Drivers of density in ornate tree lizards (*Urosaurus ornatus*)

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Abstract

Explaining spatial and temporal variation in the abundance of species is one of the primary goals of ecology. Habitat selection, the behaviour that organisms use to choose habitat patches that maximize fitness, can explain patterns in abundance between patches at small spatial scales within the dispersal capacity of the species. However, habitat selection models assume there is a reduction in individual fitness as population density increases due to increased competition between individuals. Ectotherms, which often select habitats based on temperature, a density-independent resource, may not display density-dependent responses if temperature limits energy assimilation more than finite food resources limit energy acquisition. As predicted by their dependence on environmental temperatures, some ectotherms select habitat largely independently of population density when temperatures are far from the optimal temperature for performance. But, is density-dependence prevalent in ectotherm populations when temperatures are close to the optimal temperature for performance? Habitat selection models also assume that all individuals of a population exhibit the same strategy for maximizing fitness through habitat selection. However, differences in morphology and behaviour (e.g., reproductive strategy) can modify the optimal habitat selection strategy for different phenotypes. Finally, observed patterns in habitat selection and abundance can also be modified by competition with other species. Quantifying the relative importance of these different factors that affect habitat selection behaviour will improve our ability to predict the spatial distribution and relative abundance of organisms.

The objective of my thesis was to explain spatial variation in the abundance of ectotherms, using the ornate tree lizard (*Urosaurus ornatus*) as a study species. In chapter one, I tested whether density-dependent habitat selection explained patterns in abundance and fitness of lizards between two habitats differing in suitability. In chapter two, I tested whether density dependent habitat selection in tree lizards was caused by intraspecific competition for food that limited body size and growth. In chapter three, I tested whether variation in reproductive strategy, as indicated by throat colour phenotype, affected space use and habitat selection in male tree lizards. Finally, in chapter four, I tested whether interspecific competition with another lizard species affected habitat selection, fitness, and abundance of tree lizards.

My thesis emphasizes the importance of intraspecific competition in shaping patterns of habitat selection and abundance in terrestrial ectotherms. I show that habitat selection is strongly density-dependent despite differences in thermal quality between habitats. I show that density-dependent mortality and growth lower the fitness of individuals when populations reach high densities, and this likely caused habitat selection to be density-dependent. Despite this evidence for density-dependent habitat selection, I show considerable variation between individuals in habitat selection and space use. Males with different throat colour phenotypes select habitats differently, demonstrating that variation in morphology can influence habitat selection patterns within a population. Finally, I show that interspecific competition with another lizard affects space use and how frequently tree lizards switch habitats, but this does not lead to differences in fitness or in the relative abundance of tree lizards in habitats. Therefore, intraspecific competition for resources was the dominant force shaping the relative abundance of tree lizards in different habitats.

Résumé

Un des principaux buts de l'écologie est d'expliquer les variations spatiales et temporelles de l’abondance des espèces est l’un des buts principaux de l’écologie. La sélection de l’habitat est définie comme un comportement de choix des parcelles de l’habitat par les organismes pour maximiser leur aptitude phénotypique. La sélection de l’habitat peut expliquer les variations d’abondance entre les parcelles à une petite échelle spatiale. Cependant, les modèles de sélection d’habitat supposent qu’il y a une réduction de l’aptitude en fonction de la densité de la population dû à une réduction des ressources et à un accroissement de la compétition. Les ectothermes choisissent surtout leur habitat en fonction de la température, indépendamment de la densité de population; ils peuvent échapper à l’effet limitant de la densité de population s’ils sont plus fortement limités par la température (limitant l’assimilation d’énergie) que par l’abondance des ressources (limitant l’acquisition d’énergie). Comme prédit par leur forte dépendance à la température, certains ectothermes choisissent des habitats indépendamment de la densité de population si la température est relativement basse. Mais est-ce que la densité de population prévaut si la température est proche de l’optimum de température pour la performance? De plus, les modèles de sélection de l’habitat supposent que tous les individus d’une population utilisent la même stratégie pour maximiser leur aptitude via la sélection de l’habitat. Toutefois, les différences morphologiques et comportementales (par exemple la stratégie de reproduction) peuvent modifier l’optimum de sélection de l’habitat pour les différents phénotypes. Finalement, les motifs de sélection de l’habitat et de l’abondance des populations peuvent aussi être modifiés par la compétition avec d’autres espèces. Quantifier l’importance relative de ces différents facteurs affectant le comportement de sélection de l’habitat améliorera notre habilité à prédire la distribution spatiale et l’abondance relative des organismes.

L'objectif de ma thèse est d'expliquer la variation spatiale de l'abondance des ectothermes en utilisant le lézard arboricole orné (*Urosaurus ornatus*) comme espèce modèle. Dans le chapitre un, je teste si la sélection de l'habitat en fonction de la densité de population explique les motifs d'abondance et l'aptitude des lézards entre deux habitats qui diffèrent en qualité. Dans le chapitre deux, je teste si la sélection de l'habitat en fonction de la densité de population est causée par la compétition intraspécifique pour la nourriture limitant la taille et la croissance. Dans le chapitre trois, je teste si les différentes stratégies de reproduction indiquées par les différents phénotypes de coloration du cou affectent l'utilisation de l'espace et le choix de l'habitat chez les mâles. Finalement, dans le chapitre quatre, je teste si la compétition interspécifique avec une autre espèce de lézard affecte la sélection de l'habitat, l'aptitude et l'abondance des lézards arboricoles ornés.

Ma thèse souligne l'importance de la compétition intraspécifique dans la formation des motifs de sélection de l'habitat et d'abondance chez les ectothermes terrestres. Je montre que la sélection de l'habitat dépend fortement de la densité malgré une différence de qualité thermique entre les habitats. Je montre aussi que la mortalité associée à des densités élevées peut causer la dépendance du choix de l'habitat en fonction de la densité de population. Malgré l'évidence d'une sélection de l'habitat dépendante de la densité de population, je révèle la présence d'une importante variation interindividuelle dans le choix de l'habitat et dans l'utilisation de l'espace. Les mâles avec différents phénotypes de coloration du cou choisissent différents habitats, démontrant que la variation morphologique peut influencer les motifs de sélection de l'habitat au sein d'une population. Finalement, je montre que la compétition avec une autre espèce de lézard affecte l'utilisation de l'espace ainsi que la fréquence de changement d'habitat, mais sans modifier l’aptitude ou l’abondance relative du lézard arboricole orné. Par conséquent, la compétition intraspécifique pour les ressources est la force dominante influençant l’abondance relative des lézards arboricoles ornés dans différents habitats.

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List of abbreviations

Chapter 1

JS	Jolly-Seber
Φ	apparent monthly survival probability
p	detection probability
$\hat{N}$	total number of individuals available to enter the population
pent	probability of new individuals from $\hat{N}$ entering the site at each occasion
$\mathrm{AIC_c}$	bias-corrected Akaike's information criterion
$\mathrm{QAIC_c}$	quasi-likelihood $\mathrm{AIC_c}$
c	probability a marked individual is recaptured
$f0$	number of individuals in the population that are never captured
T_{set}	preferred body temperature range
T_b	body temperature
T_e	environmental temperature
$\hat{c}$	variance inflation factor

Chapter 2

T_{set}	preferred body temperature range
VBG	von Bertalanffy growth model
t	age (months)
L_t	mean body length at age t
L_∞	mean maximum size
K	exponential rate of approach to L_∞

t_0	age when mean length is zero
SVL	snout-vent length
LAG	line of arrested growth
g	density-dependent parameter on maximum body size
d	mean habitat density (lizards/ha)
T_e	environmental temperature

Chapter 3

IFD	Ideal Free Distribution
T_b	body temperature
T_{set}	preferred temperature range
PCA	principal component analysis
DFA	discriminant function analyses
SVL	snout-vent length
d_b	the accuracy of T_b measured as the absolute deviation between T_b and T_{set}

Chapter 4

SVL	snout-vent length
p	detection probability
ϕ	apparent monthly survival probability
$\hat{N}$	super-population size
$pent$	probability of new individuals from $\hat{N}$ entering the population
$\hat{c}$	variance inflation factor

AIC_c	bias-corrected Akaike's information criterion
QAIC_c	quasi-likelihood AIC_c
S	probability that a lizard survives and remains in the same habitat
Ψ	probability that a lizard transitions between states (habitats)

List of Appendices

Appendix 1. List of additional publications completed during my Ph.D. that are not thesis chapters.

General Introduction

A major goal of ecology is to explain spatial variation in the distribution and abundance of organisms (Krebs 2001). While there are many factors that limit where species occur and how abundant species are, factors can broadly be categorized as either abiotic or biotic factors. At broad spatial and temporal scales, a species' distribution is often limited by physiological tolerances to environmental conditions (abiotic factors), such as temperature and precipitation (Hawkins et al. 2003, Kearney and Porter 2009, Sexton et al. 2009). At finer spatial scales, a species' distribution may also be limited by biotic factors, such as predators, parasites, and competitors (Robertson 1996, Jackson et al. 2001, Boulangeat et al. 2012). The combination of abiotic and biotic conditions required for survival and reproduction describe a species' multidimensional niche (Hutchinson 1959, Brown 1984, Pulliam 2000). Determining the relative importance of these different factors that limit the realized niche (Soberon and Nakamura 2009) describing where species actually occur will increase the accuracy with which we can predict the abundance and distribution of species in different habitats.

Abiotic factors are important influences on the distribution and abundance of species because they affect physiological performance (Huey 1991). Two of the most important environmental factors that influence species are temperature and precipitation because they are related to organism body temperature (Huey and Stevenson 1979) and water balance (Stephenson 1990). For example, precipitation and drought sensitivity shape the distributions of tropical trees (Engelbrecht et al. 2007). Considering temporal changes in abiotic factors also emphasizes their importance in determining the distribution and abundance of species. For example, changes in temperature due to climate change caused population extinctions in high altitude lizards because of limitations on activity time at high temperatures (Sinervo et al. 2010).

Therefore, a mechanistic understanding of species abundance requires considering variation in environmental conditions, such as temperature and precipitation.

Biotic factors can play a significant role in limiting the abundance of species. Competition can be a strong ecological and evolutionary force in communities (Day and Young 2004) that can act both within (intraspecific) and between (interspecific) species. Intraspecific competition for food, space or other resources affects the spatial distribution of organisms between habitats (Fretwell 1969). Interspecific competition can also limit the abundance and distribution of species between habitats (Schoener 1983, Robertson 1996). Measuring the effects of competition between species is difficult, however, and often requires manipulations of abundance (Schoener 1983). Predators can have strong effects on the abundance (Leibold 1996, Connell 1998) and spatial distribution of prey (Hugie and Dill 1994, Calsbeek and Irschick 2007) by increasing mortality rates in some habitats or by changing the behaviour of prey. Thus, spatial variation in biotic interactions can have strong effects on the abundance of species.

Abiotic and biotic conditions are not equally distributed across space, thus the habitat an animal selects strongly influences its fitness (Morris 1989, Matthiopoulos et al. 2015). The spatial heterogeneity of resource distribution provides an opportunity for organisms to maximize their fitness by choosing the highest quality habitat available. Habitat selection, the choice made by organisms to occupy certain habitats, has been the focus of many ecologists in theoretical modeling (Fretwell and Lucas 1969, Rosenzweig 1981, Morris 2003) and in field studies (Partridge 1974, Morris 1989, Doligez 2002).

Theoretical models predicting habitat selection focus on density dependent effects 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. 2013). If organisms choose habitats that maximize fitness and are free to colonize any habitat, then individual fitness is predicted to equalize across habitats (Fretwell and Lucas 1969). This model of habitat selection, known as the ideal free distribution (IFD; (Fretwell and Lucas 1969, Fretwell 1972, Rosenzweig 1981), forms one theoretical framework for explaining the distribution of organisms among habitats. The IFD assumes competitors are equal, individuals have perfect knowledge of habitat suitability, and individuals are free to choose patches based on density and habitat suitability. Natural animal populations rarely meet these assumptions (Kennedy and Gray 1993, Matsumura et al. 2010), but the IFD has nonetheless been very useful for predicting spatial variation in abundance of organisms between habitats (Milinski 1979, Walhström and Kjellander 1995, Haché and Bayne 2013).

The IFD also assumes that resources affecting habitat selection are finite and divisible (such as food) and that populations are regulated through density-dependence. However, habitat selection can be density-independent if resources are not divisible or if organisms occur at low densities because stochastic variation in abiotic factors, not competition, limit abundance (Greene and Stamps 2001). For ectotherms, thermal quality of a habitat may be more important than food resources and may strongly affect patch quality through physiological and locomotor limitations (Huey et al. 1989, Huey 1991, Buckley et al. 2012). Therefore, ectotherm habitat selection and abundance may be limited by the assimilation of resources (thermal quality) rather than the acquisition of energy (food abundance). If so, ectotherm habitat selection should not follow an IFD and should be density independent. In a review of 483 populations, Buckley et al. (2008) did not find evidence that environmental temperatures limited lizard density, but the spatial resolution of the analyses was too broad and may not have been adequate to detect ecologically relevant differences in thermal quality between habitats. A stronger test would be to measure population density and temperature at resolutions relevant to individual habitat selection. For example, habitat selection is only weakly density-dependent in snakes (Halliday and Blouin-Demers 2016), but snakes are not usually as abundant as lizards. Do lizards, which often reach high densities, display density-dependent habitat selection?

The IFD also assumes that all individuals have the same strategy that maximizes fitness through habitat selection. However, life stages (e.g., juveniles versus adults), sexes, and phenotypes may have different habitat preferences that maximize fitness. This can result from differences in morphology, physiology, and behaviour between individuals. For example, male and female pipefishes display differences in preference for sea grass leaf type and density that are probably related to energetic requirements for reproduction (Steffe et al. 1989). Male side-blotched lizards exhibit correlated morphological and behavioural differences in reproductive strategy (Sinervo and Lively 1996) that could affect habitat selection strategy. Differences between phenotypes in behaviour, morphology, and physiology could significantly affect the observed distribution of organisms, habitat specific population dynamics (Parker and Sutherland 1986), and whether observed distributions of organisms follow the IFD. While the IFD has been modified to include differences between individuals in competitive ability (Parker and Sutherland 1986), individuals are still assumed to be using the same strategy. Therefore, considering variability in habitat selection within a population should increase the predictive ability of habitat selection models.

The general goal of my thesis was to test hypotheses explaining variation in abundance among habitats in ectotherms. I used ornate tree lizards (*Urosaurus ornatus*) as a study system because they occur in different habitat types, vary in abundance, have small and stable home ranges, and are short-lived. In general, I tested how habitat selection, fitness, and abundance in different habitats are influenced by environmental conditions, intraspecific competition, and interspecific competition. More specifically, my thesis chapters attempt to answer the following questions:

1) Is tree lizard habitat selection density-dependent when habitats differ in thermal quality and abundance is high?
2) Do population density and habitat selection affect growth rates in tree lizards?
3) Is throat colour polymorphism in tree lizards related to alternative space use and habitat selection strategies?
4) Does interspecific competition with another lizard species affect habitat selection, fitness, and abundance of tree lizards?

In chapter one, I tested the hypothesis that density-dependent habitat selection can explain patterns of abundance of tree lizards. I used a two-habitat system with differences in temperature and the abundance of food resources for lizards. Using mark-recapture data, I tested the prediction that mean survival rates, a component of fitness, decline with density in a habitat. Next, I tested the prediction that habitat selection depends on density using isodar analyses. Finally, I tested the prediction that fitness equalizes between habitats by comparing survival rates between the two habitats.

In chapter two, I tested the hypothesis that competition for resources limited growth of tree lizards. I used skeletochronology to age lizards and tested whether growth rates decline with density in a habitat and if growth rates differed between the wash and upland habitat.

In chapter three, I tested the hypothesis that ornate tree lizard male throat colour affects space use and habitat selection because of differences in morphology and behaviour between males of distinct throat colours. This chapter required that there be throat colour polymorphism and that it could be quantified, so I include in Appendix 1 an abstract of a paper in which I quantified throat colour polymorphism with a novel method. The male throat colour polymorphism is linked to reproductive strategy (Moore et al. 1998), so I predicted that male throat colour would affect morphology, the distance that lizards travel, and habitat selection.

In chapter four, I tested the hypothesis that local abundance of tree lizards is driven by competition with striped plateau lizards (*Sceloporus virgatus*) using a field experiment. I removed a likely dominant competitor to test whether tree lizards shift their habitat and space use in response to the density of lizards from another closely related species. I also tested whether the removal of a competitor increased the fitness and abundance of tree lizards. In addressing this fourth question, one possibility was that the two species could be competing for thermal resources in addition to or in lieu of more traditional axes of competition. This prompted me to assess the strength of evidence for thermal resource partitioning in ectotherms in general. I included in Appendix 1 an abstract of a paper in which I assess the quality of evidence for thermal resource partitioning based on a literature review.

