

Tree lizard (*Urosaurus ornatus*) growth decreases with population density, but increases with habitat quality

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Funding information

Natural Sciences and Engineering Research Council of Canada (NSERC); an NSERC scholarship and Ontario Graduate Scholarship

Abstract

Habitat selection models can explain spatial patterns in the relative abundance of animals in different habitats based on the assumption that fitness declines as density in a habitat increases. Ectotherms, such as lizards, may not follow predictions of density-dependent habitat selection models because temperature, which is unaffected by density, strongly influences their habitat selection. If competition for limited resources decreases fitness, then crowding should cause a decrease in body size and growth rates. We used skeletochronology and body size data from tree lizards (*Urosaurus ornatus*) at six sites that each spanned two habitats varying in quality to test the hypothesis that habitat selection is density dependent because growth is limited by competition for resources and by habitat quality. First, we tested that the maximum body size of lizards decreased with higher densities in a habitat by comparing growth between sites. Second, we tested whether body size and growth were higher in the habitat with more resources by controlling for density in a habitat and comparing growth between habitats in different sites. We found evidence of density-dependent growth in females, but not in males. Females in more crowded sites reached a smaller maximum size. Females in the higher quality habitat also grew larger than females in the lower quality habitat after controlling for differences in density between the habitats. Therefore, we found partial support for our hypothesis that competition for resources limits growth and causes density-dependent habitat selection.

KEYWORDS

density dependence, growth, Ideal Free Distribution, ornate tree lizard, skeletochronology, *Urosaurus ornatus*

1 | INTRODUCTION

At small spatial scales, variation in animal density can largely be explained by habitat selection, where organisms choose habitats that maximize their fitness. Habitat selection can affect fitness because survival (DeCesare et al., 2014; Matthiopoulos, Fieberg, Aarts, Beyer, & Morales, 2015) and reproductive output (Pierotti, 1982) depend on resource availability, competitor density, and predation risk in habitat patches. If organisms are free to choose any habitat, then organisms should be distributed between habitats in proportion to

their suitability such that mean fitness is equalized (the Ideal Free Distribution; Fretwell & Lucas, 1969). The Ideal Free Distribution assumes individuals are free to choose any habitat, have perfect knowledge of habitat suitability and of the distribution of competitors, and are equal competitors (Fretwell & Lucas, 1969). Despite its unrealistic assumptions (Kennedy & Gray, 1993), the Ideal Free Distribution and its extensions have been useful for predicting the spatial distribution of organisms between habitats (Haché & Bayne, 2013; Milinski, 1979; Walhström & Kjellander, 1995). Another central assumption of habitat selection models, however, is that

populations experience density dependence (Clutton-Brock, Major, Albon, & Guinness, 1987; Morris, 1989; Skogland, 1985). Density dependence is the negative effect of crowding on fitness because of reduced resources (per capita) and increased intraspecific competition (Hassell, 1975). Population growth in a wide variety of species is limited by density dependence (Brook & Bradshaw, 2006), but density dependence may not occur if species are limited by resources that are unaffected by crowding (Halliday & Blouin-Demers, 2016).

Temperature is often the most important aspect of patch quality affecting ectotherm habitat selection (Blouin-Demers & Weatherhead, 2001; Halliday & Blouin-Demers, 2016; Hughes & Grand, 2000; Lelièvre et al., 2011; Monasterio, Salvador, Iraeta, & Díaz, 2009; Picard, Carrière, & Blouin-Demers, 2011) because it modulates body temperature and body temperature dictates performance (Huey, 1991) and ultimately fitness (Huey & Berrigan, 2001). Temperature, however, is unaffected by population density. Therefore, ectotherm fitness and habitat selection may not be strongly linked to population density and ectotherms may thus be more limited by their ability to process resources rather than by their ability to acquire resources. The strength of density dependence increases as temperature approaches the preferred temperature range (T_{set}) in laboratory experiments with flour beetles (Halliday, Thomas, & Blouin-Demers, 2015), but does density dependence affect the abundance and habitat selection of ectotherms in nature? Density-dependent habitat selection has been detected in some ectotherms, including salmonids (Falcu, 2015; Knight, Morris, & Haedrich, 2008), lizards (Calsbeek & Sinervo, 2002), and insects (Kiflawi, Blaustein, & Mangel, 2003). In some species like garter snakes (*Thamnophis sirtalis*), however, habitat selection is density independent because of the high fitness cost of occupying thermally inferior habitats (Halliday & Blouin-Demers, 2016). Thus, the relationship between temperature, ectotherm abundance, and habitat selection is still largely unknown. When density dependence is present in ectotherms, what is the mechanism that causes fitness to decline with increased population density?

