

Research

Density-dependent habitat selection predicts fitness and abundance in a small lizard

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Density-dependent habitat selection has been used to predict and explain patterns of abundance of species between habitats. Thermal quality, a density-independent component of habitat suitability, is often the most important factor for habitat selection in ectotherms which comprise the vast majority of animal species. Ectotherms may reach high densities such that individual fitness is reduced in a habitat due to increased competition for finite resources. Therefore, density and thermal quality may present conflicting information about which habitat will provide the highest fitness reward and ectotherm habitat selection may be density-independent. Using ornate tree lizards *Urosaurus ornatus* at 10 sites each straddling two adjacent habitats (wash and upland), we tested the hypothesis that habitat selection is density-dependent even when thermal quality differs between habitats. We first tested that fitness proxies decline with density in each habitat, indicating density-dependent effects on habitat suitability. We also confirmed that the two habitats vary in suitability (quantified by food abundance and thermal quality). Next, we tested the predictions that habitat selection depends on density with isodar analyses and that fitness proxies are equal in the two habitats within a site. We found that monthly survival rates decreased with density, and that the wash habitat had more prey and higher thermal quality than the upland habitat. Lizards preferred the habitat with more food and higher thermal quality, lizard densities in the two habitats were positively correlated, and fitness proxies of lizards did not differ between habitats. These patterns are consistent with density-dependent habitat selection, despite differences in thermal quality between habitats. We expect that density-dependent habitat selection is widespread in terrestrial ectotherms when densities are high and temperatures are close to their optimal performance range. In areas where thermal quality is low, however, we expect that depletable resources, such as food, become less limiting because assimilating resources is more difficult.

Introduction

Explaining spatial and temporal patterns in the abundance of species is one of the major goals of ecology (Krebs 2001). Within the geographical range of a species, habitat selection can strongly influence the distribution and abundance of individuals



(Morris 1989, Binckley and Resetarits 2005, Resetarits 2005). Resources are not equally distributed across space and time, and the habitat an animal chooses to occupy thus has profound impacts on its growth, survival, reproduction, and, ultimately, fitness (Morris 1989, Matthiopoulos et al. 2015). The spatial and temporal heterogeneity of resource distribution provides an opportunity for organisms to maximize their fitness by choosing the highest quality habitat available. The quality or suitability of a habitat is determined by the average success rate (survival and reproductive success) of individuals that occupy the habitat, and depends on factors such as food abundance, shelter availability, and nest site quality (Fretwell and Lucas 1969).

If organisms choose habitats to maximize fitness and are free to occupy any habitat, then individual fitness is predicted to equalize across habitats due to the negative effects of population density on individual fitness (Fretwell and Lucas 1969). This model of habitat selection, known as the ideal free distribution (Fretwell and Lucas 1969, Fretwell 1972, Rosenzweig 1981), forms the theoretical base for explaining the distribution of organisms between habitats. The ideal free distribution can be modified to incorporate territoriality (Fretwell 1972), predators (Hugie and Dill 1994), and competition with other species (Morris 2003). Habitat selection patterns can be analysed with isodars (Morris 1988) which are lines on density-density plots for each habitat pair where fitness is equalized. The shape and parameters (coefficients and intercept) of the isodars can be used to infer whether habitat selection depends on density, which habitat is preferred, and whether there is an effect of territoriality on habitat use. These theoretical distributions have been important in predicting the distribution of organisms between habitats and the fitness consequences of habitat selection (Petit and Petit 1996, Krivan et al. 2008, Matthiopoulos et al. 2015), but the models were developed for organisms for which habitat suitability depends strongly on depletable resources.

Habitat selection models rely on density-dependence where fitness in a habitat decreases as density increases (Skogland 1985, Clutton-Brock et al. 1987, Morris 1989, Krebs 2001). The negative effects of crowding, including reduced resource availability, increased competition, and increased risk of disease transmission, reduce individual fitness and population growth rates (Harms et al. 2000, Ohman and Hirche 2001, Mugabo et al. 2015). As the most suitable habitats become crowded, mean fitness declines until individuals start to achieve the same fitness by settling in a less suitable habitat that is less crowded. These negative effects of crowding can be detected in fitness proxies, such as individual growth rates, reproductive output, and survival rates. Density-dependent habitat selection has received widespread empirical support in observational and in experimental studies (Morris 1987, 1989, Barkae et al. 2014, Falcy 2015). However, there is much less known about habitat selection when there is conflicting information about the expected fitness in a habitat, such as when habitats are crowded, but contain an important density-independent resource.

Thermal quality is often one of the most important factors for habitat selection in ectotherms (Hughes and Grand 2000, Blouin-Demers and Weatherhead 2001, Monasterio et al. 2009, Lelièvre et al. 2011, Picard et al. 2011, Halliday and Blouin-Demers 2016). Thermal quality is important for habitat selection in ectotherms because physiological performance (Huey 1991) and fitness (Huey and Berrigan 2001) are related to body temperature and because ectotherms use habitat selection to thermoregulate. Therefore, habitat suitability for ectotherms is often strongly related to temperature; abundance and habitat selection may be more affected by their ability to process resources than by their ability to acquire resources. Because thermal quality should not decline with population density, ectotherm habitat selection, and thus distribution between habitats, may not respond to density. For example, some snakes select habitats independently of density because of the high fitness costs associated with occupying habitats of poor thermal quality (Halliday and Blouin-Demers 2016). Although it is possible that basking sites (Calsbeek and Sinervo 2002) or thermal refuges (Downes and Shine 1998) are finite and individuals compete for these resources (Magnuson et al. 1979), evidence of species competing for and partitioning thermal resources is equivocal (Paterson and Blouin-Demers 2017a). The magnitude of density-dependent effects in ectotherms may depend on environmental temperatures, and may only occur when temperatures are close to where performance is maximized. In beetles, for instance, the strength of density-dependence increases as temperature approaches the optimal temperature for performance (Halliday et al. 2015). Considering the conflicting and variable effects of density on ectotherm populations, the relationship between temperature, competition, and habitat selection remains largely unresolved. The tradeoff between density-dependent costs and the benefits of high thermal quality is an example of animals presented with conflicting information about the expected fitness rewards of a habitat. High densities will likely reduce fitness in a habitat, but the fitness benefits of choosing a habitat with high thermal quality may outweigh the fitness costs of crowding. Conflicting information for habitat selection may also occur with other aspects of habitat suitability that are density-independent, such as risk of mortality from abiotic factors (Sinclair 1989) or predation (Blancher and Robertson 1985).