Chapter 1

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

This chapter formed the basis for the following publication:

Paterson, J.E. and Blouin-Demers, G. 2017. Density-dependent habitat selection predicts fitness and abundance in a small lizard. Oikos, *in press.*

Abstract

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), I tested the hypothesis that habitat selection is density-dependent even when thermal quality differs between habitats. I first tested that fitness proxies decline with density in each habitat, indicating density-dependent effects on habitat suitability. I also confirmed that the two habitats vary in suitability using prey abundance and temperature. Next, I 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. I 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, habitat selection depended on density, and fitness proxies did not differ between habitats. These patterns are consistent with density-dependent habitat selection, despite differences in thermal quality between habitats. I 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, I 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 that 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 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). However, the effect of temperature on density-dependent habitat selection has not been tested in other species. Therefore, the relationship between temperature, competition, and habitat selection remains largely untested. The trade-off 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).

I tested the hypothesis that density-dependent habitat selection can explain patterns of abundance of ornate tree lizards (*Urosaurus ornatus*) between two habitats. 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 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. 1987a, 1990, Thompson and Moore 1991a). Habitat selection usually occurs at multiple spatial scales (Johnson 1980) and there can be trade-offs in the use of different habitats within a home range (Mysterud and Ims 1998), but I focused 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), I first tested that fitness proxies decline with density, indicating density-dependent effects on habitat suitability. I also confirmed that the two habitats differ in food abundance and in thermal quality. I 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, I 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 at a site.

Methods

Study area & study species

I studied tree lizards in the Chiricahua Mountains of southeastern Arizona, USA. This species occurs in several habitats, but I used adjacent treed (upland) and open canopy creek bed (wash) habitats (Supplementary information: Figure 1-S1) in canyons because these provide an obvious difference in structure that is likely to affect 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 information: Figure 1-S2). 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 my 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 in total) and were 300 m by 50 m, and four additional sites were monitored in 2016 (two capture sessions in total) and were 50 m by 50 m (Supplementary information: Figure 1-S2; Table 1-S1). The four sites added in 2016 increased my 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 Sillero 2010). The entire plot was searched at least three times per session and I recorded the total search effort (in person hours) for each survey. I 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. I 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). I 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. The mean distance between captures for males and females was 10.7 m and 7.8 m, respectively. Therefore, I assigned males to the wash habitat if their mean coordinates were less than 10.7 m from the wash and I assigned females to the wash habitat if their mean coordinates were less than 7.8 m from the wash. I did not assign individuals to an edge habitat because the wash was on average narrower than the radius of the home range (Supplementary information: Figure 1-S1). This habitat assignment assumes that lizards that have home ranges overlapping the wash have access to the food and thermal resources in that habitat. To confirm that lizards on the edge of the upland habitat also had access to the wash habitat, I used mark-recapture data and targeted behavioural observations to determine the extent to which individuals switched between habitats (Supplementary information). 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 information: Figure 1-S4). Therefore, I believe my habitat assignment is an accurate depiction of lizard habitat use. My habitat assignment also assumes that home ranges are approximately circular and that the mean coordinates accurately represent space use. Because tree lizards are very territorial in similar habitat types to this study (M'Closkey et al. 1987a, 1987b, Mahrt 1998) and because of the short distances between captures of the same individual, I believe this assumption is justified.

Density dependence of fitness proxies

I 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 (R Core Team 2014). To estimate survival at each site, I 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. I 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, I 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). I used a principal component analysis 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), I did not include it as a covariate for detection probability because I did not survey for lizards on days with a lot of precipitation. I 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 I 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. I tested the assumptions of the models by assessing goodness-of-fit for the general model at each site (Supplementary information).

I 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 information) 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), I 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. I removed inactive days during the winter when lizards were unlikely to grow (November 1 to April 1; Dunham 1982). Since most growth occurs in the first year of life, I restricted growth analyses to individuals that hatched the previous summer. 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).

I 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, I 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, I estimated population size using closed population models (Otis et al. 1978); the two capture events occurred less than a month apart (Supplementary information: Table 1-S2), 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 $f0$ (the number of individuals in the population that are never captured). Because there were only two capture events at each site, I used a general model where $c = p$ and varied with habitat, and $f0$ varied with habitat. At each of the four sites, I 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 $f0$ to the number of marked individuals at each site.

To test the assumption that fitness declines with density, I examined how population density was related to survival and individual growth rates with linear regressions. First, I tested how population density was related to monthly survival. I used mean monthly survival in a habitat (one estimate per habitat in each site) as the response, and population density in the habitat, habitat type, and the interaction between habitat and population density as predictor variables. Second, I tested how individual growth rate for yearlings was related to population density in a habitat, habitat type, and the interaction between density and habitat type. I included sex as a 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).

Habitat suitability

To determine which habitat had a higher suitability, I quantified food abundance and thermoregulatory opportunities in upland and wash habitats. Tree lizards are generalist arthropod predators (Aspland 1964), so I 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 any taxonomic bias in capture probability was likely 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). I used the total number of prey items as an indicator of prey abundance in each habitat. I 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, I believe my 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 buried flush to the ground with 2 – 4 cm of water and a few drops of soap. Traps were set for 24 hours 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, I constructed a linear mixed-effects model 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. I included site as a random effect. I also tested whether food availability was correlated with total population density at a site with a linear regression.

Thermal quality was measured in each habitat with temperature loggers whose readings were compared to the species' preferred body temperature (T_{set}). I measured the T_{set} of tree lizards with a thermal gradient in controlled conditions at the Southwestern Research Station. During May – June 2014, I captured tree lizards in the same habitat types near the 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 hours). During the trial, lizard skin temperature was measured on the dorsal surface every half hour for eight hours with an infrared thermometer (± 0.1°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. I measured T_e with temperature loggers (Maxim Thermochron iButton, ± 0.5 °C) covered with a rubber coating (Plasti Dip) and painted brown to reflect the thermal properties of tree lizards (Herczeg et al. 2006). I validated that my thermal models accurately predicted the body temperature of tree lizards (Supplementary information: Figure 1-

S3; $R^2 = 0.99$). 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 my 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, I calculated the number of hours per day a lizard could achieve T_{set}. For each hour, I calculated the maximum and minimum T_e available to lizards in a habitat at a site based on all measurements. I 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}. I used measurements between 07:00 and 17:00 because this is when tree lizards are most active (this time interval comprised 95 % of all my captures).

To compare thermal quality between sites and habitats, I 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. I included site as a random effect. I also tested whether total population density at a site depended on the mean number of hours per day within T_{set} with a linear regression.

Isodar analyses

To test the prediction that lizard habitat selection responds to density, I constructed isodars (Morris 1989b) comparing density between habitats. 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, I used the density of lizards in the wash as the dependent variable and the density of lizards in the upland habitat as the independent variable in a linear mixed-effects model with site as a random effect. I 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. The area of the wash at each site included the buffered area used to assign individuals to each habitat.

Habitat differences in fitness proxies

To compare relative fitness between upland and wash habitats, I used estimated monthly survival rates and individual growth rates at the six sites monitored for three years. I compared survival between habitats at a site using a paired *t*-test. Growth rates were compared between habitats using a linear model with habitat, sex, and an interaction between habitat and sex as independent variables.

Results

Density dependence of fitness proxies

Monthly survival estimates varied from 0.56 – 0.97. The detection probability at each capture occasion varied from 0.11 – 0.66. The most supported mark-recapture models are summarized in Supplementary information for JS models estimating survival and population size at each site studied for three years (Tables 1-S4 – 1-S9) and closed population models estimating population size at each site studied for one year (Tables 1-S10 – 1-S13). The top-ranking JS models at four 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 12 – 116 lizards/ha in the upland habitat (mean 62 lizards/ha, SD = 32) and from 31 – 206 lizards/ha in the wash habitat (mean 97 lizards/ha, SD = 59; Supplementary information: Table 1-S14). Estimated monthly survival probability decreased with density (F = 17.23, df = 1, 9, *P* = 0.0025, Figure 1-1) by 0.04 for every increase in density of 25 lizards/ha. Monthly survival probability was unaffected by habitat (F = 2.13, df = 1, 9, *P* = 0.18) and there was no interaction between habitat and density (F = 0.73, df = 1, 8, *P* = 0.42). I did not include an effect of sex in the survival analysis because there was no support in mark-recapture models (Tables 1-S4 – 1-S9) for differences in monthly survival between males and females. Growth rate did not decrease with density (F = 1.05, df = 1, 123, *P* = 0.31, Figure 1-2) in yearling lizards when controlling for sex. There was also no difference in growth rate between habitats (F = 1.25, df = 1, 123, *P* = 0.27) and no interaction between habitat and density (F = 0.53, df = 1, 122, *P* = 0.47) 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 (F = 9.71, df = 1, 393, *P* = 0.002), but there was no significant effect of month (F = 2.71, df = 2, 398, *P* = 0.07). There was a 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. Population density was not correlated with food availability at the 10 study sites (F = 0.78, df = 1, 8, *P* = 0.40).

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 (Figure 1-3). Lizards in the wash habitat had, on average, an additional 2.2 hours of activity per day (SD = 0.4 hours) within T_{set} than in the upland habitat (F = 33.08, df = 1, 825, $P < 0.0001$; Figure 1-3). 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*month interaction, F = 7.52, $P < 0.0006$). In June, the wash habitat had, on average, an additional 0.8 hours of activity per day (SD = 0.48 hours) within T_{set} than in the upland habitat. Therefore, the wash habitat had a higher thermal quality than the upland habitat. Population density was not correlated with the number of hours per day within T_{set} at the six study sites where I measured thermal quality (F = 0.01, df = 1, 4, $P = 0.94$).

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 6.15 (95 % CI = -23.44 – 29.23) and a slope of 1.40 (95 % CI = 1.09 – 1.70, F = 74.71, df = 1, 17, $P < 0.001$, Figure 1-4). The isodar explained 65 % 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 (slope = 1.52, 95 % CI = 1.23 – 1.84) when I removed the four sites only studied in 2016 from the analysis ($R^2 = 0.84$, F = 85.53, df = 1, 16, $P < 0.001$). 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: $-4.7 \times 10^{-3} – 2.7 \times 10^{-3}$) and was not significantly different from zero ($t = -0.571$, df = 17, $P = 0.58$). Yearling growth rate was related to sex ($F = 17.65$, df = 1, 97, $P < 0.001$), but not to habitat ($F = 0.75$, df = 1, 97, $P = 0.39$). There was no interaction between sex and habitat on yearling growth rate ($F = 1.65$, df = 1, 96, $P = 0.20$). Therefore, fitness proxies were equal in each habitat at a site.

Discussion

My 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, I 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, I 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 that maximizes fitness benefits.

Survival rates of tree lizards were highest at low densities and decreased with density within a habitat. The differences in monthly survival translated to large differences in the probability of surviving a breeding season. For example, the highest estimate of monthly survival (0.97) translates to a breeding season survival probability of 0.90 (0.97^4; assuming the breeding season lasts four months). The lowest estimate of monthly survival (0.56) translates to 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 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 1994a, Mugabo et al. 2013), so it is surprising I 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, I may not have detected a negative relationship between density and growth rates because of error in my estimates of population size.

I chose two fitness proxies: growth and survival. I 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 I 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).

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 1995a, Taylor and Lattanzio 2016), so I was 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.

I 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), my study demonstrates that resource competition in lizards can cause trade-offs in habitat choice. The observed difference in habitat selection patterns between snakes and lizards may be due to differences in population densities. 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 that maximize fitness. My 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).

My 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). I 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. I hypothesize that ectotherms at extreme latitudes (or altitudes) are more limited by thermal resources and energy assimilation than by energy acquisition, and I thus predict that habitat selection should become more independent of density as thermal quality declines.

I 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.

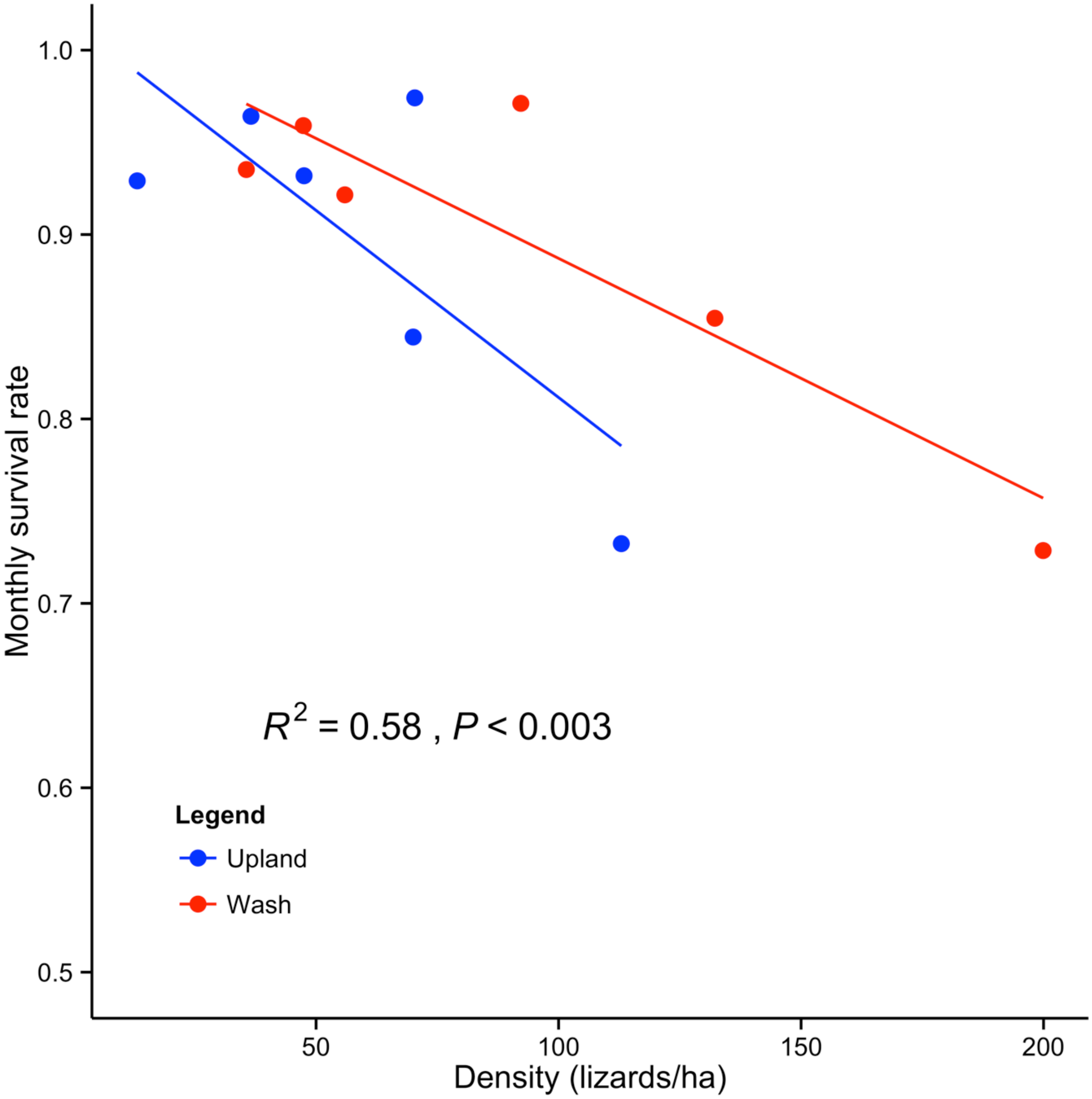

Figure 1-1. Estimated monthly survival rate of ornate tree lizards (*Urosaurus ornatus*) decreased with population density in two habitats at six sites in the Chiricahua Mountains of Arizona, USA.