If density dependence through resource depletion is an important factor in ectotherm habitat selection and fitness, then crowding should reduce the amount of resources acquired per individual. Reduced resources per individual should lead to a decrease in body size and growth rate. The body size and growth rate of an organism are potentially important mechanisms of density dependence because they are positively correlated with reproductive output and survival. For example, female clutch or litter size increases with body size (Landwer, 1994; Martin, 1977; Meiri, Brown, & Sibly, 2012). Body size is also generally positively related to fitness because it affects locomotor performance for escaping predators (Johnson, Swoap, Bennett, & Josephson, 1993) and fighting ability with conspecifics (Arnott & Elwood, 2009; Carpenter, 1995). Growth rate is also correlated with fitness because fast growth allows individuals to reproduce earlier in life, escape size-selective predators, and better survive stochastic environmental stressors (Benrey & Denno, 1997; Werner & Gilliam, 1984). Bold and fast-growing individuals may however suffer higher mortality (Stamps, 2007). In fish populations, growth is frequently density dependent and linked to

reproductive output or survival (Lorenzen & Enberg, 2002). Also, field experiments with fish (Jenkins, Diehl, Kratz, & Cooper, 1999) and lizards (Massot, Clobert, Pilorge, Lecomte, & Barbault, 1992; Mugabo, Perret, Legendre, & Le Galliard, 2013) have shown that growth rates change in response to manipulations of density. Thus, body size and growth rate are important determinants of fitness and represent a likely mechanism for density dependence in populations because they provide a mechanistic link between resource depletion and fitness.

The Ideal Free Distribution predicts that organisms will choose the habitat that provides the highest fitness benefit and that mean fitness will decline as density in a habitat increases (Fretwell & Lucas, 1969). Thus, at a given density per habitat, mean fitness is predicted to be higher in a habitat with more resources, even though fitness is predicted to equalize between habitats at a given total population density (Figure 1a). The relationship between growth and density per habitat in two habitats should demonstrate higher growth in the habitat with more resources at a specific density per habitat (Figure 1b).

Growth rates decline as lizards get larger (El Mouden, Znari, & Brown, 1999; Rotger, Igual, Smith, & Tavecchia, 2016). Thus, it is necessary to use nonlinear equations to describe variation in growth rates as body size reaches a maximum value. The von Bertalanffy growth (VBG) curve (Fabens, 1965) describes changes in mean body length (L_t) through time (t) by incorporating a decrease in growth rates as organisms get larger:

$$L_t = L_\infty \times (1 - e^{-K \times (t-t_0)}).$$

There are three parameters in this growth model: the mean maximum size (L_∞) forms an asymptote, the growth parameter (K), and the age when mean length is zero (t_0). The growth parameter, K , describes the rate at which body size approaches L_∞ . The parameter t_0 is an artefact of the model formulation and has no biological interpretation. In general, the VBG is a good fit to growth data in lizards (El Mouden et al., 1999; James, 1991; Rotger et al., 2016).

We tested the hypothesis that ornate tree lizard (*Urosaurus ornatus*) habitat selection is density dependent because growth is limited by intraspecific competition for resources and habitat quality. We have previously reported a negative relationship between ornate tree lizard survival and population density in two habitats (Paterson & Blouin-Demers, 2018), but we found no relationship between growth rate and population density using mark-recapture data. However, population density effects on body size and growth often manifest themselves as differences in asymptotic body size, rather than growth rates (Beverton & Holt, 2012; Lorenzen, 1996). If tree lizard populations are limited by resource acquisition and density dependence, then body size and growth rate should be inversely related to density. First, we tested the prediction that the asymptotic body size of lizards is inversely related to density per habitat by comparing growth curves in different sites. Second, we tested the prediction that lizards reach a higher asymptotic body size sooner in life in the habitat with more food and higher thermal quality while