We tested the hypothesis that density-dependent habitat selection can explain patterns of abundance of ornate tree lizards *Urosaurus ornatus* between two habitats with different vegetation structure that affects thermal quality and prey abundance. Lizards are a good system to test the importance of density-dependence in habitat selection by ectotherms because they occur at high densities and thus food may be limited, especially in warmer regions, and because their habitat selection is strongly influenced by temperature (Huey 1991, Smith and Ballinger 2001). Furthermore, lizards are generally easy to capture, facilitating estimates of fitness proxies. Tree lizards in particular are a good species to test

this hypothesis because they vary in density, have small stable home ranges, and their demography, thermoregulation, and reproduction have been well documented (M'Closkey et al. 1987, 1990, Thompson and Moore 1991). Habitat selection usually occurs at multiple spatial scales (Johnson 1980) and there can be tradeoffs in the use of different habitats within a home range (Myserud and Ims 1998), but we focussed on habitat selection at the home range scale. Using mark–recapture data on lizards at 10 sites each straddling the same two habitats (wash and upland), we first tested that fitness proxies decline with density, indicating density-dependent effects on habitat suitability. We also confirmed that the two habitats differ in food abundance and in thermal quality. We then tested whether habitat selection is density-dependent using isodar analyses (Morris 1988). If habitat selection is density-dependent, then the isodar should have a slope different than zero and density in one habitat should increase as density in the other habitat increases. Finally, we tested whether fitness proxies are equal in each habitat. If lizards are selecting habitats in a density-dependent manner, then mean fitness should equalize between habitats within a site.

Material and methods

Study area and study species

We studied tree lizards in the Chiricahua Mountains of south-eastern Arizona, USA. This species occurs in several habitats, but we used adjacent treed (upland) and open canopy creek bed (wash) habitats (Supplementary material Appendix 1 Fig. A1) in canyons because it provides an obvious difference in structure that likely affects both food (arthropod) abundance and thermoregulatory opportunities. Tree lizard density was measured at 10 sites that were centred on a wash and extended 50 m from the high-water mark into the upland habitat (Supplementary material Appendix 1 Fig. A2). Sites were at least 300 m apart, which is beyond the upper 95th percentile of reported dispersal distances of side-blotched lizards *Uta stansburiana*, a closely related species (Doughty et al. 1994). In addition, no marked individuals moved between sites during our study. Vegetation in the wash was sparse and mostly herbaceous; the upland habitat consisted of pine–oak woodlands. Six sites were monitored from 2014 to 2016 (12 capture sessions) and were 300 m by 50 m, and four additional sites were monitored in 2016 (two capture sessions) and were 50 m by 50 m (Supplemental material Appendix 1 Table A1). The four sites added in 2016 increased our sample size for comparing density in each habitat type.

For each capture session, observers searched the entire plot and captured lizards by noose (García-muñoz and Silero 2010). The entire plot was searched at least three times per session and we recorded the total search effort (in person hours) for each survey. One of us (JP) was present during every capture session and trained other researchers on finding and catching tree lizards. In addition, researchers often helped one another to capture lizards. Therefore,

researcher identity likely had little effect on detection probability during surveys. The capture location of each lizard was marked with a hand-held GPS unit (accuracy ± 3 m) and individuals were released at their capture location on the same day. We measured the snout–vent length (SVL) with digital calipers (± 0.1 mm) and mass with a digital scale (± 0.01 g). Individuals were marked with a medical cauterizer and given a unique code on their ventral side (Winne et al. 2006, Ekner et al. 2011). We assumed these markings are permanent: several lizards marked early in the study were recaptured with identifiable marks more than two years later.

Individual lizards were assigned to the upland or to the wash habitat based on the mean coordinates of their capture locations. We did not assign individuals to an edge habitat because the wash was on average narrower than the radius of the home range. This habitat assignment assumes that lizards that have home ranges in the wash have access to the food and thermal resources in that habitat. We used mark–recapture data and targeted behavioural observations to determine the extent to which individuals switched between habitats (Supplementary material Appendix 2). Lizards in the wash habitat and the edge of the upland habitat switched between habitats during behavioural observations and lizards closer to the wash were more likely to switch between habitat types (Supplementary material Appendix 2). The proportion of habitat switching was, however, similar in both directions (wash to upland, and upland to wash). Therefore, we believe our habitat assignment is an accurate depiction of lizard habitat use. Our habitat assignment also assumes that the mean coordinates accurately represent space use. Because tree lizards are very territorial (Mahrt 1998) and because of the short distances between our captures (mean of 11 m for males and 8 m for females), we believe this assumption is justified.