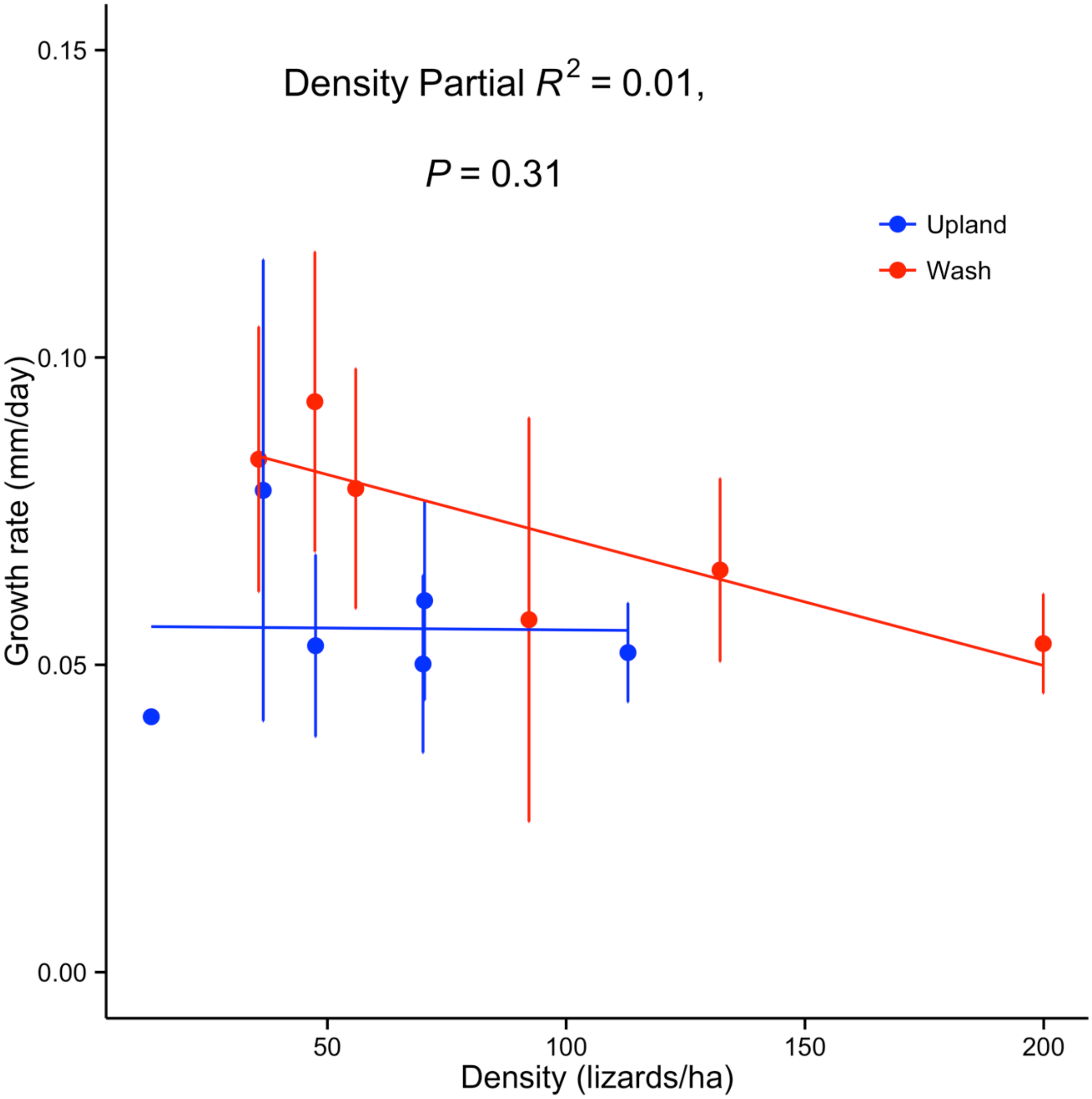

Figure 1-2. Yearling ornate tree lizard (*Urosaurus ornatus*) growth rate (n = 127) did not decline with population density in two habitats at six sites in the Chiricahua Mountains of Arizona, USA. The mean growth rate (mm/day) is displayed for each density (one estimate per habitat per site) and the bars represent one standard error.

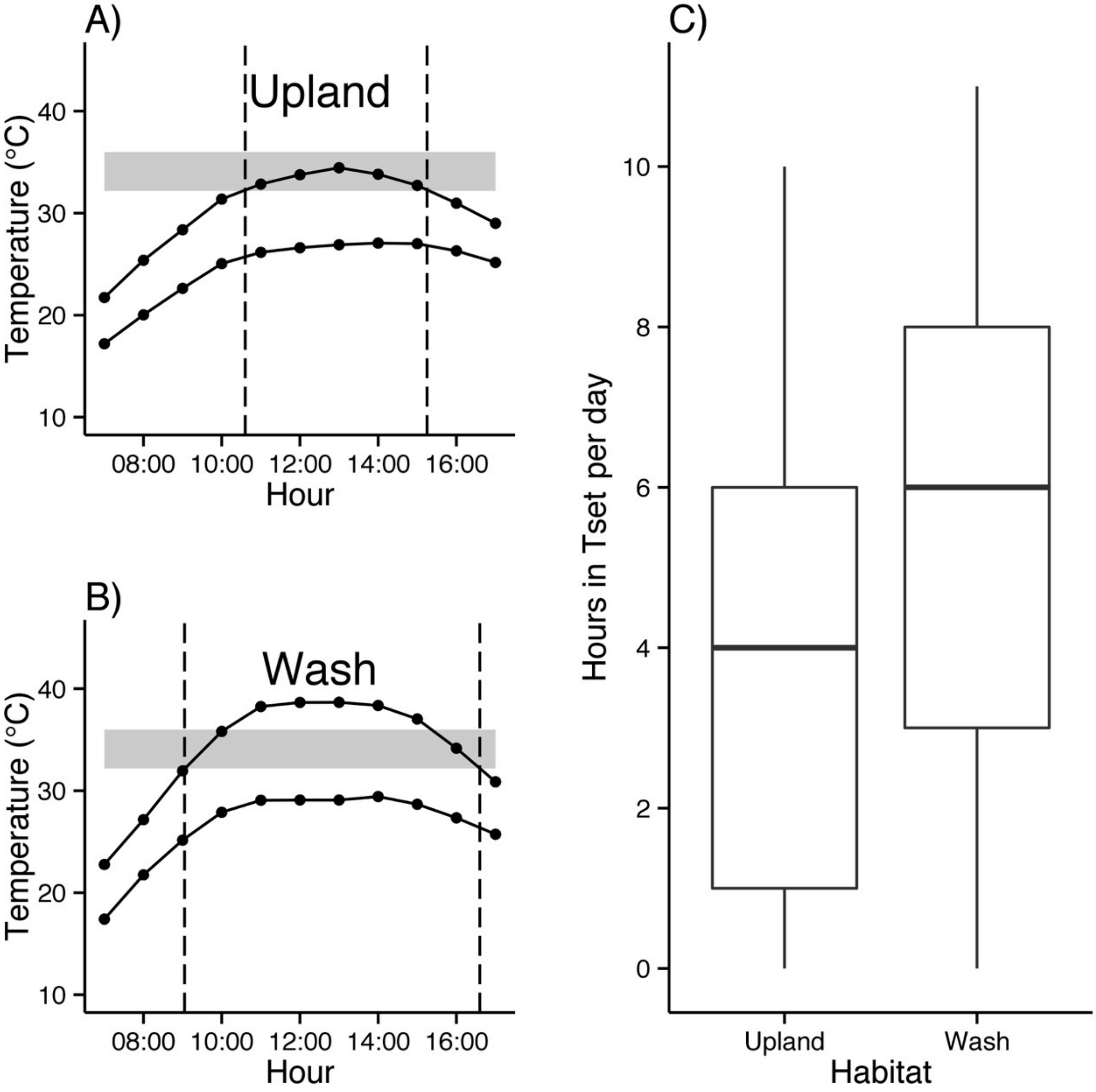

Figure 1-3. Thermal quality of A) upland and B) wash habitats showing the mean daily maximum and minimum temperatures for each hour (solid lines) in relation to the preferred body temperature (T_{set}, shaded areas) of ornate tree lizards (*Urosaurus ornatus*) in the Chiricahua Mountains of Arizona, 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 was higher in the wash that in upland habitat.

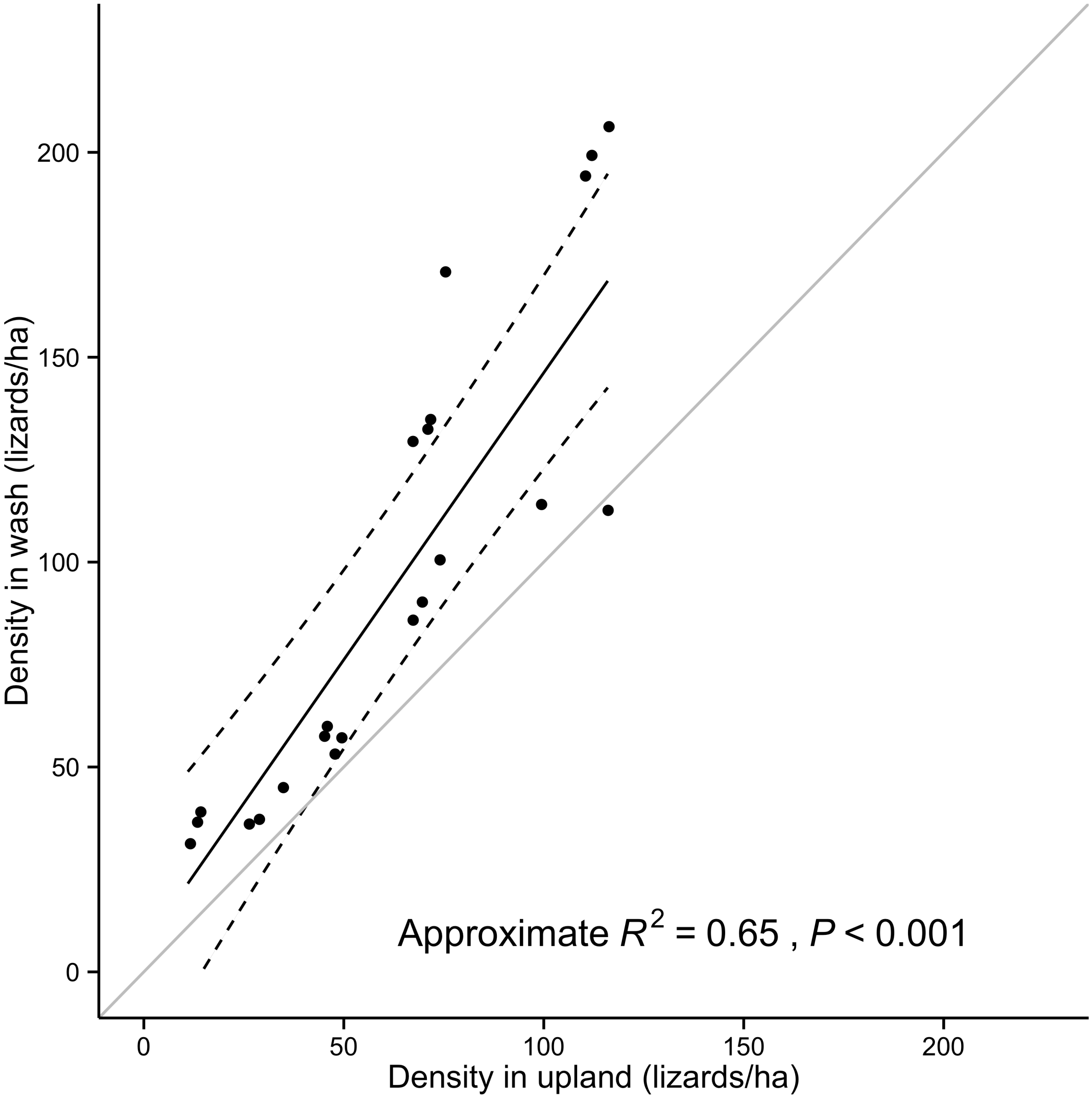

Figure 1-4. The isodar (black line, with dashed 95 % confidence intervals from a linear mixed-effects model with a random effect of site) for ornate tree lizards (*Urosaurus ornatus*) in upland and wash habitats for 10 sites (one estimate per site per year) in the Chiricahua Mountains of Arizona, USA. The grey line represents no habitat preference (equal density in each habitat).

Supplementary information for Chapter 1

Validating thermal models

In May 2014, I tested how well a thermal model matched the body temperature (T_b) of actual ornate tree lizards (*Urosaurus ornatus*). Using a tree lizard that died from unknown causes, I inserted a temperature logger (iButton) into the body cavity. The dead lizard was placed next to a thermal model consisting of a temperature logger coated in Plasti Dip and painted brown to have similar reflectance as a tree lizard. Both temperature loggers recorded data every 15 min and were placed in the field for 24 hrs. The lizard T_b was compared to the thermal model temperature using a linear regression and a paired t-test.

There was a high correlation between lizard temperature and thermal model temperature ($R^2 = 0.99$; Fig. 1-S3). The thermal model had significantly different temperatures than the lizard (paired $t = 6.01$, $df = 96$, $P < 0.001$), but the mean difference in temperature was 0.78 °C, which is close to the accuracy of the temperature logger (± 0.5 °C). Therefore, in further analyses I assumed the thermal model was a good representation of the T_b that a tree lizard would experience.

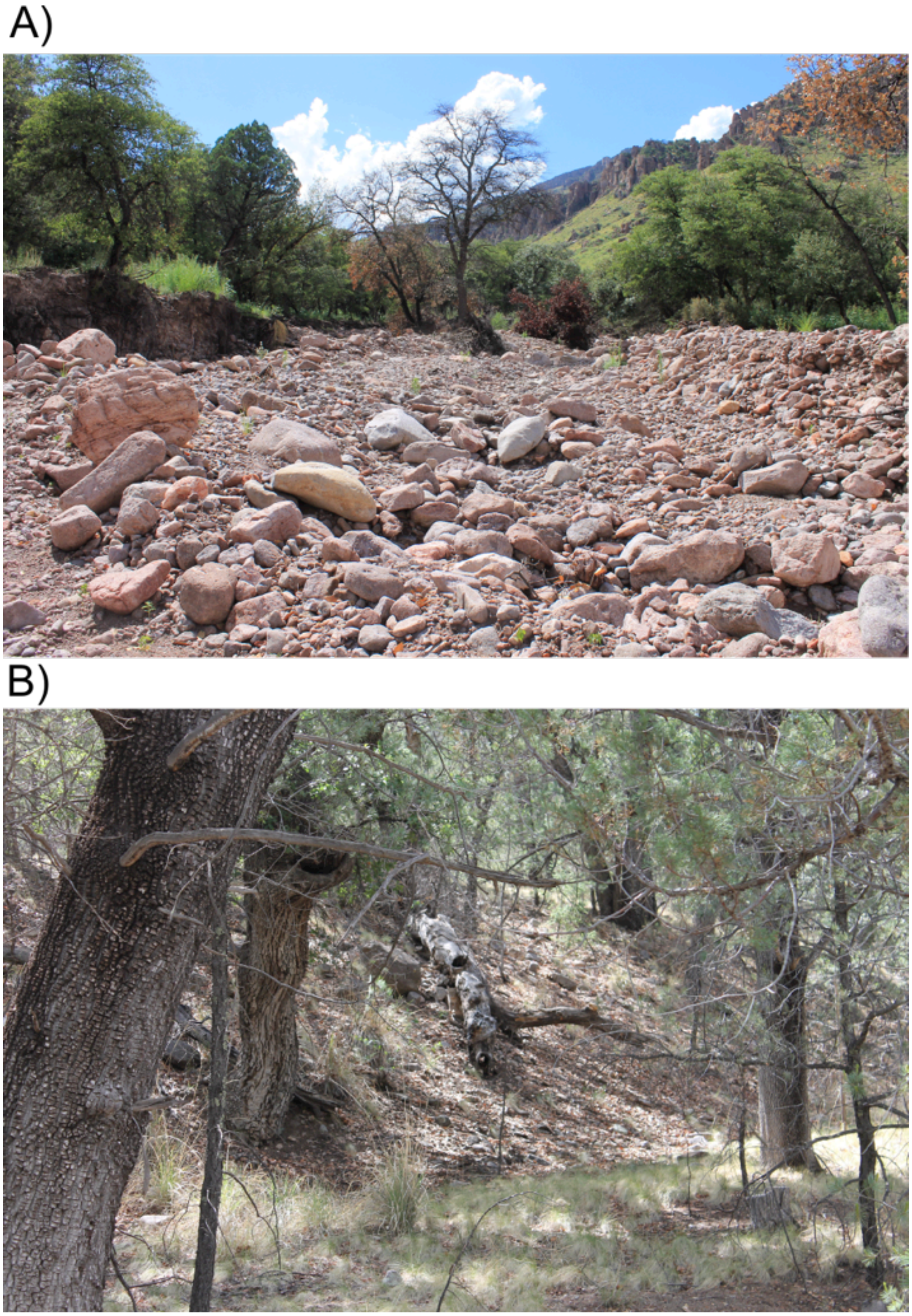

Figure 1-S1. Photographs of the two habitats used to study habitat selection by ornate tree lizards (*Urosaurus ornatus*): A) wash habitat had a rocky substrate and an open canopy with little vegetation, and B) upland habitat was treed with some undergrowth vegetation.