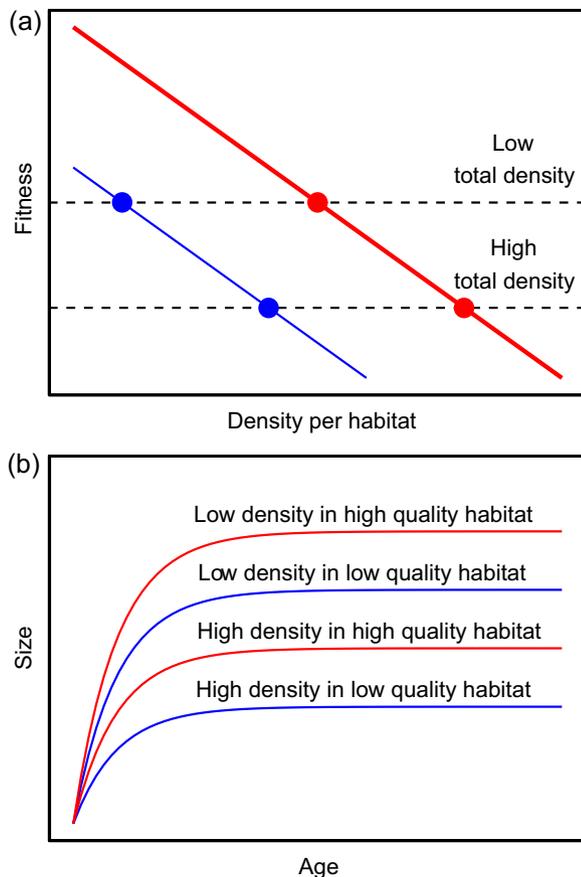


FIGURE 1 (a) The predicted decline in fitness as density in a habitat increases for a low quality (blue) and high quality (red) habitat. The horizontal dashed lines represent two total population densities where individuals are in an Ideal Free Distribution with equal fitness in both habitats. Note that at a given density per habitat, fitness is higher in the high quality habitat. (b) The predicted decline in growth and body size due to population density and habitat quality for the high quality (red; more resources) and low quality (blue; fewer resources) habitats at two levels of density per habitat [Color figure can be viewed at wileyonlinelibrary.com]

controlling for density. In the two-habitat system we studied, tree lizards preferred the habitat with more food and higher thermal quality. If tree lizards are limited by competition for finite food resources, then growth should be higher in the habitat with more food at the same density per habitat (Figure 1b). We tested these predictions with natural variation in density per habitat and body size in ornate tree lizards. To measure growth, we aged lizards with skeletochronology.

2 | MATERIALS AND METHODS

2.1 | Study site and species

We studied ornate tree lizards at six sites in the Chiricahua Mountains of Arizona, United States. Animal use was approved by the University of Ottawa Animal Care Committee (protocols BL286 and BL-2300-R1). Each site was along a creek bed (wash habitat) and

extended 50 m into the adjacent wooded area (upland habitat). The wash habitat had an open canopy and sparse herbaceous vegetation, and the upland habitat consisted of pine-oak woodlands. The two habitats differed in quality relevant to lizard fitness; the wash had more arthropod prey and allowed lizards to achieve their T_{set} (32.2–36.0°C) for a longer period in a day than the upland habitat (Paterson & Blouin-Demers, 2018). Ornate tree lizards preferred the wash habitat and occurred at higher densities in that habitat (Paterson & Blouin-Demers, 2018).

We surveyed each site for lizards 12 times between 1 May 2014 to 5 August 2016. During a survey, we caught lizards (1,000 individuals captured 1,542 times) with a noose and pole while walking through sites and marked the capture location with a handheld GPS unit (± 3 m). We gave each lizard a unique mark with a medical cauterizer (Ekner, Sajkowska, Dudek, & Tryjanowski, 2011; Winne, Willson, Andrews, & Reed, 2006). On a subset ($n = 417$) of captured lizards, we clipped the fourth toe on the right hind limb after disinfecting the foot with chlorhexadine. We stored clipped toes in 95% ethanol. We measured the lizards' snout-vent length (SVL; ± 0.1 mm) with digital calipers and released lizards at their site of capture within 4 hr. Toe-clipping, especially on a single toe as was the case here, is unlikely to affect survival rates compared with the rest of the population because many individuals lose single toes to predators or following aggressive interactions with other lizards and toe-clipping does not affect survival in other small lizards (Wilson, 1991). Clipping multiple toes from individuals, however, would have been likely to decrease survival (McCarthy & Parris, 2004) or other fitness components.

Skeletochronology is the use of cross sections of bone to age individuals that have a distinct annual period with little to no growth (Castanet, 1994). Lines of arrested growth (LAGs) form during periods of nongrowth, such as winter, and can be stained with haematoxylin (Acker, Kruse, & Krehbiel, 1986; Figure S1). We decalcified the second and third phalange using Cal-Ex Decalcifier (Thermo Fisher Scientific, Waltham, MA), and then rinsed toes in deionized water. We sectioned the diaphysis (middle of the bone) of the phalanges at -20°C with a Leica 1850 cryostat (Leica Biosystems Inc., Concord, Ontario, Canada). We stained cross sections in Harris' haematoxylin (Thermo Fisher Scientific), which stains nuclear material purple. We photographed at least five representative sections for each lizard at $\times 100$ magnification under a light microscope and estimated the number of LAGs to determine each lizard's age. Three observers independently counted the number of LAGs for lizards, and the median count was used for estimating a lizard's age.

We calculated the age of lizards in months when growth was possible because tree lizards do not grow during the winter (Dunham, 1982). We used temperature loggers and weather station data to estimate that lizards could grow from 4 May to 1 October (Supporting Information). When calculating age, we assumed all individuals hatched on 1 September (Dunham, 1982).