Density dependence of fitness proxies

We used two fitness proxies, survival and growth rate, to assess whether there was density dependence in tree lizard populations. Survival was estimated in each habitat for the six sites monitored for three years using mark–recapture models in the package 'RMark' (Laake 2013) to access the program MARK (White and Burnham 1999) in R (< www.r-project.org >). We could not estimate monthly survival at the four sites sampled for one year because we only had two capture sessions only a few weeks apart for these four sites. To estimate survival at each site monitored for three years, we used the POPAN formulation (Schwarz and Arnason 1996) of the Jolly–Seber (JS) open population model (Jolly 1965, Seber 1965). The POPAN formulation of the JS model has four parameters estimated through maximum likelihood to model populations open to births, deaths, immigration, and emigration. The probability of observing an individual at a capture event is estimated with parameters for apparent survival (Φ) and detection probability (p). The other two parameters model the probability of new individuals entering the population: \hat{N} , the total number of individuals available to enter the population and $pent$, the probability of new individuals

from \hat{N} entering the site at each occasion. We started with a general model that allowed Φ to vary with habitat, sex, season (active or overwinter) and year. The general model allowed p to vary with habitat, sex, search effort (person hours per capture event), and weather. To include a covariate of weather, we used daily summaries of precipitation, maximum temperature, minimum temperature, and mean observed temperature from a nearby weather station operated by the National Oceanic and Atmospheric Administration at the Southwestern Research Station (Menne et al. 2012). We used a principal component analysis (function: 'princomp') to summarize weather data for each day, and the first principal component (capturing 51% of the total variation in daily weather) was used as a covariate for detection probability. The first principal component describing daily variation in weather had a positive loading for precipitation (0.16) and negative loadings for maximum temperature (-0.66), minimum temperature (-0.39), and mean temperature (-0.62). Although the second principal component had a positive loading for precipitation (0.76), we did not consider it as a covariate for detection probability because we did not survey for lizards on days with a lot of precipitation. We used one \hat{N} for each site, and the general model allowed $pent$ to vary with habitat, sex, and year. The estimates for $pent$ during the active season were all close to zero, so we fixed the parameters to zero during this time so that new individuals could only enter the population between breeding seasons. This is consistent with the natural history of tree lizards because recruitment from egg hatching does not occur until late summer or fall and individuals are unlikely to immigrate during the breeding season. We tested the assumptions of the models by assessing goodness-of-fit for the general model at each site (Supplementary material Appendix 3).

We constructed all possible subsets of the general model and ranked them based on AIC_c (or $QAIC_c$ if there was evidence of over dispersion; Supplementary material Appendix 3) to determine the most supported models for each site (Burnham and Anderson 2002). Using a subset of models with moderate support ($\Delta AIC_c < 4$ compared to the most supported model), we averaged model predictions based on their relative support to account for model uncertainty (Burnham and Anderson 2002, Cade 2015). The estimates for Φ were used to test predictions of density-dependence and habitat differences in fitness.

Individual growth rates were estimated from differences in size in recaptured lizards. The difference in SVL (SVL at last capture - SVL at first capture) was divided by the number of days since the lizard was last captured. We removed inactive days during the winter when lizards were unlikely to grow (1 November to 1 April; Dunham 1982). Since most growth occurs in the first year of life, we restricted growth analyses to individuals less than one year old. Lizards were classified as yearlings when their initial SVL was smaller than the minimum size of a lizard known to have been alive the previous breeding season (4.58 cm for females, 4.75 cm for males).

We estimated population size at the beginning of each breeding season, which is from May to August, when adult density is highest. For the six sites monitored for three years, we used the estimated abundances from the POPAN formulation (Schwarz and Arnason 1996) of the Jolly-Seber (JS) open population model (Jolly 1965, Seber 1965). Population size at each occasion was derived with the model-averaged parameter predictions. For the four sites monitored for one year, we estimated population size using closed population models (Otis et al. 1978); the two capture events occurred less than a month apart (Supplementary material Appendix 1 Table A1), thus the assumption of closure was reasonable. Closed population models have three parameters: c (the probability a marked individual is recaptured), p (the probability an unmarked individual is captured), and $f\theta$ (the number of individuals in the population that are never captured). Because there were only two capture events at each site, we used a general model where $c=p$ and varied with habitat, and $f\theta$ varied with habitat. We constructed all four possible models and averaged parameters for well-supported models ($\Delta AIC_c < 4$ from most supported model). Population size was estimated by adding the estimates for $f\theta$ to the number of marked individuals at each site. We calculated habitat density by dividing the population size for each habitat by the area of each habitat.

To test the assumption that fitness declines with density, we examined how population density was related to survival and individual growth rates. First, we tested how monthly survival was related to population density in a habitat with a linear model (function 'lm'). We used mean monthly survival in a habitat (one estimate per habitat in each of the six sites with survival estimates) as the response, and mean population density in the habitat, habitat type, and the interaction between habitat and population density as predictor variables. We did not include separate estimates of survival for each of the three years with a random effect of site because we only had six sites and because there was little variation in survival between years at a site (SD of survival 0 to 0.18). Second, we tested how individual growth rate for yearlings at all 10 sites was related to population density in a habitat, habitat type, and the interaction between density and habitat type using a linear mixed-effects model (function 'lmer') with the package 'lme4' (Bates et al. 2014). We included sex as a fixed control variable in the growth regression model because growth rate often differs between sexes in lizards (El Mouden et al. 1999, Haenel and John-Alder 2002). We also included site as a random effect.