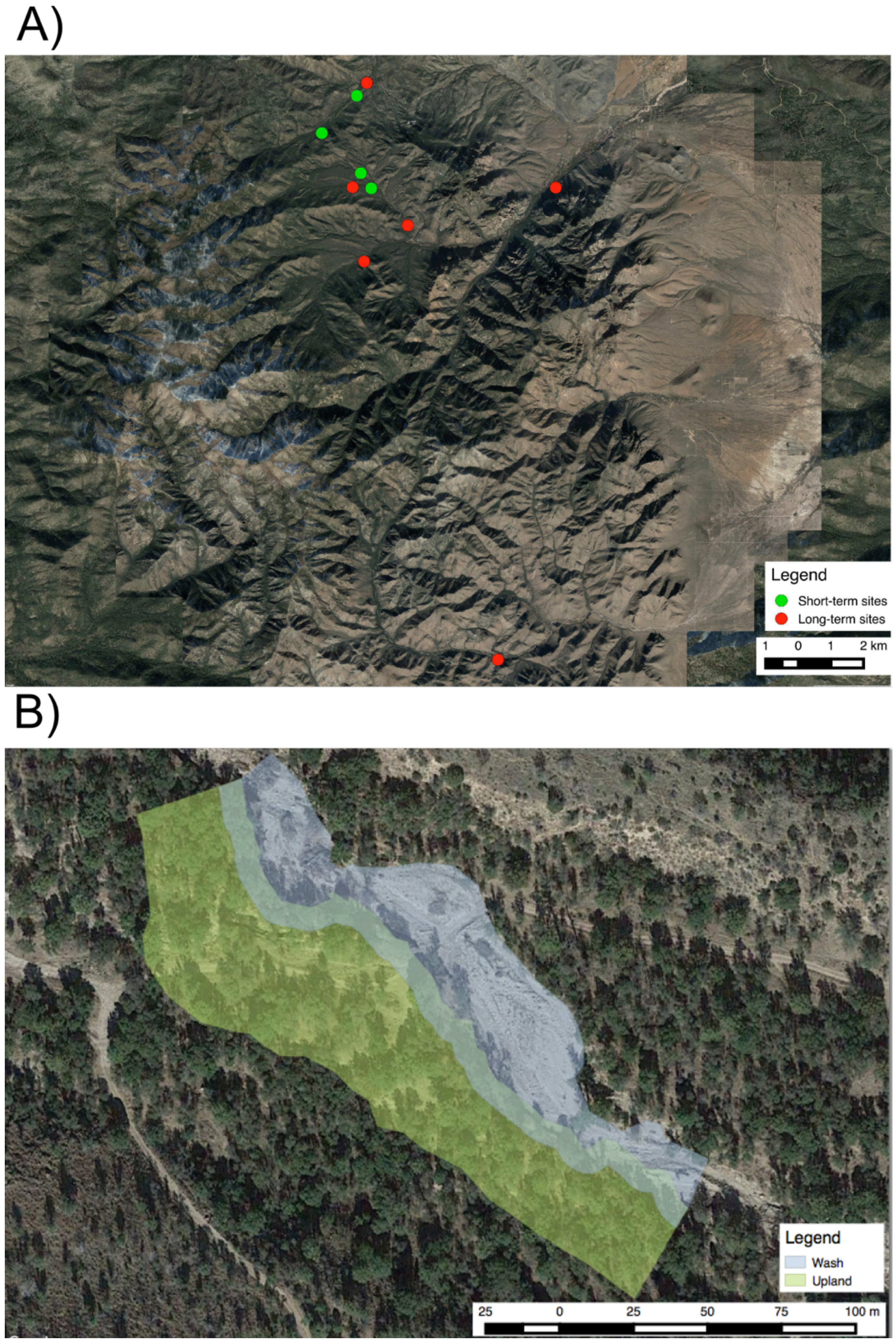

Figure 1-S2. A) Location of study sites where ornate tree lizards (*Urosaurus ornatus*) were studied for one (n = 4; green) or three (n = 6; red) active seasons in the Chiricahua Mountains of Arizona, USA. B) The two habitats at one representative study site (site 2) showing the wash (blue), upland (green), and buffer zone (overlap) for assigning lizards to each habitat.

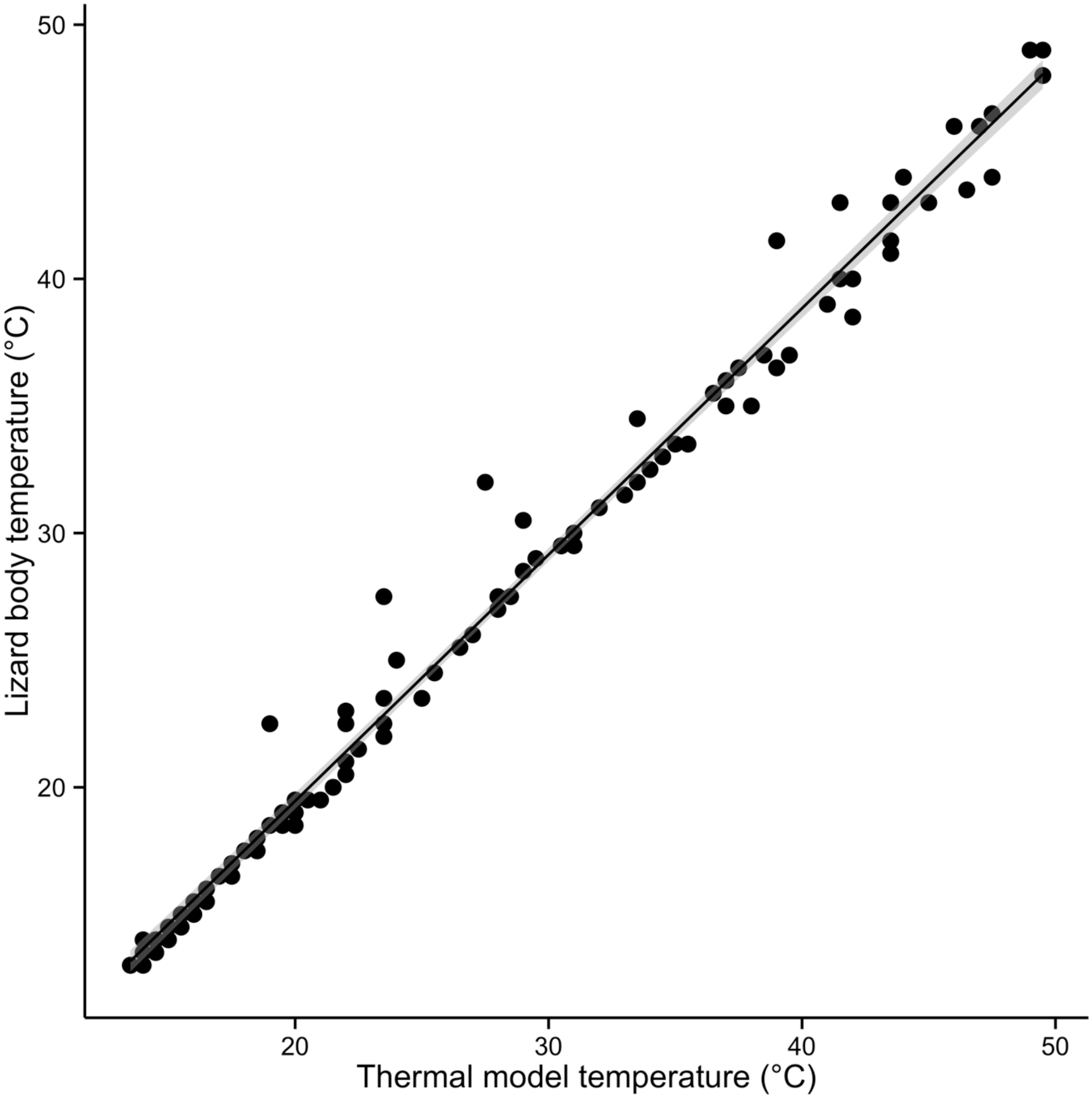

Figure 1-S3. The relationship between the temperature in a thermal model and the body temperature of an ornate tree lizard (*Urosaurus ornatus*) over 24 hrs in the Chiricahua Mountains of Arizona, USA. The regression line is black and the grey shading displays the 95% confidence interval.

Table 1-S1. Coordinates (UTM, zone 12R) of study sites where ornate tree lizards (*Urosaurus ornatus*) were studied for three (Site 1-6) or one (Site 7 - 10) or active seasons in the Chiricahua Mountains of Arizona, USA.

Site	**E**	**N**
1	667700	3530564
2	672389	3516224
3	668088	3528306
4	668081	3533752
5	673919	3530657
6	669406	3529429
7	667943	3530998
8	666727	3532199
9	668271	3530541
10	667781	3533355

Table 1-S2. Dates of capture sessions for ornate tree lizards (*Urosaurus ornatus*) at 10 sites in the Chiricahua Mountains of Arizona, USA.

Date	Capture Event	Site
2014-May-18	1	1
2014-May-31	2	1
2014-Jun-25	3	1
2014-Jul-7	4	1
2014-Jul-25	5	1
2015-May-14	6	1
2015-Jun-6	7	1
2015-Jul-4	8	1
2016-May-14	9	1
2016-Jun-2	10	1
2016-Jun-29	11	1
2016-Jul-20	12	1
2014-May-12	1	2
2014-Jun-19	2	2
2014-Jul-21	3	2
2015-May-3	4	2
2015-Jun-4	5	2
2015-Jul-12	6	2
2015-Aug-2	7	2
2016-May-6	8	2
2016-May-25	9	2
2016-Jun-18	10	2
2016-Jul-14	11	2
2016-Aug-3	12	2
2014-May-2	1	3
2014-May-20	2	3
2014-Jun-9	3	3
2014-Jun-28	4	3
2014-Jul-8	5	3
2015-May-18	6	3
2015-Jun-14	7	3
2015-Jul-7	8	3
2016-May-16	9	3
2016-Jun-4	10	3
2016-Jun-30	11	3
2016-Jul-21	12	3
2014-May-19	1	4
2014-Jun-1	2	4

2014-Jun-17	3	4
2014-Jun-29	4	4
2014-Jul-13	5	4
2015-May-9	6	4
2015-May-24	7	4
2015-Jun-19	8	4
2015-Jul-21	9	4
2016-May-13	10	4
2016-Jun-3	11	4
2016-Jul-17	12	4
2014-May-9	1	5
2014-May-27	2	5
2014-Jun-24	3	5
2014-Jul-6	4	5
2014-Jul-15	5	5
2015-May-17	6	5
2015-Jun-10	7	5
2015-Jun-27	8	5
2016-May-19	9	5
2016-May-20	9	5
2016-Jun-12	10	5
2016-Jul-8	11	5
2016-Jul-28	12	5
2014-May-3	1	6
2014-May-25	2	6
2014-Jun-18	3	6
2014-Jun-30	4	6
2014-Jul-14	5	6
2015-May-11	6	6
2015-Jun-11	7	6
2015-Jun-28	8	6
2016-May-18	9	6
2016-Jun-6	10	6
2016-Jul-3	11	6
2016-Aug-1	12	6
2016-Jun-5	1	7
2016-Jul-9	2	7
2016-Jun-13	1	8
2016-Jul-10	2	8
2016-May-23	1	9
2016-Jun-15	2	9
2016-May-29	1	10
2016-Jun-26	2	10

Assessing habitat switching in ornate tree lizards (Urosaurus ornatus)

To assess the extent to which ornate tree lizards switch between the wash and upland habitats, I used mark-recapture data and focal behavioural observations. The mark-recapture data indicated that 25% of recaptured individuals (96 of 382) switched between wash and upland habitats on at least one occasion. Therefore, lizards were usually recaptured in the same habitat, but habitat switching did occur. I calculated the mean distance to the wash for each lizard and used a mixed-effects logistic regression model with the *lme4* package to test whether the probability of switching between habitats was related to the distance to the wash or sex. I included a random effect of site. The probability of a tree lizard switching habitats was higher in males than in females ($X^2 = 5.02$, $P = 0.025$) and declined sharply as distance to the wash habitat increased ($X^2 = 32.11$, $P < 0.001$; Figure 1-S4).

I also assessed habitat switching with focal observations of lizards (n = 36). After locating a tree lizard, observers recorded lizard behaviour for 1 hour from a distance of at least 5 m with binoculars to determine how far lizards travelled and whether lizards switched between habitats. The sexes differed in the distance travelled during observations (F = 11.32, df = 1, 30, $P = 0.002$): females moved shorter distances than males (3 m ± 2.2 and 11 m ± 1.99, respectively). The distance travelled by lizards did not depend on the habitat type lizards started in (F = 0.05, df = 1, 30, $P = 0.82$). Six out of 17 (35%) lizards that started in the wash switched between habitats during the trial. Five out of 19 (26%) lizards that started in the upland switched between habitats. Considering that my estimates of the proportion of lizards switching habitats (~25-35%) were similar using focal behavioural observations and mark-recapture data, I believe my habitat assignments based on the mean distance travelled by lizards as a home range buffer is justified. Furthermore, the estimates of distances travelled were very similar using mark-recapture data and behavioural observations.

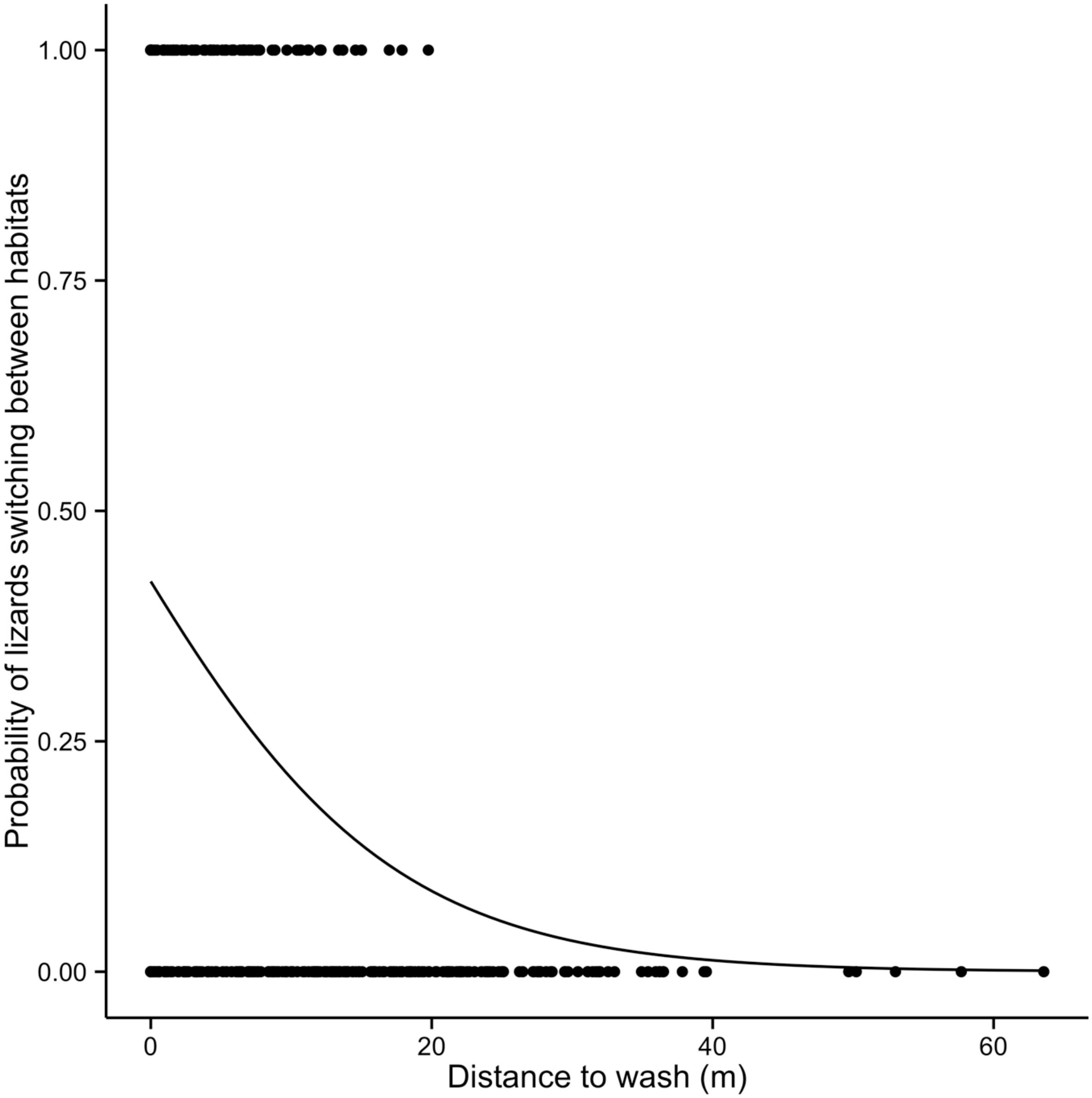

Figure 1-S4. The probability of ornate tree lizards (*Urosaurus ornatus*) switching between the wash and upland habitat as a function of the mean distance from a lizard to the wash (n = 380 individuals caught at least twice).