2.2 | Validation of skeletochronology

There can be considerable variation in bone growth patterns between individuals of the same age (Cope & Punt, 2007). To test

whether LAGs were deposited annually and whether they accurately represented a lizard's age, we compared the estimated age from skeletochronology to the known age of lizards based on mark-recapture data. Tree lizards hatch from eggs in early fall and reach sexual maturity the following spring as yearlings (Dunham, 1982). For mark-recapture data, we assigned lizards as yearlings if their initial SVL was smaller than the minimum size of a lizard known to be alive the previous year (4.75 cm for males and 4.56 cm for females). We then used known-age lizards that had their toes sampled to compare age estimates between mark-recapture data and skeletochronology. Since we sampled lizards from 2014 to 2016, the oldest lizards in our validation sample hatched in 2013 and had their toes sampled in 2016 (a maximum of three winters). We used a paired *t* test to compare age estimates from the two methods.

2.3 | Population density and habitat quality

We used the typical formulation of the VBG curve (Fabens, 1965) to describe ornate tree lizard growth using SVL and age (months). To test the prediction that density negatively affects growth in tree lizards, we tested whether L_{∞} declined with density per habitat. We used the modified VBG curve for incorporating density dependence (Beverton & Holt, 2012; Lorenzen, 1996; Lorenzen & Enberg, 2002):

$$L_t = (L_{\infty} - (g \times d)) \times (1 - e^{-K \times (t - t_0)}).$$

The parameter g is the density-dependent parameter and d is the mean density per habitat (lizards/ha). We calculated population size in each habitat at the beginning of the breeding season from open-population mark-recapture models with one estimate per site in each year (for detailed model descriptions and density data, see Paterson & Blouin-Demers, 2018). One of us (J. E. P.) walked the boundary of each habitat with a handheld GPS unit and calculated the area in QGIS (QGIS Development Team, 2009). Since density per habitat differed between the three years of this study and lizards experienced different densities through time, we used the mean density per habitat. If density per habitat is inversely related to maximum body size, then g should be greater than zero.

To test whether growth rates differed between the wash and the upland habitat, we constructed VBG models with and without separate L_{∞} , g , K , and t_0 parameters for the two habitats. Although we predicted growth rates should be higher in the wash habitat because it has more prey items and higher thermal quality, we did not have a priori predictions for which growth curve parameters would differ between habitats and the parameters are often correlated with each other (Pilling, Kirkwood, & Walker, 2002). Therefore, we constructed all possible model subsets ($n = 15$ models) and compared their fit in an information-theoretic framework (Burnham & Anderson, 2002) using bias-corrected Akaike's information criterion (AIC_c) calculated with the package AIC_{modavg} (Mazerolle, 2017). We constructed separate models for males and females because growth rates and maximum body size differ between the sexes in this species (Tinkle & Dunham, 1983). We ranked

models based on AIC_c and predicted that models with separate parameter estimates for the two habitats would have a lower AIC_c than the models with only one estimate per parameter. We compared the fit of the top-ranking model to the common parameter model (no habitat differences) with likelihood ratio tests. We used bootstrapped coefficient estimates from the top-ranking model of each sex to derive 95% confidence intervals (CIs) on predictions of SVL to compare growth in the wash and upland habitat.

We assigned individuals to a habitat using their mean GPS coordinates for captures. Thus, we assigned individuals to the wash habitat if the mean coordinates were within the wash. All other lizards were assigned to the upland habitat. This habitat assignment assumes that lizard home ranges are circular and stable. The habitat assignment also assumes that lizards with mean coordinates within the wash habitat have access to the thermal and food resources in the wash.

3 | RESULTS

3.1 | Validation of skeletochronology

In 92% of samples, two out of three observers agreed on the number of LAG's observed. In 32% of samples, all three observers agreed on the number of LAG's observed. For the 113 individuals with known ages based on mark-recapture data, age estimates from the two methods were not different ($t = 0.94$, $df = 112$, $P = 0.35$). The mean difference in age between the two methods was 0.18 months (95% CI = -0.55-0.20). Out of the 113 known age individuals, 95 (84%) were correctly aged using skeletochronology.

3.2 | Population density and habitat quality

For females, the growth curve with the lowest AIC_c (Table 1) had a common L_{∞} (5.07, 95% CI = 5.00-5.21) and separate estimates for g , K , and t_0 for lizards in the upland ($g = 0.0024$, 95% CI = 0.0011-0.0038; $K = 2.90$, 95% CI = 0.20-11.70; $t_0 = 0.47$, 95% CI = -0.14-1.07) and the wash ($g = 0.000010$, 95% CI = -0.00061-0.00083; $K = 0.85$, 95% CI = 0.32-1.89; $t_0 = -1.76$, 95% CI = -5.75-2.32) habitats. The estimates of g were positive in both habitats and maximum body size declined with density per habitat (Figure 2a). The top-ranking model fit the data better than the model without differences in growth between habitats ($\Delta AIC_c = 9.79$, $F = 5.44$; $df = 3, 194$, $P = 0.0013$). Using bootstrapped estimates of the growth curve coefficients in the top-ranked model to generate 95% CIs of predicted body size, female lizards reached larger maximum sizes in the wash habitat at the mean density per habitat (76 lizards/ha; Figure 3a).