Habitat suitability

To determine which habitat had a higher suitability, we quantified food abundance and thermoregulatory opportunities in upland and wash habitats. Tree lizards are generalist arthropod predators (Aspland 1964), so we measured prey abundance with pitfall traps to sample arthropods. Pitfall traps are known to be biased towards more active species

(Greenslade 1964, Topping and Sunderland 1992), but we assumed any taxonomic bias in capture probability was the same in both habitats. It is possible, however, that there was some bias in the pitfall trap captures and, consequently, that the detectability of arthropods varied between habitats (Melbourne 1999, Koivula et al. 2003). We used the total number of prey items as an indicator of prey abundance in each habitat. We chose to analyze prey number rather than prey volume because the prey volume data were extremely skewed and strongly violated the assumptions of the models. Total volume of prey was strongly and positively correlated with the number of arthropod prey in a trap ($r=0.55$, $p < 0.00001$). Therefore, we believe our approach to quantifying differences in arthropod abundance between habitats based on the number of prey caught per trap is justified. Pitfall traps consisted of plastic cups (9.5 cm diameter) buried flush to the ground with 2–4 cm of water and a few drops of soap. Traps were set for 24 h in 10 locations on each trapping day (five per habitat). Trap locations were chosen using a stratified random design, with random locations in both habitats within 50 m blocks for sites studied for three years and within 10 m blocks for sites studied for one year. At the six sites studied for three years, food abundance was measured three times (once each in May, June and July) per year to account for possible seasonal changes in arthropod abundance. At the four sites studied for one year, arthropods were only sampled in June. To compare food availability between habitats, we constructed a linear mixed-effects model (function: 'lmer') using the package 'lme4' (Bates et al. 2014) with the number of prey caught per trap (log transformed) as the dependent variable, and habitat (wash or upland), month, year, and the interaction between habitat and month as independent variables. We included site as a random effect.

Thermal quality was measured in each habitat with temperature loggers whose readings were compared to the species' preferred body temperature (T_{set}). We measured the T_{set} of tree lizards with a thermal gradient in controlled conditions at the Southwestern Research Station. During May–June 2014, we captured tree lizards ($n=41$) in the same habitat types near our study sites to measure T_{set} . The thermal gradient was heated at one end with heating pads to create a smooth temperature gradient of 20 to 50°C. The minimum gradient temperature was below the preferred temperature and the maximum was above the critical thermal maximum for most iguanid lizards (Kour and Hutchison 1970). Lizards were acclimatized to the gradient overnight (12 h). During the trial, lizard skin temperature was measured on the dorsal surface every half hour for eight hours with an infrared thermometer ($\pm 0.1^\circ\text{C}$). Measuring skin temperature with an infrared thermometer is a good estimate of internal body temperature (T_b) in small-bodied lizards (Herczeg et al. 2006, Carretero 2012, Bouazza et al. 2016). The central 50% of the distribution of T_b (25th – 75th quantiles) was used as the T_{set} for each lizard in the thermal gradient. The means of the 25th and 75th quantiles were used as the T_{set} for the species.

Operative environmental temperatures (T_e) represent the range of T_b a lizard could experience in a given habitat. We measured T_e with temperature loggers (Maxim Thermo-chron iButton, $\pm 0.5^\circ\text{C}$) covered with a rubber coating and painted brown to reflect the thermal properties of tree lizards (Herczeg et al. 2006). We validated that our thermal models accurately predicted the body temperature of tree lizards (Supplementary material Appendix 1 Fig. A3; $R^2=0.99$). Models were randomly placed on rocks and on tree trunks (at 1.5 m height) to represent common perching areas of lizards at each site. In our observations where perch location was noted ($n=529$), 64% of lizards perched on trees or rocks and these were the most common perching microhabitats. There was one pair of models at each site and they were moved between microhabitats approximately once per month. To quantify the thermal quality of each habitat, we calculated the number of hours per day a lizard could achieve T_{set} . For each hour, we calculated the maximum and minimum T_e available to lizards in a habitat at a site. We considered T_{set} achievable as long as the maximum temperature was above the lower bound of T_{set} and the minimum temperature was below the upper bound of T_{set} . We used measurements between 07:00 and 17:00 because this is when tree lizards are most active (this time interval comprised 95% of all our captures).

To compare thermal quality between sites and habitats, we used a linear mixed effects model to test whether the number of hours a lizard could reach T_{set} was related to habitat, month, and the interaction between habitat and month. We included site as a random effect.

To test whether habitat density depended on habitat quality, we used a linear mixed effects model (function 'lmer') in the package 'lme4' (Bates et al. 2014). We used density in a habitat as the dependent variable. We used the mean number of prey caught in pitfall traps, the mean number of hours in T_{set} , and habitat type as fixed effects. We included site as a random effect.

To test whether fitness proxies of lizards were affected by habitat quality, we used linear models. We used a linear model (function 'lm') with monthly survival as the dependent variable, and we used the mean number of prey caught in pitfall traps, the mean number of hours in T_{set} , habitat type, and habitat density as fixed effects. We used a linear mixed-effects model (function 'lmer') in the package 'lme4' (Bates et al. 2014) with growth rate as the dependent variable, and the mean number of prey caught in pitfall traps, the mean number of hours in T_{set} , habitat type and habitat density as fixed effects. We included site as a random effect.

Isodar analyses

To test the prediction that lizard habitat selection responds to density, we constructed isodars (Morris 1989) comparing density between habitats using linear mixed-effects models (function 'lmer'; package 'lme4'; Bates et al. 2014). If lizard habitat selection does not respond to density, the isodar has a slope of zero or is undefined (vertical or horizontal line,

depending on which habitat was preferred). If lizard habitat selection is density-dependent, the isodar is linear or curved with density in one habitat increasing as density in the other habitat increases. Curved isodars occur when individuals are territorial and competitively exclude subordinates from settling in the higher quality habitat (Knight et al. 2008). For the isodar analyses, we used the density of lizards in the wash as the dependent variable, the density of lizards in the upland habitat as the fixed independent variable, and site as a random effect. We included estimates from the sites studied for three years each year they were studied because there was high population turnover between years and less than 20% of adults survived to the next breeding season at each site.

Habitat differences in fitness proxies

To compare relative fitness between upland and wash habitats, we used estimated monthly survival rates at the six sites monitored for three years and individual growth rates at all 10 sites. The analysis above relating survival to habitat density included a habitat effect, the analysis compared differences in the y-intercept of survival at a given habitat density. The present analysis tests a different prediction than the habitat effect in the density analysis by pairing habitats at each site. At a given total population density, organisms following an ideal free distribution should be distributed so that mean fitness is equal in all habitat types. We compared survival between habitats at a site using a paired Wilcoxon rank test (function: 'wilcox.test') on mean monthly survival averaged between the three years. Growth rates were compared between habitats at a site using a linear mixed-effects model (Bates et al. 2014) with habitat, sex, and an interaction between habitat and sex as fixed effect variables. We included a random effect of site.