Goodness-of-fit for mark-recapture models

Jolly-Seber (Jolly 1965, Seber 1965) mark-recapture models (JS) assume that:

1. All marked and unmarked individuals have the same probability of recapture.
2. All marked individuals have the same probability of surviving to the next time step.
3. Marks on individuals are not lost, missed, or misidentified.
4. Sampling is instantaneous relative to the time differences between samples, and releases are immediately after capture.

Assumptions 3 and 4 are difficult to test empirically, but since all individuals were carefully checked for marks, and all individuals were released the day of capture, there were likely no violations of these assumptions. To assess assumptions 1 and 2 and test the goodness-of-fit for the general models at each site, I estimated the variance inflation factor (ĉ) using: bootstrapping, the median ĉ method, and the Fletcher method (Lebreton et al. 1992, Cooch and White 2012, Fletcher 2012) on the analogous Cormack-Jolly-Seber models (Cormack 1989) estimating survival and detection probability. Both the Cormack-Jolly-Seber and JS models estimate survival and detection probability using the same likelihood components (Cooch and White 2012). If the general models fit the data reasonably well and all assumptions are met, then ĉ will be one. Extra-binomial variation caused by either sparse data or incorrect model structure because of assumption violations causes increases in ĉ. In general, when ĉ is larger than three, the structure of the general model does not adequately fit the data (Lebreton et al. 1992). However, when ĉ is greater than one, but less than three, model results can be adjusted by changing ĉ. To be conservative regarding the fit of the general models, I adjusted ĉ to be the highest estimate of the three methods used for each site, and used quasi-likelihood methods ($QAIC_c$) to rank models when ĉ was greater than one (Burnham and Anderson 2002). The estimated ĉ for each method and site is presented in Table 1-S3.

Table 1-S3. Variance inflation estimates (ĉ) for general Jolly-Seber mark-recapture models at six sites in the Chiricahua Mountains of Arizona, USA for ornate tree lizards (*Urosaurus ornatus*) using bootstrapping (1000 iterations), the median ĉ method, and Fletcher's ĉ.

	ĉ estimates		
Site	**Bootstrapping**	**Median**	**Fletcher**
1	1.11	1.07	1.00
2	0.81	0.99	0.99
3	0.95	0.99	0.99
4	1.43	1.14	1.00
5	1.58	1.00	0.98
6	1.07	1.05	1.01

Table 1-S4. Most supported (< 4 ΔQAIC$_c$ of most supported model) Jolly-Seber models at site 1 for ornate tree lizards (_Urosaurus ornatus_) in the Chiricahua Mountains of Arizona, USA. The inflation factor ($\hat{c}$) has been adjusted to 1.11. The full model was: Φ(~hab * sex + season + year)_p_(~hab * sex + effort * weather)_pent_(~hab * sex + year)$\hat{N}$(~1). k = number of parameters in a model; QAIC$_c$ = quasi-likelihood Akaike's information criterion for a model; ΔQAIC$_c$ = difference in QAIC$_c$ between a model and the top-ranked model; ω = Akaike weight for a model.

model	**k**	**QAIC$_c$**	**ΔQAIC$_c$**	**ω**
Φ(~season)_p_(~effort * weather)_pent_(~1)$\hat{N}$(~1)	8	705.88	0.00	0.09
Φ(~hab + season)_p_(~effort * weather)_pent_(~1)$\hat{N}$(~1)	9	706.46	0.58	0.07
Φ(~1)_p_(~effort * weather)_pent_(~1)$\hat{N}$(~1)	7	706.64	0.76	0.06
Φ(~season)_p_(~hab + effort * weather)_pent_(~1)$\hat{N}$(~1)	9	706.84	0.95	0.06
Φ(~hab)_p_(~effort * weather)_pent_(~1)$\hat{N}$(~1)	8	707.14	1.25	0.05
Φ(~1)_p_(~hab + effort * weather)_pent_(~1)$\hat{N}$(~1)	8	707.55	1.67	0.04
Φ(~sex + season)_p_(~effort * weather)_pent_(~1)$\hat{N}$(~1)	9	707.91	2.02	0.03
Φ(~season)_p_(~effort * weather)_pent_(~sex)$\hat{N}$(~1)	9	707.95	2.06	0.03
Φ(~season)_p_(~effort * weather)_pent_(~hab)$\hat{N}$(~1)	9	708.01	2.13	0.03
Φ(~season)_p_(~sex + effort * weather)_pent_(~1)$\hat{N}$(~1)	9	708.02	2.13	0.03
Φ(~hab + season)_p_(~hab + effort * weather)_pent_(~1)$\hat{N}$(~1)	10	708.29	2.40	0.03
Φ(~hab + sex + season)_p_(~effort * weather)_pent_(~1)$\hat{N}$(~1)	10	708.50	2.62	0.02
Φ(~hab + season)_p_(~effort * weather)_pent_(~sex)$\hat{N}$(~1)	10	708.55	2.66	0.02
Φ(~hab + season)_p_(~effort * weather)_pent_(~hab)$\hat{N}$(~1)	10	708.61	2.72	0.02
Φ(~hab + season)_p_(~sex + effort * weather)_pent_(~1)$\hat{N}$(~1)	10	708.61	2.73	0.02
Φ(~1)_p_(~effort * weather)_pent_(~sex)$\hat{N}$(~1)	8	708.69	2.80	0.02
Φ(~season)_p_(~effort * weather)_pent_(~year)$\hat{N}$(~1)	10	708.73	2.84	0.02
Φ(~1)_p_(~effort * weather)_pent_(~hab)$\hat{N}$(~1)	8	708.75	2.87	0.02
Φ(~sex)_p_(~effort * weather)_pent_(~1)$\hat{N}$(~1)	8	708.76	2.88	0.02
Φ(~1)_p_(~sex + effort * weather)_pent_(~1)$\hat{N}$(~1)	8	708.76	2.88	0.02
Φ(~sex + season)_p_(~hab + effort * weather)_pent_(~1)$\hat{N}$(~1)	10	708.84	2.96	0.02
Φ(~season)_p_(~hab + effort * weather)_pent_(~hab)$\hat{N}$(~1)	10	708.91	3.02	0.02
Φ(~season)_p_(~hab + effort * weather)_pent_(~sex)$\hat{N}$(~1)	10	708.91	3.03	0.02
Φ(~season)_p_(~sex + hab + effort * weather)_pent_(~1)$\hat{N}$(~1)	10	708.99	3.11	0.02
Φ(~hab)_p_(~hab + effort * weather)_pent_(~1)$\hat{N}$(~1)	9	709.06	3.18	0.02
Φ(~hab)_p_(~effort * weather)_pent_(~sex)$\hat{N}$(~1)	9	709.21	3.32	0.02
Φ(~hab + sex)_p_(~effort * weather)_pent_(~1)$\hat{N}$(~1)	9	709.27	3.38	0.02
Φ(~hab)_p_(~sex + effort * weather)_pent_(~1)$\hat{N}$(~1)	9	709.27	3.38	0.02
Φ(~hab)_p_(~effort * weather)_pent_(~hab)$\hat{N}$(~1)	9	709.27	3.39	0.02
Φ(~season)_p_(~sex * hab + effort * weather)_pent_(~1)$\hat{N}$(~1)	11	709.32	3.43	0.02

Φ(~hab + season)p(~effort * weather)$pent$(~year)$\hat{N}$(~1)	11	709.35	3.46	0.02
Φ(~1)p(~hab + effort * weather)$pent$(~hab)$\hat{N}$(~1)	9	709.61	3.72	0.01
Φ(~1)p(~hab + effort * weather)$pent$(~sex)$\hat{N}$(~1)	9	709.61	3.72	0.01
Φ(~1)p(~sex + hab + effort * weather)$pent$(~1)$\hat{N}$(~1)	9	709.68	3.80	0.01
Φ(~sex)p(~hab + effort * weather)$pent$(~1)$\hat{N}$(~1)	9	709.68	3.80	0.01
Φ(~season + year)p(~effort * weather)$pent$(~1)$\hat{N}$(~1)	10	709.73	3.84	0.01
Φ(~season)p(~hab + effort * weather)$pent$(~year)$\hat{N}$(~1)	11	709.74	3.85	0.01
Φ(~season)p(~1)$pent$(~1)$\hat{N}$(~1)	5	709.78	3.89	0.01

Table 1-S5. Most supported (< 4 ΔAIC_c of most supported model) Jolly-Seber models at site 2 for ornate tree lizards (*Urosaurus ornatus*) in the Chiricahua Mountains of Arizona, USA. k = number of parameters in a model; AIC_c = Akaike's information criterion for a model; ΔAIC_c = difference in AIC_c between a model and the top-ranked model; ω = Akaike weight for a model.

model	**k**	**AIC_c**	**ΔAIC_c**	**ω**
Φ(~season * year)*p*(~sex + hab + effort * weather)*pent*(~sex)$\hat{N}$(~1)	14	1017.88	0.00	0.13
Φ(~season * year)*p*(~hab + effort * weather)*pent*(~sex)$\hat{N}$(~1)	13	1017.92	0.04	0.12
Φ(~season * year)*p*(~sex + hab + effort * weather)*pent*(~1)$\hat{N}$(~1)	13	1018.78	0.90	0.08
Φ(~year)*p*(~sex + hab + effort * weather)*pent*(~sex)$\hat{N}$(~1)	12	1019.24	1.36	0.06
Φ(~season * year)*p*(~hab + effort * weather)*pent*(~1)$\hat{N}$(~1)	12	1019.82	1.94	0.05
Φ(~season * year)*p*(~sex + hab + effort * weather)*pent*(~hab + sex)$\hat{N}$(~1)	15	1019.92	2.04	0.05
Φ(~season * year)*p*(~hab + effort * weather)*pent*(~hab + sex)$\hat{N}$(~1)	14	1019.95	2.07	0.04
Φ(~season * year)*p*(~sex * hab + effort * weather)*pent*(~sex)$\hat{N}$(~1)	15	1020.03	2.15	0.04
Φ(~hab + year)*p*(~sex + hab + effort * weather)*pent*(~sex)$\hat{N}$(~1)	13	1020.13	2.25	0.04
Φ(~year)*p*(~hab + effort * weather)*pent*(~sex)$\hat{N}$(~1)	11	1020.24	2.36	0.04
Φ(~year)*p*(~sex + hab + effort * weather)*pent*(~1)$\hat{N}$(~1)	11	1020.69	2.81	0.03
Φ(~season + year)*p*(~sex + hab + effort * weather)*pent*(~sex)$\hat{N}$(~1)	13	1020.70	2.82	0.03
Φ(~season * year)*p*(~sex + hab + effort * weather)*pent*(~hab)$\hat{N}$(~1)	14	1020.74	2.87	0.03
Φ(~sex + year)*p*(~hab + effort * weather)*pent*(~sex)$\hat{N}$(~1)	12	1020.89	3.01	0.03
Φ(~season * year)*p*(~sex * hab + effort * weather)*pent*(~1)$\hat{N}$(~1)	14	1020.92	3.04	0.03
Φ(~hab + year)*p*(~hab + effort * weather)*pent*(~sex)$\hat{N}$(~1)	12	1021.18	3.30	0.02
Φ(~sex + year)*p*(~sex + hab + effort * weather)*pent*(~sex)$\hat{N}$(~1)	13	1021.22	3.34	0.02
Φ(~year)*p*(~sex + hab + effort * weather)*pent*(~hab + sex)$\hat{N}$(~1)	13	1021.34	3.46	0.02
Φ(~year)*p*(~sex * hab + effort * weather)*pent*(~sex)$\hat{N}$(~1)	13	1021.37	3.49	0.02
Φ(~year)*p*(~sex + hab + effort + weather)*pent*(~sex)$\hat{N}$(~1)	11	1021.40	3.52	0.02
Φ(~hab * sex + season * year)*p*(~hab + effort * weather)*pent*(~sex)$\hat{N}$(~1)	16	1021.45	3.57	0.02
Φ(~hab + year)*p*(~sex + hab + effort * weather)*pent*(~1)$\hat{N}$(~1)	12	1021.48	3.61	0.02
Φ(~season + year)*p*(~hab + effort * weather)*pent*(~sex)$\hat{N}$(~1)	12	1021.54	3.66	0.02

Φ(~season * year)p(~hab + effort * weather)$pent$(~hab)$\hat{N}$(~1)	13	1021.78	3.90	0.02

Table 1-S6. Most supported (< 4 ΔAIC_c of most supported model) Jolly-Seber models at site 3 for ornate tree lizards (*Urosaurus ornatus*) in the Chiricahua Mountains of Arizona, USA. k = number of parameters in a model; AIC_c = Akaike's information criterion for a model; ΔAIC_c = difference in AIC_c between a model and the top-ranked model; ω = Akaike weight for a model.

model	**k**	**AIC_c**	**ΔAIC_c**	**ω**
$\Phi(\sim\text{season})p(\sim 1)\mathit{pent}(\sim 1)\hat{N}(\sim 1)$	5	559.92	0.00	0.04
$\Phi(\sim\text{season})p(\sim 1)\mathit{pent}(\sim\text{year})\hat{N}(\sim 1)$	7	561.06	1.14	0.02
$\Phi(\sim\text{season})p(\sim\text{sex})\mathit{pent}(\sim 1)\hat{N}(\sim 1)$	6	561.12	1.20	0.02
$\Phi(\sim 1)p(\sim\text{effort} * \text{weather})\mathit{pent}(\sim 1)\hat{N}(\sim 1)$	7	561.15	1.23	0.02
$\Phi(\sim\text{season})p(\sim\text{effort})\mathit{pent}(\sim 1)\hat{N}(\sim 1)$	6	561.19	1.27	0.02
$\Phi(\sim 1)p(\sim 1)\mathit{pent}(\sim 1)\hat{N}(\sim 1)$	4	561.27	1.35	0.02
$\Phi(\sim\text{season})p(\sim\text{effort} * \text{weather})\mathit{pent}(\sim 1)\hat{N}(\sim 1)$	8	561.54	1.62	0.02
$\Phi(\sim\text{season})p(\sim 1)\mathit{pent}(\sim\text{hab})\hat{N}(\sim 1)$	6	561.67	1.75	0.02
$\Phi(\sim\text{hab} + \text{season})p(\sim 1)\mathit{pent}(\sim 1)\hat{N}(\sim 1)$	6	561.74	1.82	0.02
$\Phi(\sim\text{season})p(\sim\text{weather})\mathit{pent}(\sim 1)\hat{N}(\sim 1)$	6	561.76	1.84	0.02
$\Phi(\sim\text{season})p(\sim\text{hab})\mathit{pent}(\sim 1)\hat{N}(\sim 1)$	6	561.81	1.89	0.02
$\Phi(\sim\text{sex} + \text{season})p(\sim 1)\mathit{pent}(\sim 1)\hat{N}(\sim 1)$	6	561.87	1.95	0.02
$\Phi(\sim 1)p(\sim\text{effort})\mathit{pent}(\sim 1)\hat{N}(\sim 1)$	5	561.93	2.01	0.01
$\Phi(\sim\text{sex})p(\sim\text{sex})\mathit{pent}(\sim 1)\hat{N}(\sim 1)$	6	561.99	2.07	0.01
$\Phi(\sim\text{season})p(\sim 1)\mathit{pent}(\sim\text{sex})\hat{N}(\sim 1)$	6	562.06	2.14	0.01
$\Phi(\sim\text{sex})p(\sim\text{sex} + \text{effort} * \text{weather})\mathit{pent}(\sim 1)\hat{N}(\sim 1)$	9	562.16	2.24	0.01
$\Phi(\sim\text{season})p(\sim\text{sex})\mathit{pent}(\sim\text{year})\hat{N}(\sim 1)$	8	562.18	2.26	0.01
$\Phi(\sim 1)p(\sim\text{sex} + \text{effort} * \text{weather})\mathit{pent}(\sim 1)\hat{N}(\sim 1)$	8	562.20	2.28	0.01
$\Phi(\sim 1)p(\sim\text{sex})\mathit{pent}(\sim 1)\hat{N}(\sim 1)$	5	562.23	2.31	0.01
$\Phi(\sim\text{sex} + \text{season})p(\sim\text{sex})\mathit{pent}(\sim 1)\hat{N}(\sim 1)$	7	562.31	2.39	0.01
$\Phi(\sim\text{sex})p(\sim\text{sex})\mathit{pent}(\sim\text{year})\hat{N}(\sim 1)$	8	562.31	2.39	0.01
$\Phi(\sim\text{season})p(\sim\text{sex} + \text{effort})\mathit{pent}(\sim 1)\hat{N}(\sim 1)$	7	562.42	2.50	0.01
$\Phi(\sim 1)p(\sim 1)\mathit{pent}(\sim\text{year})\hat{N}(\sim 1)$	6	562.44	2.52	0.01
$\Phi(\sim\text{hab})p(\sim\text{effort} * \text{weather})\mathit{pent}(\sim 1)\hat{N}(\sim 1)$	8	562.50	2.58	0.01
$\Phi(\sim\text{hab})p(\sim 1)\mathit{pent}(\sim 1)\hat{N}(\sim 1)$	5	562.57	2.65	0.01
$\Phi(\sim\text{season})p(\sim\text{effort})\mathit{pent}(\sim\text{year})\hat{N}(\sim 1)$	8	562.70	2.78	0.01
$\Phi(\sim\text{sex})p(\sim\text{sex} + \text{effort})\mathit{pent}(\sim 1)\hat{N}(\sim 1)$	7	562.71	2.79	0.01
$\Phi(\sim\text{season})p(\sim 1)\mathit{pent}(\sim\text{hab} + \text{year})\hat{N}(\sim 1)$	8	562.82	2.90	0.01
$\Phi(\sim\text{hab} + \text{season})p(\sim 1)\mathit{pent}(\sim\text{year})\hat{N}(\sim 1)$	8	562.85	2.93	0.01
$\Phi(\sim\text{season})p(\sim\text{sex})\mathit{pent}(\sim\text{hab})\hat{N}(\sim 1)$	7	562.86	2.94	0.01
$\Phi(\sim\text{sex} + \text{season})p(\sim\text{sex})\mathit{pent}(\sim\text{year})\hat{N}(\sim 1)$	9	562.87	2.95	0.01
$\Phi(\sim\text{sex} + \text{season})p(\sim 1)\mathit{pent}(\sim\text{year})\hat{N}(\sim 1)$	8	562.88	2.96	0.01
$\Phi(\sim\text{season})p(\sim\text{sex} + \text{effort} * \text{weather})\mathit{pent}(\sim 1)\hat{N}(\sim 1)$	9	562.89	2.97	0.01
$\Phi(\sim 1)p(\sim\text{sex} + \text{effort})\mathit{pent}(\sim 1)\hat{N}(\sim 1)$	6	562.90	2.98	0.01