For males, the growth curve with the lowest AIC_c (Table 2) had a common L_{∞} (5.12, 95% CI = 5.03-5.36), g (-0.00026, 95% CI = -0.00069-0.00017), K (0.34, 95% CI = 0.11-0.73), and t_0 (-6.17, 95% CI = -18.55 to -2.07) for lizards in both habitats. The top-ranking model did not include any differences in growth between habitats. The estimate of g was negative, but the CI overlapped with zero and the predicted maximum body size did not change with habitat density (Figure 2b). Using bootstrapped estimates of the growth curve

TABLE 1 von Bertalanffy growth curves of female ornate tree lizards (*Urosaurus ornatus*) comparing growth in the upland ($n = 89$) and wash ($n = 109$) habitats from six sites in the Chiricahua Mountains of Arizona, United States

| Model | AIC _c | ΔAIC _c | k | ω |
|---|------------------|-------------------|---|------|
| $L_{\infty}(\sim 1)g(\sim \text{hab})K(\sim \text{hab})t_0(\sim \text{hab})$ | 31.10 | | 7 | 0.34 |
| $L_{\infty}(\sim 1)g(\sim \text{hab})K(\sim \text{hab})t_0(\sim 1)$ | 31.93 | 0.83 | 6 | 0.22 |
| $L_{\infty}(\sim \text{hab})g(\sim \text{hab})K(\sim \text{hab})t_0(\sim \text{hab})$ | 33.08 | 1.98 | 8 | 0.12 |
| $L_{\infty}(\sim 1)g(\sim \text{hab})K(\sim 1)t_0(\sim \text{hab})$ | 33.26 | 2.16 | 6 | 0.11 |
| $L_{\infty}(\sim \text{hab})g(\sim \text{hab})K(\sim \text{hab})t_0(\sim 1)$ | 34.10 | 2.99 | 7 | 0.08 |
| $L_{\infty}(\sim \text{hab})g(\sim 1)K(\sim \text{hab})t_0(\sim \text{hab})$ | 35.11 | 4.00 | 7 | 0.05 |
| $L_{\infty}(\sim \text{hab})g(\sim 1)K(\sim \text{hab})t_0(\sim 1)$ | 36.38 | 5.27 | 6 | 0.02 |
| $L_{\infty}(\sim 1)g(\sim \text{hab})K(\sim 1)t_0(\sim 1)$ | 36.48 | 5.37 | 5 | 0.02 |
| $L_{\infty}(\sim \text{hab})g(\sim \text{hab})K(\sim 1)t_0(\sim 1)$ | 37.67 | 6.57 | 6 | 0.01 |
| $L_{\infty}(\sim \text{hab})g(\sim 1)K(\sim 1)t_0(\sim \text{hab})$ | 37.68 | 6.58 | 6 | 0.01 |
| $L_{\infty}(\sim \text{hab})g(\sim 1)K(\sim 1)t_0(\sim 1)$ | 40.27 | 9.17 | 5 | 0.00 |
| $L_{\infty}(\sim 1)g(\sim 1)K(\sim 1)t_0(\sim 1)$ | 40.89 | 9.79 | 4 | 0.00 |
| $L_{\infty}(\sim 1)g(\sim 1)K(\text{hab})t_0(\sim 1)$ | 41.41 | 10.30 | 5 | 0.00 |
| $L_{\infty}(\sim 1)g(\sim 1)K(\sim 1)t_0(\sim \text{hab})$ | 41.46 | 10.36 | 5 | 0.00 |
| $L_{\infty}(\sim 1)g(\sim 1)K(\sim \text{hab})t_0(\sim \text{hab})$ | 43.37 | 12.27 | 6 | 0.00 |

Note. AIC_c: Akaike's information criterion for a model; g : the effect of density on maximum body size; k : number of parameters in a model; K : the rate at which lizards approach the asymptotic body size; L_{∞} : the mean maximum body size before density dependent effects; t_0 : the age when average length is zero; ΔAIC_c: difference in AIC_c between a model and the top-ranked model; ω : Akaike weight for a model; ~ 1 : one estimate for all female lizards; $\sim \text{hab}$: different estimates for the wash and upland habitat.

coefficients in the top-ranked model that included habitat differences to generate 95% CI of predicted body size, male lizards at the mean density per habitat (76 lizards/ha) reached similar sizes in the upland and wash habitats. The 95% CI of predicted SVL in the wash and upland overlapped for the whole range of ages that we sampled (Figure 3b).

4 | DISCUSSION

Our data partially support the hypothesis that ornate tree lizard growth is limited by competition for resources and habitat quality. Maximum body size decreased as density per habitat increased in females, but there was no effect of density on body size in males. In females, there was evidence that habitat quality affected growth; lizards in the wash reached a higher maximum body size than lizards in the upland habitat when controlling for density per habitat. There was no evidence that habitat quality influenced growth rate or maximum body size in males.