Data deposition

Data available from the Dryad Digital Repository: < <http://dx.doi.org/10.5061/dryad.pn090> > (Paterson and Blouin-Demers 2017b).

Results

Density dependence of fitness proxies

Monthly survival estimates varied from 0.56–0.98. The detection probability at each capture occasion varied from 0.06–0.60. The most supported mark–recapture models are summarized in Supplementary material Appendix 3 for JS models estimating survival and population size at each site studied for three years (Supplementary material Appendix 3 Tables A3–A8) and closed population models estimating population size at each site studied for one year (Supplementary material Appendix 3 Table A9–A12). The top-ranking JS models at five of the six sites had differences in survival between the breeding season and the rest of the year. None

of the top-ranking JS models included differences in survival between males and females.

Estimated population density ranged from 11–113 lizards ha^{-1} in the upland habitat (mean 60 lizards ha^{-1} , $\text{SD}=31$) and from 45–251 lizards ha^{-1} in the wash habitat (mean 129 lizards ha^{-1} , $\text{SD}=70$; Supplementary material Appendix 3 Table A13). Estimated monthly survival probability decreased with density (linear model, $F=8.99$, $\text{df}=1$, 9 , $p=0.015$, Fig. 1) by 0.03 for every increase in density of 25 lizards ha^{-1} . Monthly survival probability was unaffected by habitat ($F=1.85$, $\text{df}=1$, 9 , $p=0.21$) and there was no interaction between habitat and density ($F=1.18$, $\text{df}=1$, 8 , $p=0.31$). We did not include an effect of sex in the survival analysis because there was no support in mark–recapture models (Supplementary material Appendix 3 Table A3–A8) for differences in monthly survival between males and females. Growth rate did not decrease with density (linear mixed-effects model, $F=0.59$, $\text{df}=1$, 5 , $p=0.47$, Fig. 2) in yearling lizards when controlling for sex ($F=24.17$, $\text{df}=1$, 99 , $p < 0.001$). There was also no difference in growth rate between habitats ($F=0.84$, $\text{df}=1$, 23 , $p=0.37$) and no interaction between habitat and density ($F=0.02$, $\text{df}=1$, 31 , $p=0.89$) in yearling lizards.

Habitat suitability

The 410 pitfall traps caught 14 293 arthropods and 12 267 (89 %) of those were in orders known to be consumed by tree lizards (Aspland 1964). There were significantly more arthropod prey caught in the wash habitat than in the upland habitat (linear mixed-effects model, $F=9.71$, $\text{df}=1$, 393 , $p=0.002$), but there was no significant effect of month ($F=2.71$, $\text{df}=2$, 398 , $p=0.07$). There was a

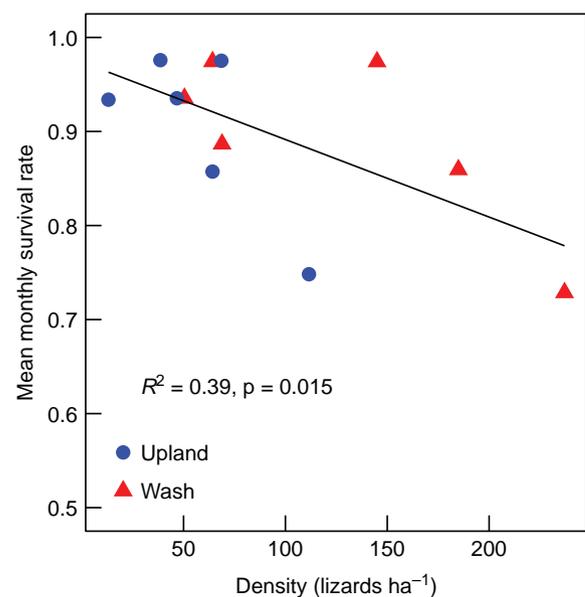


Figure 1. Mean monthly survival rate of ornate tree lizards *Urosaurus ornatus* decreased with population density in two habitats at six sites in the Chiricahua Mountains of Arizona, USA.

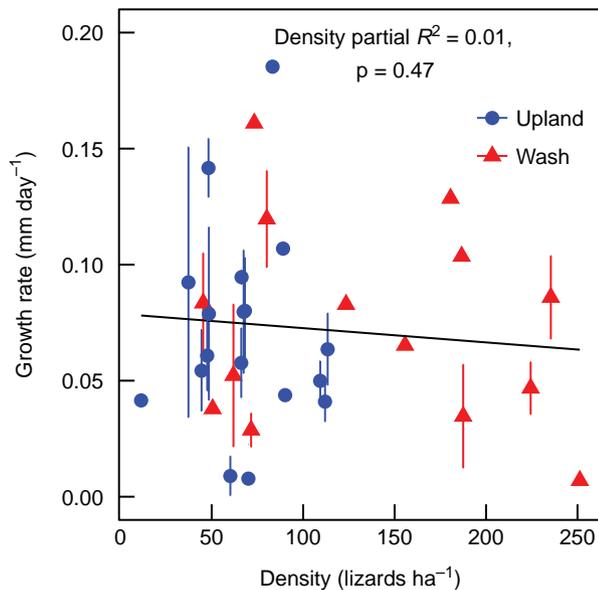


Figure 2. Yearling ornate tree lizard *Urosaurus ornatus* growth rate ($n=103$) did not decline with population density in two habitats at six sites in the Chiricahua Mountains of Arizona, USA. The mean growth rate (mm day^{-1}) is displayed for each density (one estimate per habitat per site per year) and the bars represent one standard error.

marginally significant interaction between habitat and month ($F=3.11$, $df=2$, 393 , $p=0.05$); the number of prey captured per trap was the same in both habitats in July. The model predicted mean number of prey captured per trap was 75 % ($SD=29\%$) higher in the wash habitat than in the upland habitat during May and June. Therefore, the wash had more food for lizards than the upland habitat during spring.