Φ(~hab + season)p(~sex)$pent$(~1)$\hat{N}$(~1)	7	562.91	2.99	0.01
Φ(~sex)p(~effort * weather)$pent$(~1)$\hat{N}$(~1)	8	562.93	3.01	0.01
Φ(~season)p(~weather)$pent$(~year)$\hat{N}$(~1)	8	562.95	3.03	0.01
Φ(~sex)p(~1)$pent$(~1)$\hat{N}$(~1)	5	562.96	3.04	0.01
Φ(~hab)p(~hab)$pent$(~1)$\hat{N}$(~1)	6	562.97	3.05	0.01
Φ(~season)p(~effort)$pent$(~hab)$\hat{N}$(~1)	7	562.98	3.06	0.01
Φ(~season)p(~hab)$pent$(~year)$\hat{N}$(~1)	8	562.98	3.06	0.01
Φ(~season)p(~sex + weather)$pent$(~1)$\hat{N}$(~1)	7	562.99	3.07	0.01
Φ(~1)p(~1)$pent$(~hab)$\hat{N}$(~1)	5	563.01	3.09	0.01
Φ(~1)p(~effort * weather)$pent$(~hab)$\hat{N}$(~1)	8	563.03	3.11	0.01
Φ(~hab + season)p(~effort)$pent$(~1)$\hat{N}$(~1)	7	563.03	3.11	0.01
Φ(~1)p(~hab + effort * weather)$pent$(~1)$\hat{N}$(~1)	8	563.06	3.14	0.01
Φ(~season)p(~sex + hab)$pent$(~1)$\hat{N}$(~1)	7	563.07	3.15	0.01
Φ(~1)p(~hab)$pent$(~1)$\hat{N}$(~1)	5	563.07	3.15	0.01
Φ(~hab)p(~hab + effort * weather)$pent$(~1)$\hat{N}$(~1)	9	563.10	3.18	0.01
Φ(~season)p(~hab + effort)$pent$(~1)$\hat{N}$(~1)	7	563.12	3.20	0.01
Φ(~hab + sex)p(~sex)$pent$(~1)$\hat{N}$(~1)	7	563.12	3.20	0.01
Φ(~sex + season)p(~effort)$pent$(~1)$\hat{N}$(~1)	7	563.17	3.25	0.01
Φ(~hab + season)p(~hab)$pent$(~1)$\hat{N}$(~1)	7	563.19	3.27	0.01
Φ(~season)p(~sex)$pent$(~sex)$\hat{N}$(~1)	7	563.21	3.29	0.01
Φ(~season)p(~1)$pent$(~sex + year)$\hat{N}$(~1)	8	563.23	3.31	0.01
Φ(~hab)p(~effort)$pent$(~1)$\hat{N}$(~1)	6	563.24	3.32	0.01
Φ(~season)p(~effort + weather)$pent$(~1)$\hat{N}$(~1)	7	563.25	3.33	0.01
Φ(~hab + sex)p(~sex + hab)$pent$(~hab)$\hat{N}$(~1)	9	563.26	3.34	0.01
Φ(~1)p(~sex)$pent$(~year)$\hat{N}$(~1)	7	563.29	3.37	0.01
Φ(~hab + sex)p(~sex + hab)$pent$(~1)$\hat{N}$(~1)	8	563.32	3.40	0.01
Φ(~hab + sex)p(~sex + effort * weather)$pent$(~1)$\hat{N}$(~1)	10	563.33	3.41	0.01
Φ(~1)p(~effort * weather)$pent$(~sex)$\hat{N}$(~1)	8	563.34	3.42	0.01
Φ(~hab + season)p(~1)$pent$(~hab)$\hat{N}$(~1)	7	563.35	3.43	0.01
Φ(~season)p(~effort)$pent$(~sex)$\hat{N}$(~1)	7	563.35	3.43	0.01
Φ(~1)p(~weather)$pent$(~1)$\hat{N}$(~1)	5	563.38	3.46	0.01
Φ(~1)p(~1)$pent$(~sex)$\hat{N}$(~1)	5	563.39	3.47	0.01
Φ(~hab + sex)p(~sex)$pent$(~year)$\hat{N}$(~1)	9	563.40	3.48	0.01
Φ(~season)p(~hab)$pent$(~hab)$\hat{N}$(~1)	7	563.41	3.49	0.01
Φ(~season)p(~effort * weather)$pent$(~hab)$\hat{N}$(~1)	9	563.41	3.49	0.01
Φ(~hab)p(~hab)$pent$(~hab)$\hat{N}$(~1)	7	563.42	3.50	0.01
Φ(~sex)p(~sex)$pent$(~sex)$\hat{N}$(~1)	7	563.44	3.52	0.01
Φ(~hab)p(~sex)$pent$(~1)$\hat{N}$(~1)	6	563.45	3.53	0.01
Φ(~hab + season)p(~effort * weather)$pent$(~1)$\hat{N}$(~1)	9	563.47	3.55	0.01
Φ(~hab)p(~sex + effort * weather)$pent$(~1)$\hat{N}$(~1)	9	563.49	3.57	0.01
Φ(~sex)p(~sex)$pent$(~sex + year)$\hat{N}$(~1)	9	563.50	3.58	0.01
Φ(~sex)p(~sex + effort)$pent$(~year)$\hat{N}$(~1)	9	563.51	3.59	0.01
Φ(~hab + sex)p(~sex + hab)$pent$(~year)$\hat{N}$(~1)	10	563.51	3.59	0.01

Φ(~1)*p*(~effort)*pent*(~year)$\hat{N}$(~1)	7	563.53	3.61	0.01
Φ(~season)*p*(~weather)*pent*(~hab)$\hat{N}$(~1)	7	563.53	3.61	0.01
Φ(~sex)*p*(~sex)*pent*(~hab)$\hat{N}$(~1)	7	563.56	3.64	0.01
Φ(~season)*p*(~hab + effort * weather)*pent*(~1)$\hat{N}$(~1)	9	563.56	3.64	0.01
Φ(~sex + season)*p*(~effort * weather)*pent*(~1)$\hat{N}$(~1)	9	563.59	3.67	0.01
Φ(~hab + season)*p*(~weather)*pent*(~1)$\hat{N}$(~1)	7	563.61	3.69	0.01
Φ(~sex + season)*p*(~1)*pent*(~hab)$\hat{N}$(~1)	7	563.61	3.69	0.01
Φ(~hab + sex)*p*(~sex + hab)*pent*(~hab + year)$\hat{N}$(~1)	11	563.62	3.70	0.01
Φ(~sex)*p*(~effort)*pent*(~1)$\hat{N}$(~1)	6	563.65	3.73	0.01
Φ(~sex + season)*p*(~sex + effort)*pent*(~1)$\hat{N}$(~1)	8	563.66	3.74	0.01
Φ(~hab)*p*(~hab + effort)*pent*(~1)$\hat{N}$(~1)	7	563.67	3.75	0.01
Φ(~season)*p*(~hab + weather)*pent*(~1)$\hat{N}$(~1)	7	563.68	3.76	0.01
Φ(~hab + sex + season)*p*(~1)*pent*(~1)$\hat{N}$(~1)	7	563.68	3.76	0.01
Φ(~hab)*p*(~1)*pent*(~year)$\hat{N}$(~1)	7	563.69	3.77	0.01
Φ(~hab + sex)*p*(~sex + hab + effort * weather)*pent*(~1)$\hat{N}$(~1)	11	563.70	3.78	0.01
Φ(~1)*p*(~effort)*pent*(~hab)$\hat{N}$(~1)	6	563.71	3.79	0.01
Φ(~sex + season)*p*(~weather)*pent*(~1)$\hat{N}$(~1)	7	563.73	3.81	0.01
Φ(~season)*p*(~effort * weather)*pent*(~sex)$\hat{N}$(~1)	9	563.76	3.84	0.01
Φ(~1)*p*(~hab + effort)*pent*(~1)$\hat{N}$(~1)	6	563.76	3.84	0.01
Φ(~sex + season)*p*(~hab)*pent*(~1)$\hat{N}$(~1)	7	563.76	3.84	0.01
Φ(~sex)*p*(~sex + hab)*pent*(~1)$\hat{N}$(~1)	7	563.83	3.91	0.01
Φ(~season)*p*(~1)*pent*(~hab + sex)$\hat{N}$(~1)	7	563.84	3.92	0.01
Φ(~hab + sex)*p*(~sex + effort)*pent*(~1)$\hat{N}$(~1)	8	563.85	3.93	0.01
Φ(~season)*p*(~sex + effort)*pent*(~year)$\hat{N}$(~1)	9	563.86	3.94	0.01
Φ(~year)*p*(~effort * weather)*pent*(~1)$\hat{N}$(~1)	9	563.87	3.95	0.01
Φ(~sex)*p*(~sex)*pent*(~hab + year)$\hat{N}$(~1)	9	563.88	3.96	0.01
Φ(~sex)*p*(~sex + effort * weather)*pent*(~hab)$\hat{N}$(~1)	10	563.89	3.97	0.01
Φ(~sex)*p*(~sex + effort * weather)*pent*(~sex)$\hat{N}$(~1)	10	563.89	3.97	0.01
Φ(~hab + season)*p*(~1)*pent*(~sex)$\hat{N}$(~1)	7	563.90	3.98	0.01
Φ(~hab)*p*(~sex + hab)*pent*(~1)$\hat{N}$(~1)	7	563.91	3.99	0.01

Table 1-S7. Most supported (< 4 ΔQAIC$_c$ of most supported model) Jolly-Seber models at site 4 for ornate tree lizards (*Urosaurus ornatus*) in the Chiricahua Mountains of Arizona, USA. The inflation factor ($\hat{c}$) has been adjusted to 1.43. k = number of parameters in a model; QAIC$_c$ = quasi-likelihood Akaike's information criterion for a model; ΔQAIC$_c$ = difference in QAIC$_c$ between a model and the top-ranked model; ω = Akaike weight for a model.

model	**k**	**QAIC$_c$**	**ΔQAIC$_c$**	**ω**
Φ(~season)*p*(~hab + effort)*pent*(~1)$\hat{N}$(~1)	7	662.24	0.00	0.09
Φ(~1)*p*(~hab + effort + weather)*pent*(~1)$\hat{N}$(~1)	7	663.55	1.31	0.05
Φ(~season)*p*(~hab + effort)*pent*(~hab)$\hat{N}$(~1)	8	663.74	1.50	0.04
Φ(~season)*p*(~hab + effort + weather)*pent*(~1)$\hat{N}$(~1)	8	663.86	1.62	0.04
Φ(~1)*p*(~hab + effort)*pent*(~1)$\hat{N}$(~1)	6	663.93	1.69	0.04
Φ(~season)*p*(~hab + effort)*pent*(~sex)$\hat{N}$(~1)	8	663.97	1.73	0.04
Φ(~hab + season)*p*(~hab + effort)*pent*(~1)$\hat{N}$(~1)	8	663.98	1.75	0.04
Φ(~sex + season)*p*(~hab + effort)*pent*(~1)$\hat{N}$(~1)	8	664.27	2.03	0.03
Φ(~1)*p*(~hab + weather)*pent*(~1)$\hat{N}$(~1)	6	664.35	2.11	0.03
Φ(~hab + season)*p*(~effort)*pent*(~1)$\hat{N}$(~1)	7	664.53	2.29	0.03
Φ(~1)*p*(~hab)*pent*(~1)$\hat{N}$(~1)	5	664.85	2.61	0.03
Φ(~1)*p*(~sex + hab + effort + weather)*pent*(~1)$\hat{N}$(~1)	8	665.06	2.83	0.02
Φ(~1)*p*(~hab + effort + weather)*pent*(~hab)$\hat{N}$(~1)	8	665.11	2.88	0.02
Φ(~season)*p*(~sex + hab + effort + weather)*pent*(~1)$\hat{N}$(~1)	9	665.13	2.89	0.02
Φ(~1)*p*(~hab + effort * weather)*pent*(~1)$\hat{N}$(~1)	8	665.16	2.92	0.02
Φ(~hab + season)*p*(~effort)*pent*(~hab)$\hat{N}$(~1)	8	665.28	3.04	0.02
Φ(~1)*p*(~hab + effort + weather)*pent*(~sex)$\hat{N}$(~1)	8	665.30	3.06	0.02
Φ(~hab + season)*p*(~hab + effort)*pent*(~hab)$\hat{N}$(~1)	9	665.32	3.09	0.02
Φ(~season)*p*(~hab * sex + effort)*pent*(~1)$\hat{N}$(~1)	9	665.40	3.16	0.02
Φ(~season)*p*(~hab + effort + weather)*pent*(~hab)$\hat{N}$(~1)	9	665.40	3.17	0.02
Φ(~1)*p*(~hab + effort)*pent*(~hab)$\hat{N}$(~1)	7	665.43	3.19	0.02
Φ(~season)*p*(~hab + effort)*pent*(~hab + sex)$\hat{N}$(~1)	9	665.53	3.29	0.02
Φ(~season)*p*(~hab)*pent*(~1)$\hat{N}$(~1)	6	665.53	3.30	0.02
Φ(~season)*p*(~hab + effort * weather)*pent*(~1)$\hat{N}$(~1)	9	665.54	3.30	0.02
Φ(~sex)*p*(~hab + effort + weather)*pent*(~1)$\hat{N}$(~1)	8	665.54	3.30	0.02
Φ(~hab + season)*p*(~sex + effort)*pent*(~1)$\hat{N}$(~1)	8	665.55	3.32	0.02
Φ(~hab)*p*(~hab + effort + weather)*pent*(~1)$\hat{N}$(~1)	8	665.58	3.34	0.02
Φ(~season)*p*(~hab + effort + weather)*pent*(~sex)$\hat{N}$(~1)	9	665.61	3.37	0.02
Φ(~1)*p*(~hab + effort)*pent*(~sex)$\hat{N}$(~1)	7	665.66	3.42	0.02
Φ(~hab + season)*p*(~hab + effort + weather)*pent*(~1)$\hat{N}$(~1)	9	665.70	3.46	0.02
Φ(~hab + season)*p*(~hab + effort)*pent*(~sex)$\hat{N}$(~1)	9	665.72	3.48	0.02
Φ(~sex + season)*p*(~hab + effort)*pent*(~hab)$\hat{N}$(~1)	9	665.78	3.55	0.02