Female tree lizard body size was limited by resource competition: maximum body size decreased with density per habitat based on our predictions of body size. The top three models (all within two AIC units) included differences in growth parameters between habitat types. Density-dependent growth is common in other ectotherms, such as fish (Imre, Grant, & Cunjak, 2005; Lorenzen & Enberg, 2002;

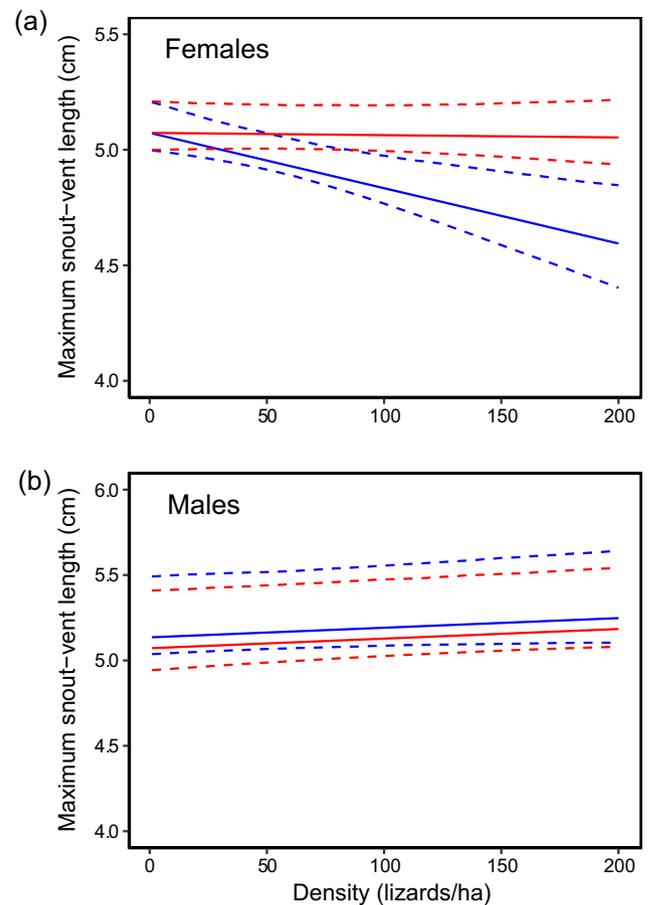


FIGURE 2 The relationship between density per habitat and maximum snout-vent length ($L_{\infty} - (g \times d)$) for ornate tree lizards (*Urosaurus ornatus*) using von Bertalanffy growth curves with a density-dependent term for (a) females and (b) males in the upland (low quality, blue) and wash (high quality, red) habitats. The top-ranked model for males completely overlaps in both habitats. Dashed lines represent 95% CI of predicted maximum lengths using bootstrapping [Color figure can be viewed at wileyonlinelibrary.com]

Post, Parkinson, & Johnston, 1999) and some lizards (Massot et al., 1992; Mugabo et al., 2013). However, density-dependent growth has not previously been linked to habitat selection in wild lizard populations. We found a negative effect of population density on maximum body size in females, but was the effect biologically relevant (as opposed to statistically significant)? The predicted change in asymptotic SVL from the minimum to maximum observed densities per habitat (0.24 cm) represents 14% of the total variation in female SVL (3.93–5.65 cm). In tree lizards, clutch size is directly related to female body size (Landwer, 1994). An increase in body size of 0.24 cm would correspond to a 22% increase in clutch size based on the mean clutch size of nine eggs for tree lizards in the Chiricahua Mountains (Dunham, 1982). Therefore, the estimated change in body size due to density dependence appears biologically relevant for female tree lizards.

There was no evidence that density per habitat affected maximum body size in male tree lizards because the estimate of g was negative and the CI overlapped zero. The differences between