T_{set} of 41 ($n=21$ females and 20 males) adult lizards in the thermal gradient was 32.2 to 36.0°C. Lizards could reach T_{set} earlier in the day in the wash habitat than in the upland habitat, and could remain active at T_{set} later in the day in the wash habitat (Fig. 3). Lizards in the wash habitat had, on average, an additional 2.2 hours of activity per day ($SD=0.4$ h) within T_{set} than in the upland habitat (linear mixed-effects model, $F=33.08$, $df=1$, 825 , $p < 0.0001$; Fig. 3). The estimated activity time within T_{set} in the wash habitat was 50% higher than in the upland habitat. The habitat difference in thermal quality was consistent in May and July, but the difference between habitats was less marked in June (habitat \times month interaction, $F=7.52$, $p < 0.0006$). In June, the wash habitat had, on average, an additional 0.8 h of activity per day ($SD=0.48$ h) within T_{set} than in the upland habitat. Therefore, the wash habitat had a higher thermal quality than the upland habitat.

Lizard density in a habitat increased with prey number (linear mixed-effects model, $F=29.46$, $df=1$, 4 , $p=0.007$) and was higher in the wash than in the upland habitat ($F=18.20$, $df=1$, 8 , $p=0.003$). Independent of habitat type,

density decreased with the number of hours during which it was possible to achieve T_{set} ($F=8.14$, $df=1$, 4 , $p=0.04$), but within a site the mean number of hours during which it was possible to achieve T_{set} was always higher in the wash habitat than in the upland habitat.

Monthly survival was higher in the wash habitat (linear model, $F=6.76$, $df=1$, 7 , $p=0.04$), but did not change with mean prey abundance ($F=0.05$, $df=1$, 7 , $p=0.82$), the mean number of hours during which it was possible to achieve T_{set} ($F=4.79$, $df=1$, 7 , $p=0.06$), or habitat density ($F=4.78$, $df=1$, 7 , $p=0.06$). Habitat density and prey abundance, however, were negatively correlated, as indicated by their variance inflation factors (VIFs; function 'vif' in the 'car' package; Fox and Weisberg 2011) of 6.7 and 7.9, respectively. Therefore, the effects of these variables on survival should be interpreted with caution due to multicollinearity. Growth rate did not differ between habitats (linear mixed-effects model, $F=0.09$, $df=1$, 11 , $p=0.77$), with prey abundance ($F=0.19$, $df=1$, 10 , $p=0.68$), with the mean number of hours during which it was possible to achieve T_{set} ($F=0.01$, $df=1$, 4 , $p=0.94$), or with habitat density ($F < 0.01$, $df=1$, 27 , $p > 0.99$). The VIFs of mean prey abundance (12.21) and of habitat density (11.73) were high, so these results should be interpreted with caution because of multicollinearity.

Isodars

At all sites, the density of lizards was higher in the wash habitat than in the upland habitat, and increased linearly with an estimated intercept of 16.79 (95 % $CI=-27.78 - 61.91$) and a slope of 1.86 (95 % $CI=1.22 - 2.49$, linear mixed-effects model, $F=28.94$, $df=1$, 11 , $p < 0.001$, Fig. 4). The isodar explained approximately 74% of the variance in lizard density in the wash habitat based on lizard density in the upland habitat. The isodar was still linear and suggested tree lizards prefer the wash habitat when we removed the four sites only studied in 2016 from the analysis (approximate $R^2=0.79$, $F=24.32$, $df=1$, 6 , $p=0.002$). Removing individuals that switched between habitats from population estimates also did not change qualitatively the results of the isodar (Supplementary material Appendix 4). Therefore, the wash habitat was preferred over the upland habitat, and habitat selection depended on density.

Differences in fitness between habitats

The mean paired difference in monthly survival between habitats (wash minus upland) was 1.0×10^{-4} (95% $CI: -5.1 \times 10^{-2} - 1.9 \times 10^{-3}$) and was not significantly different from zero (Wilcoxon rank test, $V=6$, $p=0.44$). Yearling growth rate was related to sex (linear mixed-effects model, $F=24.79$, $df=1$, 99 , $p < 0.001$), but not to habitat ($F=0.24$, $df=1$, 99 , $p=0.62$). There was no interaction between sex and habitat on yearling growth rate ($F=1.31$, $df=1$, 98 , $p=0.25$). Therefore, fitness proxies were equal in each habitat at a site.