Φ(~1)*p*(~hab + weather)*pent*(~hab)$\hat{N}$(~1)	7	665.85	3.61	0.02
Φ(~season + year)*p*(~hab + effort)*pent*(~1)$\hat{N}$(~1)	9	665.86	3.63	0.02
Φ(~sex + season)*p*(~hab + effort + weather)*pent*(~1)$\hat{N}$(~1)	9	665.90	3.66	0.01
Φ(~sex)*p*(~hab + effort)*pent*(~1)$\hat{N}$(~1)	7	665.91	3.67	0.01
Φ(~hab)*p*(~hab + effort)*pent*(~1)$\hat{N}$(~1)	7	665.93	3.70	0.01
Φ(~sex + season)*p*(~hab + effort)*pent*(~sex)$\hat{N}$(~1)	9	666.00	3.76	0.01
Φ(~hab + sex + season)*p*(~hab + effort)*pent*(~1)$\hat{N}$(~1)	9	666.06	3.82	0.01
Φ(~season)*p*(~effort)*pent*(~1)$\hat{N}$(~1)	6	666.07	3.83	0.01
Φ(~1)*p*(~hab + weather)*pent*(~sex)$\hat{N}$(~1)	7	666.07	3.83	0.01
Φ(~season)*p*(~hab + weather)*pent*(~1)$\hat{N}$(~1)	7	666.17	3.93	0.01

Table 1-S8. Most supported (< 4 ΔQAIC$_c$ of most supported model) Jolly-Seber models at site 5 for ornate tree lizards (*Urosaurus ornatus*) in the Chiricahua Mountains of Arizona, USA. The inflation factor (ĉ) has been adjusted to 1.58. k = number of parameters in a model; QAIC$_c$ = quasi-likelihood Akaike's information criterion for a model; ΔQAIC$_c$ = difference in QAIC$_c$ between a model and the top-ranked model; ω = Akaike weight for a model.

model	**k**	**QAIC$_c$**	**ΔQAIC$_c$**	**ω**
Φ(~1)*p*(~1)*pent*(~1)$\hat{N}$(~1)	4	216.33	0.00	0.10
Φ(~1)*p*(~hab)*pent*(~1)$\hat{N}$(~1)	5	217.61	1.28	0.05
Φ(~1)*p*(~1)*pent*(~sex)$\hat{N}$(~1)	5	217.89	1.56	0.05
Φ(~1)*p*(~weather)*pent*(~1)$\hat{N}$(~1)	5	217.91	1.57	0.05
Φ(~1)*p*(~sex)*pent*(~1)$\hat{N}$(~1)	5	218.01	1.68	0.04
Φ(~hab)*p*(~1)*pent*(~1)$\hat{N}$(~1)	5	218.02	1.69	0.04
Φ(~1)*p*(~effort)*pent*(~1)$\hat{N}$(~1)	5	218.31	1.97	0.04
Φ(~1)*p*(~1)*pent*(~hab)$\hat{N}$(~1)	5	218.50	2.17	0.03
Φ(~sex)*p*(~1)*pent*(~1)$\hat{N}$(~1)	5	218.51	2.18	0.03
Φ(~season)*p*(~1)*pent*(~1)$\hat{N}$(~1)	5	218.55	2.22	0.03
Φ(~1)*p*(~sex + hab)*pent*(~1)$\hat{N}$(~1)	6	219.21	2.88	0.02
Φ(~1)*p*(~hab)*pent*(~sex)$\hat{N}$(~1)	6	219.25	2.92	0.02
Φ(~1)*p*(~hab + weather)*pent*(~1)$\hat{N}$(~1)	6	219.27	2.94	0.02
Φ(~1)*p*(~sex)*pent*(~sex)$\hat{N}$(~1)	6	219.36	3.03	0.02
Φ(~hab * sex)*p*(~1)*pent*(~1)$\hat{N}$(~1)	7	219.42	3.08	0.02
Φ(~1)*p*(~weather)*pent*(~sex)$\hat{N}$(~1)	6	219.46	3.12	0.02
Φ(~hab)*p*(~1)*pent*(~sex)$\hat{N}$(~1)	6	219.62	3.29	0.02
Φ(~hab)*p*(~weather)*pent*(~1)$\hat{N}$(~1)	6	219.63	3.29	0.02
Φ(~1)*p*(~sex + weather)*pent*(~1)$\hat{N}$(~1)	6	219.64	3.31	0.02
Φ(~1)*p*(~hab + effort)*pent*(~1)$\hat{N}$(~1)	6	219.69	3.36	0.02
Φ(~hab)*p*(~sex)*pent*(~1)$\hat{N}$(~1)	6	219.77	3.43	0.02
Φ(~sex)*p*(~hab)*pent*(~1)$\hat{N}$(~1)	6	219.85	3.51	0.02
Φ(~hab)*p*(~hab)*pent*(~1)$\hat{N}$(~1)	6	219.87	3.54	0.02
Φ(~1)*p*(~effort)*pent*(~sex)$\hat{N}$(~1)	6	219.87	3.54	0.02
Φ(~1)*p*(~hab)*pent*(~hab)$\hat{N}$(~1)	6	219.90	3.57	0.02
Φ(~season)*p*(~hab)*pent*(~1)$\hat{N}$(~1)	6	219.90	3.57	0.02
Φ(~hab)*p*(~effort)*pent*(~1)$\hat{N}$(~1)	6	220.03	3.70	0.02
Φ(~1)*p*(~sex + effort)*pent*(~1)$\hat{N}$(~1)	6	220.04	3.71	0.02
Φ(~season)*p*(~weather)*pent*(~1)$\hat{N}$(~1)	6	220.07	3.74	0.02
Φ(~hab + sex)*p*(~1)*pent*(~1)$\hat{N}$(~1)	6	220.08	3.75	0.02
Φ(~1)*p*(~effort + weather)*pent*(~1)$\hat{N}$(~1)	6	220.11	3.78	0.02
Φ(~1)*p*(~1)*pent*(~hab + sex)$\hat{N}$(~1)	6	220.12	3.79	0.02

$\Phi(\sim 1)p(\sim \text{weather})pent(\sim \text{hab})\hat{N}(\sim 1)$	6	220.13	3.80	0.01
$\Phi(\sim \text{sex})p(\sim \text{weather})pent(\sim 1)\hat{N}(\sim 1)$	6	220.14	3.81	0.01
$\Phi(\sim \text{sex})p(\sim 1)pent(\sim \text{sex})\hat{N}(\sim 1)$	6	220.14	3.81	0.01
$\Phi(\sim \text{season})p(\sim 1)pent(\sim \text{sex})\hat{N}(\sim 1)$	6	220.17	3.84	0.01
$\Phi(\sim \text{hab})p(\sim 1)pent(\sim \text{hab})\hat{N}(\sim 1)$	6	220.20	3.87	0.01
$\Phi(\sim 1)p(\sim \text{sex})pent(\sim \text{hab})\hat{N}(\sim 1)$	6	220.23	3.90	0.01
$\Phi(\sim \text{sex})p(\sim \text{sex})pent(\sim 1)\hat{N}(\sim 1)$	6	220.25	3.92	0.01
$\Phi(\sim \text{hab + season})p(\sim 1)pent(\sim 1)\hat{N}(\sim 1)$	6	220.29	3.96	0.01
$\Phi(\sim \text{season})p(\sim \text{sex})pent(\sim 1)\hat{N}(\sim 1)$	6	220.30	3.97	0.01

Table 1-S9. Most supported (< 4 ΔQAIC$_c$ of most supported model) Jolly-Seber models at site 6 for ornate tree lizards (*Urosaurus ornatus*) in the Chiricahua Mountains of Arizona, USA. The inflation factor (ĉ) has been adjusted to 1.07. k = number of parameters in a model; QAIC$_c$ = quasi-likelihood Akaike's information criterion for a model; ΔQAIC$_c$ = difference in QAIC$_c$ between a model and the top-ranked model; ω = Akaike weight for a model.

model	**k**	**QAIC$_c$**	**ΔQAIC$_c$**	**ω**
Φ(~1)*p*(~1)*pent*(~sex)$\hat{N}$(~1)	5	681.37	0.00	0.02
Φ(~1)*p*(~1)*pent*(~hab * sex)$\hat{N}$(~1)	7	681.63	0.26	0.02
Φ(~hab)*p*(~1)*pent*(~sex)$\hat{N}$(~1)	6	681.76	0.39	0.02
Φ(~season)*p*(~1)*pent*(~sex)$\hat{N}$(~1)	6	681.82	0.45	0.02
Φ(~1)*p*(~hab)*pent*(~sex)$\hat{N}$(~1)	6	681.88	0.51	0.02
Φ(~1)*p*(~hab)*pent*(~hab * sex)$\hat{N}$(~1)	8	682.03	0.66	0.02
Φ(~season)*p*(~hab)*pent*(~sex)$\hat{N}$(~1)	7	682.09	0.72	0.02
Φ(~hab)*p*(~1)*pent*(~hab * sex)$\hat{N}$(~1)	8	682.12	0.74	0.02
Φ(~hab + year)*p*(~1)*pent*(~sex)$\hat{N}$(~1)	8	682.15	0.78	0.01
Φ(~season)*p*(~1)*pent*(~hab * sex)$\hat{N}$(~1)	8	682.16	0.79	0.01
Φ(~season)*p*(~hab)*pent*(~hab * sex)$\hat{N}$(~1)	9	682.30	0.93	0.01
Φ(~season + year)*p*(~1)*pent*(~sex)$\hat{N}$(~1)	8	682.45	1.08	0.01
Φ(~season + year)*p*(~hab)*pent*(~sex)$\hat{N}$(~1)	9	682.71	1.34	0.01
Φ(~hab + year)*p*(~1)*pent*(~hab * sex)$\hat{N}$(~1)	10	682.83	1.46	0.01
Φ(~year)*p*(~1)*pent*(~sex)$\hat{N}$(~1)	7	682.85	1.48	0.01
Φ(~season + year)*p*(~1)*pent*(~hab * sex)$\hat{N}$(~1)	10	683.07	1.69	0.01
Φ(~hab + season)*p*(~1)*pent*(~sex)$\hat{N}$(~1)	7	683.09	1.72	0.01
Φ(~hab + year)*p*(~weather)*pent*(~sex)$\hat{N}$(~1)	9	683.12	1.74	0.01
Φ(~1)*p*(~1)*pent*(~1)$\hat{N}$(~1)	4	683.12	1.75	0.01
Φ(~1)*p*(~1)*pent*(~hab + sex)$\hat{N}$(~1)	6	683.13	1.76	0.01
Φ(~1)*p*(~weather)*pent*(~sex)$\hat{N}$(~1)	6	683.15	1.78	0.01
Φ(~hab + year)*p*(~1)*pent*(~1)$\hat{N}$(~1)	7	683.17	1.80	0.01
Φ(~season + year)*p*(~hab)*pent*(~hab * sex)$\hat{N}$(~1)	11	683.20	1.83	0.01
Φ(~year)*p*(~1)*pent*(~hab * sex)$\hat{N}$(~1)	9	683.34	1.97	0.01
Φ(~1)*p*(~hab)*pent*(~hab + sex)$\hat{N}$(~1)	7	683.34	1.97	0.01
Φ(~1)*p*(~effort)*pent*(~sex)$\hat{N}$(~1)	6	683.35	1.98	0.01
Φ(~hab)*p*(~1)*pent*(~1)$\hat{N}$(~1)	5	683.38	2.00	0.01
Φ(~year)*p*(~hab)*pent*(~sex)$\hat{N}$(~1)	8	683.38	2.01	0.01
Φ(~sex)*p*(~1)*pent*(~sex)$\hat{N}$(~1)	6	683.42	2.05	0.01
Φ(~season)*p*(~1)*pent*(~1)$\hat{N}$(~1)	5	683.43	2.06	0.01
Φ(~1)*p*(~weather)*pent*(~hab * sex)$\hat{N}$(~1)	8	683.46	2.08	0.01
Φ(~1)*p*(~sex)*pent*(~sex)$\hat{N}$(~1)	6	683.47	2.10	0.01

Φ(~season)_p_(~effort)_pent_(~sex)$\hat{N}$(~1)	7	683.49	2.12	0.01
Φ(~hab)_p_(~hab)_pent_(~sex)$\hat{N}$(~1)	7	683.50	2.12	0.01
Φ(~hab + season)_p_(~1)_pent_(~hab * sex)$\hat{N}$(~1)	9	683.51	2.14	0.01
Φ(~hab)_p_(~weather)_pent_(~sex)$\hat{N}$(~1)	7	683.53	2.16	0.01
Φ(~season)_p_(~hab)_pent_(~hab + sex)$\hat{N}$(~1)	8	683.54	2.16	0.01
Φ(~season + year)_p_(~1)_pent_(~1)$\hat{N}$(~1)	7	683.60	2.22	0.01
Φ(~season)_p_(~1)_pent_(~hab + sex)$\hat{N}$(~1)	7	683.62	2.25	0.01
Φ(~hab)_p_(~1)_pent_(~hab + sex)$\hat{N}$(~1)	7	683.63	2.25	0.01
Φ(~1)_p_(~hab)_pent_(~1)$\hat{N}$(~1)	5	683.64	2.27	0.01
Φ(~1)_p_(~effort)_pent_(~hab * sex)$\hat{N}$(~1)	8	683.65	2.28	0.01
Φ(~season)_p_(~hab + effort)_pent_(~sex)$\hat{N}$(~1)	8	683.69	2.32	0.01
Φ(~sex)_p_(~1)_pent_(~hab * sex)$\hat{N}$(~1)	8	683.70	2.32	0.01
Φ(~1)_p_(~hab + weather)_pent_(~sex)$\hat{N}$(~1)	7	683.71	2.34	0.01
Φ(~season)_p_(~hab)_pent_(~1)$\hat{N}$(~1)	6	683.71	2.34	0.01
Φ(~hab)_p_(~effort)_pent_(~sex)$\hat{N}$(~1)	7	683.75	2.38	0.01
Φ(~year)_p_(~hab)_pent_(~hab * sex)$\hat{N}$(~1)	10	683.76	2.39	0.01
Φ(~1)_p_(~sex)_pent_(~hab * sex)$\hat{N}$(~1)	8	683.76	2.39	0.01
Φ(~hab + year)_p_(~effort)_pent_(~sex)$\hat{N}$(~1)	9	683.78	2.40	0.01
Φ(~hab)_p_(~hab)_pent_(~hab * sex)$\hat{N}$(~1)	9	683.81	2.44	0.01
Φ(~sex + season)_p_(~1)_pent_(~sex)$\hat{N}$(~1)	7	683.85	2.47	0.01
Φ(~1)_p_(~hab + effort)_pent_(~sex)$\hat{N}$(~1)	7	683.85	2.48	0.01
Φ(~hab + sex)_p_(~1)_pent_(~sex)$\hat{N}$(~1)	7	683.85	2.48	0.01
Φ(~season + year)_p_(~hab)_pent_(~1)$\hat{N}$(~1)	8	683.86	2.49	0.01
Φ(~hab)_p_(~sex)_pent_(~sex)$\hat{N}$(~1)	7	683.87	2.50	0.01
Φ(~hab + year)_p_(~weather)_pent_(~hab * sex)$\hat{N}$(~1)	11	683.90	2.53	0.01
Φ(~1)_p_(~hab + weather)_pent_(~hab * sex)$\hat{N}$(~1)	9	683.91	2.53	0.01
Φ(~season)_p_(~effort)_pent_(~hab * sex)$\hat{N}$(~1)	9	683.91	2.53	0.01
Φ(~season)_p_(~weather)_pent_(~sex)$\hat{N}$(~1)	7	683.93	2.55	0.01
Φ(~season)_p_(~sex)_pent_(~sex)$\hat{N}$(~1)	7	683.93	2.56	0.01
Φ(~hab)_p_(~weather)_pent_(~hab * sex)$\hat{N}$(~1)	9	683.93	2.56	0.01
Φ(~sex)_p_(~hab)_pent_(~sex)$\hat{N}$(~1)	7	683.95	2.57	0.01
Φ(~season)_p_(~hab + effort)_pent_(~hab * sex)$\hat{N}$(~1)	10	683.98	2.61	0.01
Φ(~1)_p_(~sex + hab)_pent_(~sex)$\hat{N}$(~1)	7	684.00	2.62	0.01
Φ(~hab + year)_p_(~weather)_pent_(~1)$\hat{N}$(~1)	8	684.02	2.65	0.01
Φ(~1)_p_(~hab + effort)_pent_(~hab * sex)$\hat{N}$(~1)	9	684.05	2.67	0.01
Φ(~year)_p_(~weather)_pent_(~sex)$\hat{N}$(~1)	8	684.05	2.67	0.01
Φ(~year)_p_(~1)_pent_(~1)$\hat{N}$(~1)	6	684.12	2.75	0.01
Φ(~sex + season)_p_(~hab)_pent_(~sex)$\hat{N}$(~1)	8	684.13	2.76	0.01
Φ(~sex)_p_(~hab)_pent_(~hab * sex)$\hat{N}$(~1)	9	684.14	2.77	0.01
Φ(~hab)_p_(~effort)_pent_(~hab * sex)$\hat{N}$(~1)	9	684.15	2.78	0.01
Φ(~hab + year)_p_(~1)_pent_(~hab + sex)$\hat{N}$(~1)	9	684.17	2.79	0.01
Φ(~1)_p_(~sex + hab)_pent_(~hab * sex)$\hat{N}$(~1)	9	684.18	2.81	0.01
Φ(~hab + season)_p_(~hab)_pent_(~sex)$\hat{N}$(~1)	8	684.19	2.82	0.01