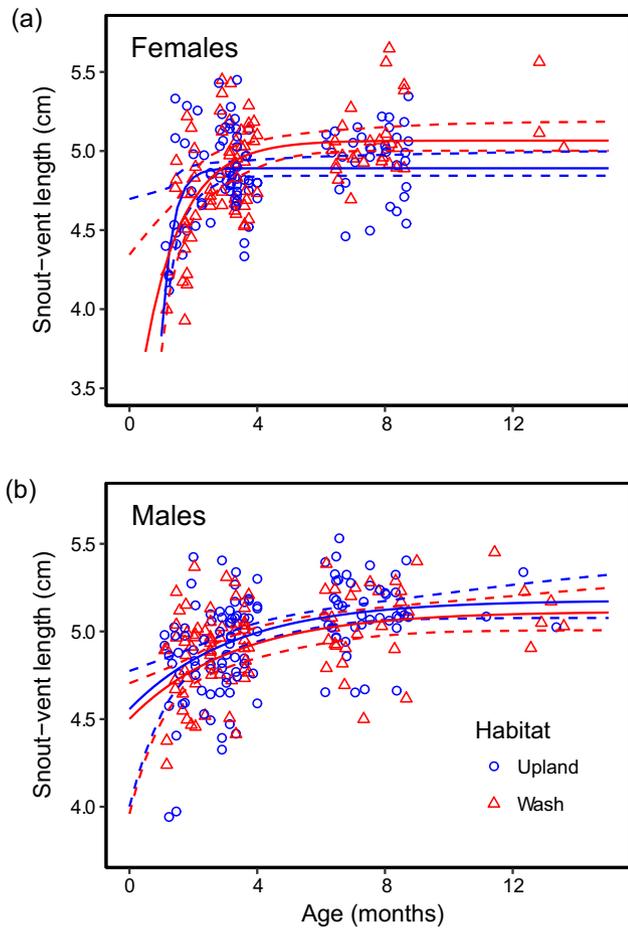


FIGURE 3 von Bertalanffy growth curves for ornate tree lizards (*Urosaurus ornatus*) in the upland (low quality, blue) and wash (high quality, red) at the mean density per habitat (76 lizards/hectare). (a) Females in the wash habitat ($n = 109$) reached a longer maximum SVL than females in the upland habitat ($n = 89$). (b) Males in the upland ($n = 92$) and wash ($n = 127$) habitats did not differ in body size or growth. Dashed lines represent 95% CI of predicted lengths using bootstrapping. CI: confidence interval; SVL: snout-vent length [Color figure can be viewed at wileyonlinelibrary.com]

males and females in the response to population density may be caused by differences in how and when each sex invests energy in growth and reproduction (Roff, 2000; Stearns, 1989). Males were larger than females at the beginning of their first breeding season and growth had already slowed down, whereas females grew rapidly during the beginning of their first breeding season until they became gravid. Female investment in egg production reduces growth rates (Landwer, 1994) and growth slows down significantly after female lizards start producing eggs. Males grow rapidly early in life because their ability to secure a territory at the beginning of the breeding season is positively related to body size (Carpenter, 1995). Therefore, the relationship between body size and fitness is different in males and females due to the timing of reproductive demands. Alternatively, we may have failed to detect an effect of density per habitat on maximum body size in males because the most rapid growth occurred when lizards were small and we did not sample during the first few months of life. Finally, there may simply be no

TABLE 2 von Bertalanffy growth curves of male ornate tree lizards (*Urosaurus ornatus*) comparing growth in the upland ($n = 92$) and wash ($n = 127$) habitats from six sites in the Chiricahua Mountains of Arizona, United States

| Model | AICc | Δ AICc | k | ω |
|---|------|---------------|---|----------|
| $L_{\infty}(\sim 1)g(\sim 1)K(\sim 1)t_0(\sim 1)$ | 4.08 | | 4 | 0.14 |
| $L_{\infty}(\sim \text{hab})g(\sim 1)K(\sim 1)t_0(\sim 1)$ | 4.26 | 0.18 | 5 | 0.13 |
| $L_{\infty}(\sim 1)g(\sim \text{hab})K(\sim 1)t_0(\sim 1)$ | 4.64 | 0.56 | 5 | 0.11 |
| $L_{\infty}(\sim 1)g(\sim 1)K(\sim \text{hab})t_0(\sim \text{hab})$ | 4.84 | 0.76 | 6 | 0.10 |
| $L_{\infty}(\sim \text{hab})g(\sim 1)K(\sim 1)t_0(\sim \text{hab})$ | 4.88 | 0.80 | 6 | 0.09 |
| $L_{\infty}(\sim \text{hab})g(\sim 1)K(\sim \text{hab})t_0(\sim 1)$ | 5.00 | 0.92 | 6 | 0.09 |
| $L_{\infty}(\sim 1)g(\sim 1)K(\text{hab})t_0(\sim 1)$ | 6.00 | 1.92 | 5 | 0.05 |
| $L_{\infty}(\sim 1)g(\sim 1)K(\sim 1)t_0(\sim \text{hab})$ | 6.17 | 2.08 | 5 | 0.05 |
| $L_{\infty}(\sim 1)g(\sim \text{hab})K(\sim 1)t_0(\sim \text{hab})$ | 6.21 | 2.12 | 6 | 0.05 |
| $L_{\infty}(\sim \text{hab})g(\sim \text{hab})K(\sim 1)t_0(\sim 1)$ | 6.36 | 2.27 | 6 | 0.04 |
| $L_{\infty}(\sim 1)g(\sim \text{hab})K(\sim \text{hab})t_0(\sim 1)$ | 6.43 | 2.34 | 6 | 0.05 |
| $L_{\infty}(\sim \text{hab})g(\sim 1)K(\sim \text{hab})t_0(\sim \text{hab})$ | 6.88 | 2.79 | 7 | 0.03 |
| $L_{\infty}(\sim 1)g(\sim \text{hab})K(\sim \text{hab})t_0(\sim \text{hab})$ | 6.93 | 2.85 | 7 | 0.03 |
| $L_{\infty}(\sim \text{hab})g(\sim \text{hab})K(\sim \text{hab})t_0(\sim 1)$ | 7.08 | 2.99 | 7 | 0.03 |
| $L_{\infty}(\sim \text{hab})g(\sim \text{hab})K(\sim \text{hab})t_0(\sim \text{hab})$ | 9.01 | 4.93 | 8 | 0.01 |