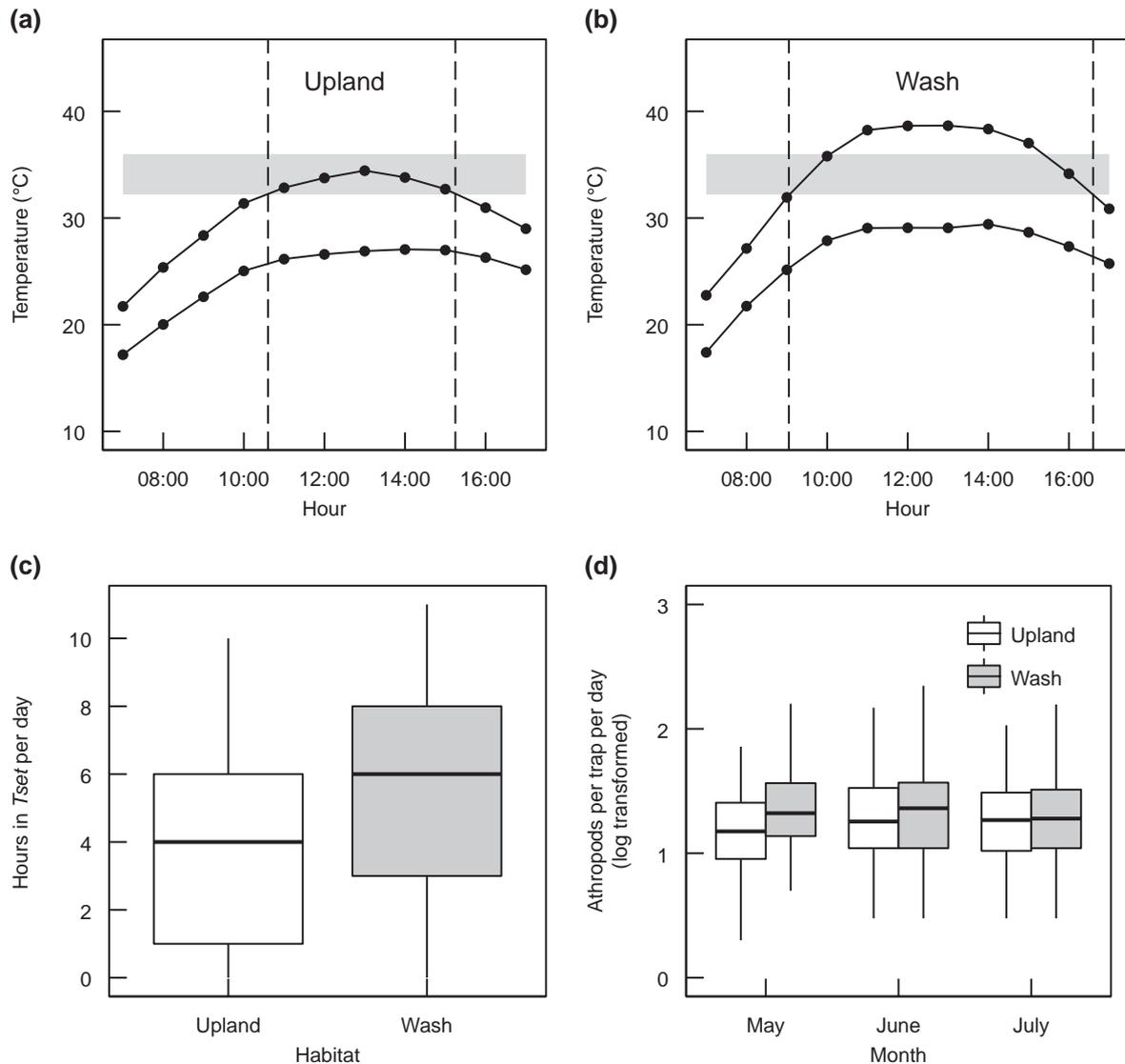


Figure 3. Thermal quality of (a) upland and (b) wash habitats showing the mean maximum and minimum temperatures for each hour in relation to the preferred body temperature (T_{set} , shaded areas) of ornate tree lizards *Urosaurus ornatus* in the Chiricahua Mountains of Arizona, USA. The vertical dashed lines bound the time when lizards could be active at T_{set} . (c) The number of hours within the range of preferred body temperatures of tree lizards is higher in wash than in upland habitat ($n = 836$). (d) The daily number of arthropods captured in pitfall traps for May, June and July in the upland and wash habitats ($n = 410$).

Discussion

Our data indicate density-dependent habitat selection in tree lizards that matches the predictions of an ideal free distribution. First, monthly survival was lowest at sites with the highest density, providing evidence for increased competition for resources at high densities. Second, we found differences in habitat suitability likely to influence fitness and habitat preference. The wash habitat had more arthropod prey and allowed lizards to achieve their preferred body temperature for longer than the upland habitat. Third, we found a clear preference for the higher quality wash habitat and lizard density was always higher in the wash than in the upland habitat. More lizards chose the upland habitat when density in the

wash habitat was high and the isodar had a positive slope over a wide range of densities. Finally, fitness proxies were equal between habitats, indicating that lizards were selecting habitat to maximize fitness benefits.

Survival rates of tree lizards were highest at low densities and decreased with density. The differences in monthly survival translated into large differences in the probability of surviving a breeding season. For example, the highest estimate of monthly survival (0.98) translated into a breeding season survival probability of 0.92 (0.98^4 ; assuming the breeding season lasts four months). The lowest estimate of monthly survival (0.56) translated into a breeding season survival probability of 0.10 (0.56^4). Obviously, surviving the breeding season has large consequences for lifetime fitness. For males, longevity

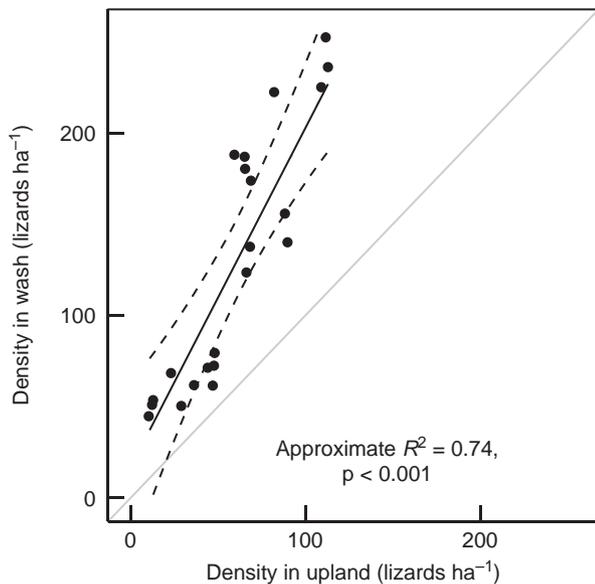


Figure 4. Isodar (black line, dashed 95% confidence interval from linear mixed-effects model) for ornate tree lizards *Urosaurus ornatus* in upland and wash habitats for 10 sites (one estimate per site per year) in the Chiricahua Mountains of Arizona, USA. Six sites were sampled for three years, and four sites were sampled for one year. The grey line represents no habitat preference (equal density in each habitat).

is expected to yield more mating opportunities. For females, the fitness consequences of breeding season survival are even clearer because they lay a single clutch of eggs at the end of the breeding season (Dunham 1982) and fitness is zero if a female does not survive to lay any eggs. Therefore, there is strong evidence for a fitness cost of crowding in tree lizard populations.

