. undulatus* using constant-temperature incubation treatments (Andrews et al. 2000). Longer hindlimbs are generally associated with increased locomotor performance (e.g., sprinting speed, Bauwens et al. 1995), and sprinting speed is frequently associated with higher fitness (i.e., survival) in hatchling/juvenile lizards (Miles 2004; Husak 2006). However, the small magnitude difference in limb length likely had minor influence on sprinting performance in hatchlings from this study. Studies often found that variation in incubation temperature results in variation in hatchling body size or body condition (e.g., Andrews et al. 2000; Brana & Ji 2000); we found no such response in our experiment.

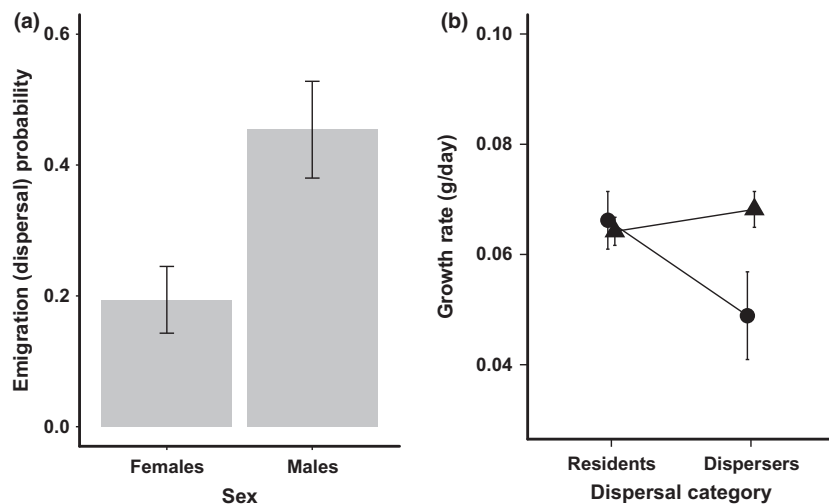
Table 2: Results of likelihood ratio tests (LRT) to evaluate the statistical significance of individual factors influencing emigration probability (psi). Model containing the sex effect on emigration probability provides significantly better fit than a model excluding this effect. Models including island and/or incubation effects do not provide significant improvement of fit over models excluding these effects. Thus, the most parsimonious model is Model 1, which includes a sex effect on emigration probability alone. Bolded number indicates the best model in each comparison based on LRT

Models compared	Tested effect (parameter)	χ^2	df	p
1 vs. 2	i + inc (psi)	3.882	2	0.144
1 vs. 3	i (psi)	1.724	1	0.189
1 vs. 4	inc (psi)	1.502	1	0.220
2 vs. 3	inc (psi)	2.158	1	0.142
2 vs. 4	i (psi)	2.381	1	0.123
2 vs. 9	sex (psi)	8.370	1	0.004

Table 3: Effect table from the model testing the effect of lizard traits on juvenile dispersal. Dispersal probability differed significantly between males and females. Statistical test used was a generalized linear mixed effects model (dispersal as the dependent variable) assuming a binomial error distribution. Dispersers were modeled with a score of 1 and residents with a score of 0

	df	χ^2	p
Body mass	1	1.731	0.188
Body condition	1	0.617	0.423
Hindlimb length	1	0.143	0.705
Sex	1	5.902	0.015

Fig. 2: Variation in recapture probability between male and female lizards estimated using Cormack–Jolly–Seber models (a) and growth rate as a function of both dispersal category and lizard sex (b). Panel b illustrates the interaction between sex and dispersal category. Females are represented in black dots, and males are represented in black triangles; error bars are 1 SE.



Capture–mark–recapture models that included incubation effects did not fit the data significantly better than models that included sex alone. This suggests incubation conditions did not significantly influence dispersal decisions of hatchling lizards in this study. Similar to the results presented in this study, temperature experienced by embryos during development did not influence dispersal in the common lizard (*Zootoca vivipara*, Massot et al. 2002). However, these authors found that the effect of temperature on dispersal depended on the habitat in which the offspring were released (humid vs. dry habitats). Furthermore, innate thermal preferences have been demonstrated to influence dispersal decisions in another lizard species (Bestion et al. 2015) such that lizards preferring cooler temperatures were more likely to disperse from warmer sites, whereas the opposite pattern was observed for lizards preferring warmer temperatures. Therefore, developmental conditions that alter thermal preferences could have an impact on dispersal decisions and therefore population dynamics. We did not quantify the environmental conditions of the microhabitats in which we released lizards or thermal preferences, so we cannot test for such interactive effects here.

Consistent with patterns predicted for species with polygynous mating systems (Greenwood 1980; but see recent reappraisals of this hypothesis (Dobson 2013; Mabry et al. 2013), we observed a significant sex bias in dispersal where males were significantly more likely to disperse than females (Fig. 1a). Interestingly, the influence of dispersal on juvenile growth rate differed between males and females (Fig. 1b). Dispersive male lizards did not differ significantly in growth rate from resident males, whereas dispersive females grew significantly slower than resident females. This result suggests that the costs and benefits of dispersal might equilibrate differently for each sex. Indeed, sexually antagonistic selection on natal dispersal distance was recently demonstrated for another lizard species, *Anolis sagrei* (Calsbeek et al. 2014). Similar to the present study, these authors detected male-biased juvenile dispersal, but also found that viability selection favored more philopatric females. It should be noted that our study was not designed as a rigorous test of the sex-specific costs and benefits of natal dispersal. Such a test would require an experimental design that manipulates the density and/or sex ratio of the population, and the number of siblings released together at a given location. However, given the sex-specific pattern of selection documented in Calsbeek et al. (2014) and the sex-

specific pattern of growth associated with dispersal observed in this study, it is possible that sexually antagonistic costs and benefits of juvenile dispersal might be more common than previously realized in polygynous species and deserves continued scrutiny.

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