Note. AICc: Akaike's information criterion for a model; g: the effect of density on maximum body size; k: number of parameters in a model; K: the rate at which lizards approach the asymptotic body size; L_{∞} : the mean maximum body size before density dependent effects; t_0 : the age when average length is zero; Δ AICc: difference in AICc between a model and the top-ranked model; ω : Akaike weight for a model; ~ 1 : one estimate for all male lizards; $\sim \text{hab}$: different estimates for the wash and upland habitat.

effect of density per habitat on male ornate tree lizard body size and growth.

Maximum female body size was higher in the wash habitat than in the upland habitat when controlling for density per habitat, but there was no significant difference in growth between habitat types for males. Thus, there was partial support for our hypothesis that habitat selection is density dependent due to growth being limited by intraspecific competition for resources and habitat quality. We predicted that maximum body size and growth rates should be higher in the wash at a given density per habitat because of increased food availability and higher thermal quality in the wash. Other studies have found evidence that habitat quality influences growth rate in amphibians (Sinsch, Leskovar, Drobig, König, & Grosse, 2007), fishes (Phelan et al., 2000; Sogard, 1992), lizards (Dunham, 1978), and turtles (Brown, Bishop, & Brooks, 1994). The growth curve with the lowest AICc for females included separate estimates of g, K, and t_0 for lizards in each habitat and the differences were in the predicted direction with a higher maximum body size in the wash habitat than the upland habitat. This top-ranking model had much higher support than a model with no differences between habitats. In males, there was no evidence that habitat quality affected body size and growth; the top-ranking model did not have any differences between habitats. Therefore, the effect of habitat quality on tree lizard body size and growth was present in females, but undetectable in males.

There are several potential reasons the male growth data do not support our prediction about differences in growth between habitats. First, it is possible there is no difference in growth between the two habitats and male lizards prefer the wash habitat because females prefer that habitat. Second, we could have failed to detect a difference in growth between habitats in males because we did not have enough observations or because we lacked body size data during the initial 2 months of life after hatching when growth rates are the highest (Tinkle & Dunham, 1983). Our study focused on individuals that already had reached sexual maturity, but competition for food resources is likely also strong in juvenile lizards because they grow rapidly. Compared with females, male growth rate had already significantly declined by the beginning of the first breeding season. Future studies examining the effect of habitat quality on male tree lizard growth should include hatchlings since growth is most rapid early in life.

Our data partially support the hypothesis that finite resources can limit the abundance and influence the distribution between habitats of ectotherms, even when there are differences in thermal quality between habitats; our hypothesis was supported in females, but not in males. If populations were limited by the ability to process resources (i.e., temperature) instead of their ability to acquire resources (i.e., food abundance), then body size and growth should be unaffected by density per habitat. The tree lizards we studied reached high densities per habitat (200 lizards/ha) where competition for finite resources reduced body size and growth, at least in females. Although thermal quality may still be important for habitat selection and performance in tree lizards, it did not limit populations enough to alleviate competition for finite food resources. This supports our hypothesis that ectotherm habitat selection and abundance are regulated by density-dependent mechanisms when temperatures are close to T_{set} . Future work should test whether environmental temperatures modulate the strength of density-dependent effects in wild populations. This could be accomplished with studies along altitudinal or latitudinal gradients.

We observed large variation in body size and growth between individuals of ornate tree lizards. We found evidence that maximum female body size is limited by density per habitat and this emphasizes the effect of intraspecific competition and density dependence on the abundance and distribution of lizards. There was no evidence that population density negatively affected maximum body size in males. We presented evidence that females became larger in the wash habitat when controlling for density per habitat, and this links individual fitness to habitat quality and habitat selection.

ACKNOWLEDGEMENTS

We thank Valérie Bertrand, Martine Doucet, Lucy Patterson, Peter Soroye, Dariya Quenneville, and Hannah Watkins for assistance with data collection in the field. Liam Eaton assisted with laboratory data collection. We are grateful for logistical support provided by the Southwestern Research Station. Lizards were collected under

Arizona Fish and Game Department Scientific Collector's Permits (Nos. SP674341, SP713940, and SP740592) and approved by Coronado National Forest. This study was funded by a Natural Sciences and Engineering Research Council of Canada (NSERC) grant to G. B. D. and an NSERC scholarship and Ontario Graduate Scholarship to J. E. P.

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How to cite this article: Paterson JE, Blouin-Demers G. Tree lizard (*Urosaurus ornatus*) growth decreases with population density, but increases with habitat quality. *J. Exp. Zool.* 2018;1–9. <https://doi.org/10.1002/jez.2216>