Tree lizard growth rates did not decrease with density. In previous studies of density-dependence in lizards, growth rate frequently decreased with density (Massot et al. 1992, Smith and Ballinger 1994, Mugabo et al. 2013), so it is surprising we found no effect of density on growth rate in yearlings over such a wide range of density. Growth rate declined strongly with initial size, however, so detecting variation in growth rate with individuals starting at different sizes may be difficult if significant growth occurs outside of the breeding season. Furthermore, we may not have detected a negative relationship between density and growth rates because of error in our estimates of population size derived from the mark-recapture models.

We chose two fitness proxies: growth and survival. We acknowledge that other fitness proxies may respond differently to population density, food availability, or thermal quality. For example, recruitment and fecundity are both likely positively related to fitness and we did not measure these fitness proxies. Growth rates are probably related to fecundity because clutch size is strongly related to female body size in tree lizards (Landwer 1994). Both recruitment (Gaillard et al. 1998, Both et al. 1999) and fecundity (Peters and Barbosa 1977, Koslow et al. 1995) are likely to decline

with population density because of increased competition for resources. It is possible, however, that recruitment and fecundity do not respond to density in tree lizards and that would change our interpretation of habitat selection in this system. If there is no density-dependence of fitness, then the test of equal fitness between habitats at a site is not meaningful because there is no benefit to using a lower quality habitat.

The isodar was straight over a wide range of densities and demonstrated that tree lizards preferred the wash habitat. Tree lizards are very territorial (Carpenter 1995, Taylor and Lattanzio 2016), so we were expecting a curved isodar. It is possible that curvature in the isodar may only become apparent at very high densities, once the habitat is completely saturated with territories.

We found evidence of density-dependent habitat selection, even though there were significant differences in thermal quality between habitats. Despite evidence in snakes that differences in thermal quality between habitats can cause habitat selection to be largely density-independent (Halliday and Blouin-Demers 2016), our study demonstrates that resource depletion in lizards can cause tradeoffs in habitat choice. Snakes usually occur at low densities and thus competition for food is unlikely, except under rare circumstances (Lindell et al. 1993). Lizards, however, can occur at very high densities where competition and resource depletion are likely (Buckley and Jetz 2007, Pafilis et al. 2009), which explains why some individuals colonize lower quality habitats at high densities to maximize fitness. Our study design does not, however, allow us to determine which finite resource is causing the observed density-dependent patterns. It is possible that density-dependent survival and habitat selection occur because of competition for limited food resources (Stamps 1977) or for another finite resource, such as basking sites (Calsbeek and Sinervo 2002).

Our test of density-dependent habitat selection in lizards implies that resource depletion can be more limiting than thermal quality in this taxon, but how widespread can this pattern be? A global review indicated only a weak relationship between lizard abundance and environmental temperature, but a strong relationship between lizard abundance and net primary productivity (Buckley et al. 2008). This implies that food availability, limited by productivity, likely limits the abundance of most lizards. The spatial resolution of large-scale temperature data used for these analyses (greater than 10' latitude and longitude), however, does not reflect the availability of temperatures relevant to lizard thermoregulation (Buckley et al. 2008). Variation in habitat use between individuals in a population may also have caused the weak observed relationship between environmental temperatures and ectotherm abundance (Shine 1987, Bestion et al. 2015). We examined lizard abundance and habitat suitability at a spatial scale relevant to thermal and prey resource use, and found that tree lizard habitat selection responds to population density and that abundance is likely limited by prey availability and not by temperature.

For ectotherms living in habitats where temperatures regularly reach their preferred temperature range, abundance

is likely to be regulated by resource depletion and by density dependence, even if habitat selection is modulated by thermal differences between habitats (Halliday et al. 2015). Many species in temperate regions, however, experience temperatures significantly below their preferred range, and thus may be more limited by their ability to process resources rather than by their ability to acquire resources. For these species, resources are unlikely to be depleted because of limits on assimilating food imposed by low temperatures. For example, fence lizards *Sceloporus undulatus* have a large geographical range and populations vary in energy assimilation rates based on differences in temperature; this causes differences in growth rates and in reproductive output across their range (Angilletta 2001). Thus, examining habitat selection in terrestrial ectotherms in areas with different thermal regimes would be fruitful to test the relationship between temperature and density-dependence in habitat selection. We hypothesize that ectotherms at extreme latitudes (or altitudes) are more limited by thermal resources and energy assimilation than by energy acquisition, and we thus predict that habitat selection should become more independent of density as thermal quality declines.

We have shown that lizards can select habitats in a density-dependent manner even in the face of sharp differences in thermal quality between habitats, so thermal quality does not always override the influence of finite resources when individuals are choosing a habitat. Linking patterns of habitat selection to habitat suitability and fitness indicators, such as growth rate and survival, is important to identify what drives differences in fitness and abundance between habitats. Future work should test the influence of thermal differences on habitat selection in ectotherms in more thermally challenging environments, such as high-altitude mountain ranges or more temperate ecosystems.

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Supplementary material (available online as Appendix oik-04758 at <www.oikosjournal.org/appendix/oik-04758>). Appendix 1–4.