Φ(~season)*p*(~hab + weather)*pent*(~sex)$\hat{N}$(~1)	8	684.19	2.82	0.01
Φ(~hab + year)*p*(~hab)*pent*(~sex)$\hat{N}$(~1)	9	684.19	2.82	0.01
Φ(~sex + season)*p*(~1)*pent*(~hab * sex)$\hat{N}$(~1)	9	684.21	2.83	0.01
Φ(~season)*p*(~sex + hab)*pent*(~sex)$\hat{N}$(~1)	8	684.22	2.85	0.01
Φ(~hab + sex)*p*(~1)*pent*(~hab * sex)$\hat{N}$(~1)	9	684.24	2.87	0.01
Φ(~season + year)*p*(~hab)*pent*(~hab + sex)$\hat{N}$(~1)	10	684.26	2.88	0.01
Φ(~hab)*p*(~sex)*pent*(~hab * sex)$\hat{N}$(~1)	9	684.27	2.90	0.01
Φ(~hab + year)*p*(~sex)*pent*(~sex)$\hat{N}$(~1)	9	684.28	2.91	0.01
Φ(~hab + sex + year)*p*(~1)*pent*(~sex)$\hat{N}$(~1)	9	684.30	2.93	0.01
Φ(~season)*p*(~weather)*pent*(~hab * sex)$\hat{N}$(~1)	9	684.30	2.93	0.01
Φ(~season)*p*(~sex)*pent*(~hab * sex)$\hat{N}$(~1)	9	684.31	2.93	0.01

Table 1-S10. Closed population mark-recapture model table for ornate tree lizards (*Urosaurus ornatus*) at site 7 in the Chiricahua Mountains of Arizona, USA. The full model was: *p*(~hab)*c*()*f0*(~hab). k = number of parameters in a model; AIC_c = Akaike's information criterion for a model; ΔAIC_c = difference in AIC_c between a model and the top-ranked model; ω = Akaike weight for a model.

model	**k**	**AIC_c**	**ΔAIC_c**	**ω**	**Deviance**
p(~1)*c*()*f0*(~1)	2	-5.27	0.00	0.54	38.15
p(~1)*c*()*f0*(~hab)	3	-3.20	2.07	0.19	38.03
p(~hab)*c*()*f0*(~1)	3	-3.07	2.20	0.18	38.15
p(~hab)*c*()*f0*(~hab)	4	-1.51	3.76	0.08	37.45

Table 1-S11. Closed population mark-recapture model table for ornate tree lizards (*Urosaurus ornatus*) at site 8 in the Chiricahua Mountains of Arizona, USA. k = number of parameters in a model; AIC_c = Akaike's information criterion for a model; ΔAIC_c = difference in AIC_c between a model and the top-ranked model; ω = Akaike weight for a model.

model	**k**	**AIC_c**	**ΔAIC_c**	**ω**	**Deviance**
p(~1)*c*()*f0*(~1)	2	20.40	0.00	0.57	14.57
p(~1)*c*()*f0*(~hab)	3	22.59	2.19	0.19	14.32
p(~hab)*c*()*f0*(~1)	3	22.72	2.32	0.18	14.45
p(~hab)*c*()*f0*(~hab)	4	25.18	4.78	0.05	14.29

Table 1-S12. Closed population mark-recapture model table for ornate tree lizards (*Urosaurus ornatus*) at site 9 in the Chiricahua Mountains of Arizona, USA. k = number of parameters in a model; AIC_c = Akaike's information criterion for a model; ΔAIC_c = difference in AIC_c between a model and the top-ranked model; ω = Akaike weight for a model.

model	**k**	**AIC_c**	**ΔAIC_c**	**ω**	**Deviance**
p(~1)*c*()*f0*(~1)	2	-20.72	0.00	0.53	19.80
p(~1)*c*()*f0*(~hab)	3	-18.83	1.89	0.21	19.53
p(~hab)*c*()*f0*(~1)	3	-18.74	1.98	0.20	19.62
p(~hab)*c*()*f0*(~hab)	4	-16.61	4.11	0.07	19.53

Table 1-S13. Closed population mark-recapture model table for ornate tree lizards (*Urosaurus ornatus*) at site 10 in the Chiricahua Mountains of Arizona, USA. k = number of parameters in a model; AIC_c = Akaike's information criterion for a model; ΔAIC_c = difference in AIC_c between a model and the top-ranked model; ω = Akaike weight for a model.

model	**k**	**AIC_c**	**ΔAIC_c**	**ω**	**Deviance**
p(~1)*c*()*f0*(~1)	2	-18.52	0.00	0.45	24.18
p(~1)*c*()*f0*(~hab)	3	-17.34	1.18	0.25	23.20
p(~hab)*c*()*f0*(~1)	3	-17.07	1.45	0.22	23.46
p(~hab)*c*()*f0*(~hab)	4	-15.11	3.41	0.08	23.19

Table 1-S14. Estimated densities by habitat of ornate tree lizards (*Urosaurus ornatus*) from 10 sites in the Chiricahua Mountains of Arizona, USA. Densities from sites 1-6 are based on Jolly-Seber open population mark-recaptures and densities from sites 7-10 are based on closed population mark-recapture models in 2016.

Site	Year	Habitat	Density (lizards/ha)
1	2014	Upland	74
1	2014	Wash	101
1	2015	Upland	70
1	2015	Wash	90
1	2016	Upland	67
1	2016	Wash	86
2	2014	Upland	110
2	2014	Wash	194
2	2015	Upland	116
2	2015	Wash	206
2	2016	Upland	112
2	2016	Wash	199
3	2014	Upland	46
3	2014	Wash	60
3	2015	Upland	35
3	2015	Wash	45
3	2016	Upland	29
3	2016	Wash	37
4	2014	Upland	67
4	2014	Wash	129
4	2015	Upland	72
4	2015	Wash	135
4	2016	Upland	71
4	2016	Wash	132
5	2014	Upland	12
5	2014	Wash	31
5	2015	Upland	13
5	2015	Wash	37
5	2016	Upland	14
5	2016	Wash	39
6	2014	Upland	45
6	2014	Wash	58
6	2015	Upland	50
6	2015	Wash	57

6	2016	Upland	48
6	2016	Wash	53
7	2016	Upland	99
7	2016	Wash	114
8	2016	Upland	26
8	2016	Wash	36
9	2016	Upland	116
9	2016	Wash	113
10	2016	Upland	75
10	2016	Wash	171

Chapter 2

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

Abstract

Habitat selection models can explain spatial patterns in the relative abundance of animals in different habitat patches, but assume that fitness declines as density in a habitat increases. Because habitat selection in ectotherms, such as lizards, is strongly influenced by temperature and because temperature is unaffected by density, ectotherms may not follow predictions of density-dependent habitat selection models. If competition for limited resources decreases fitness, then crowding should reduce the amount of resources per individual and cause a decrease in body size and growth rates. I 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. Using von Bertalanffy growth curves, I tested two predictions. First, I tested that the maximum body size of lizards decreased with higher densities in a habitat by comparing growth curves between sites. Second, I tested whether body size and growth were greater in the habitat with more resources by controlling for density in a habitat and comparing growth between habitats in different sites. I found strong evidence of density-dependent growth in females, but not in males. Females in more crowded sites had a smaller maximum body size. Female tree lizards in the higher quality habitat also grew larger than females in the lower quality habitat when controlling for density in the habitats. There was no evidence that male growth and body size differed between the two habitats. Therefore, I found partial support for my hypothesis that competition for resources limits growth and causes density-dependent habitat selection.

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 et al. 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; this pattern is the Ideal Free Distribution (Fretwell and 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 and Lucas 1969). Despite its unrealistic assumptions (Kennedy and Gray 1993), the Ideal Free Distribution and its extensions have been useful for predicting the spatial distribution of organisms between habitats (Milinski 1979, Walhström and Kjellander 1995, Haché and Bayne 2013). Another central assumption of habitat selection models, however, is that populations experience density-dependence (Skogland 1985, Clutton-Brock et al. 1987, Morris 1989). Density-dependence is the negative effect of crowding on individual fitness because of reduced resources and increased intraspecific competition (Hassell 1975). Population growth in a wide variety of species is limited by density-dependence (Brook and Bradshaw 2006), but density-dependence may not be present if species are limited by resources that are unaffected by crowding (Halliday and Blouin-Demers 2016).

Temperature is often the most important aspect of patch quality affecting ectotherm habitat selection (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) because it modulates body temperature and body temperature dictates performance (Huey 1991) and ultimately fitness (Huey and Berrigan 2001). Temperature, however, is unaffected by population density. Therefore, ectotherm fitness and habitat selection may not be strongly linked to differences in population density and ectotherms may thus be more limited by their ability to process resources 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 et al. 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 (Knight et al. 2008, Falcy 2015), lizards (Calsbeek and Sinervo 2002), and insects (Kiflawi et al. 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 and 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 (Martin 1977, Landwer 1994, Meiri et al. 2012). In males, body size is also generally positively related to fitness because it affects locomotor performance for escaping predators (Johnson et al. 1993) and fighting ability with conspecifics (Carpenter 1995a, Arnott and Elwood 2009). Growth rate is also correlated with fitness because it allows individuals to reproduce earlier in life, escape size-selective predators, and better survive stochastic environmental stressors (Werner and Gilliam 1984, Benrey and Denno 1997). In fish populations, growth is frequently density-dependent and linked to reproductive output or survival (Lorenzen and Enberg 2002). Also, field experiments with fish (Jenkins et al. 1999) and lizards (Massot et al. 1992, Mugabo et al. 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 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 and 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 2-1A). 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 2-1B).

Growth rates decline as lizards get larger (El Mouden et al. 1999, Rotger et al. 2016). Thus, it is necessary to use non-linear 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 (James 1991, El Mouden et al. 1999, Rotger et al. 2016).

I 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. In chapter one, I found a negative relationship between ornate tree lizard survival and population density in two habitats, but I found no relationship between absolute growth rate and population density using mark-recapture data. However, it is possible that I did not detect a decline in growth rate with population density because I could only age a small portion of lizards using mark-recapture data. Furthermore, population density effects on body size and growth often manifest themselves as differences in asymptotic body size, rather than absolute growth rates (Lorenzen 1996, Beverton and Holt 2012). 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, I tested the prediction that the asymptotic body size is inversely related to density per habitat by comparing growth curves in different sites. Second, I tested the prediction that the VBG curve reaches a higher asymptote sooner in the habitat with more food and higher thermal quality by comparing body size and age between habitats and controlling for density per habitat. In the two-habitat system I 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 2-1B). I tested these predictions with natural variation in density per habitat and body size in ornate tree lizards. To measure growth, I aged lizards using skeletochronology.

Methods

Study site and species

I studied ornate tree lizards at six sites in the Chiricahua Mountains of Arizona, USA. 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 (Chapter 1). Ornate tree lizards preferred the wash habitat and occurred at higher densities in that habitat (Chapter 1).

I surveyed each site for lizards 12 times between 1 May 2014 and 5 August 2016. During a survey, I caught lizards (1000 individuals captured a total of 1542 times) with a noose and pole while walking through sites and marked the capture location with a handheld GPS unit (± 3 m). I gave each lizard a unique mark with a medical cauterizer (Winne et al. 2006, Ekner et al. 2011). On a subset (n = 417) of captured lizards, I clipped the fourth toe on the right hind limb after disinfecting the foot with Chlorhexadine. I stored clipped toes in 95% ethanol. I measured the lizards' snout-vent length (SVL; ± 0.1 mm) with digital calipers and released lizards at their site of capture within four hours. Toe-clipping, especially on a single toe, is unlikely to affect survival rates negatively compared to 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).

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 non-growth, such as winter, and can be stained with haemotoxylin (Acker et al. 1986; Figure 2-2). I decalcified the second and third phalange using Cal-Ex Decalcifier (Fisher Scientific), and then rinsed toes in deionized water. I sectioned the diaphysis (middle of the bone) of the phalanges at -20 °C with a Leica 1850 cryostat. I stained cross sections in Harris' Haematoxylin (Fisher Scientific), which stains nuclear material purple. I photographed at least five representative sections for each lizard at 100x 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.

I calculated the age of lizards in months when growth was possible because tree lizards do not grow during the winter (Dunham 1982). I used temperature loggers and weather station data to estimate that lizards could grow from 12 April to 18 October (Supplementary information). When calculating age, I assumed all individuals hatched on 1 September (Dunham 1982).

Validation of skeletochronology

There can be considerable variation in bone growth patterns between individuals of the same age (Cope and Punt 2007). To test whether LAGs were deposited annually and whether they accurately represented a lizard's age, I 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, I 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). I then used known-age lizards that had their toes sampled to compare age estimates between mark-recapture data and skeletochronology. Since I sampled lizards from 2014 to 2016, the oldest lizards in my validation sample hatched in 2013 and had their toes sampled in 2016 (a maximum of 3 winters). I used a paired t-test to compare age estimates from the two methods.

Population density & habitat quality

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

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

The parameter *g* is the density-dependent parameter and *d* is the mean density per habitat (lizards/ha). I 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 (Chapter 1). I 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 and lizards experienced different densities through time, I 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, I constructed VBG models with and without separate L_∞, g, K, and t_0 parameters for the two habitats. Although I predicted growth rates should be higher in the wash habitat because it has more prey items and higher thermal quality, I 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 et al. 2002). Therefore, I constructed all possible model subsets (15) and compared their fit in an information-theoretic framework (Burnham and Anderson 2002) using bias-corrected Akaike's information criterion (AIC_c) calculated with the package *AICcmodavg* (Mazerolle 2017). I constructed separate models for males and females because growth rates and maximum body size differ between the sexes in this species (Tinkle and Dunham 1983). I 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. I compared the fit of the top-ranking model to the common parameter model (no habitat differences) with likelihood ratio tests. I used bootstrapped coefficient estimates from the top-ranking model of each sex to derive 95% confidence intervals on predictions of SVL to compare growth in the wash and upland habitat.

I assigned individuals to a habitat using their mean GPS coordinates for captures. The mean distance between captures for females and males was 8 m and 11 m, respectively. Thus, I assigned individuals to the wash habitat if the mean coordinates were within 8 m of the wash for females and 11 m of the wash for males. 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 home ranges that overlap with the wash habitat have access to the thermal and food resources in the wash. This assumption is reasonable because the probability of lizards switching between habitats is much higher when a lizard's home range is close to the habitat boundary (Chapter 1). When calculating density, I included the buffered area in the wash and not the upland.

Results

Validation of skeletochronology

In 92% of samples, two 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 = 0.9423, df = 112, P = 0.35). The mean difference in age between the two methods was 0.22 months (95% CI: -0.69 – 0.25). Out of the 113 known age individuals, 95 (84%) were correctly aged using skeletochronology.

Population density & habitat quality

The growth curve for females with the lowest AIC_c (Table 2-1) had common L_∞ (5.09, 95% CI: 5.02 – 5.19) and t_0 (0.98, 95% CI: -1.20 – 1.79) and separate estimates for g and K for lizards in the upland (g = 0.0026, 95% CI: 0.0013 – 0.0039, K = 1.64, 95% CI: 0.75 – 3.45) and the wash (g = 0.00062, 95% CI: -0.000096 – 0.0013, K = 1.19, 95% CI: 0.55 – 2.41) habitats. The estimates of g were positive in both habitats and maximum body size declined with density per habitat (Figure 2-3A). The top-ranking model fit the data better than the model without differences in growth between habitats (ΔAIC_c = 11.60; F = 8.01, df = 2, 192, P = 0.0005). Using bootstrapped estimates of the growth curve coefficients in the top-ranked model to generate 95% confidence intervals of predicted body size, female lizards reached larger maximum sizes in the wash habitat at the mean density per habitat (76 lizards/ha) after lizards reached their second breeding season (Figure 2-4A).

The growth curve for males with the lowest AIC_c (Table 2-2) had a common L_∞ (5.12, 95% CI: 5.04 – 5.33) and g (-0.00051, 95% CI: -0.0011 – 0.00012), and separate estimates of K and t_0 for lizards in the upland (K = 0.42, 95% CI: 0.13 – 0.98, t_0 = -3.00, 95% CI: -15.58 – 0.46) and wash ($K = 0.17$, 95% CI: 0.054 – 0.66, $t_0 = -13.13$, 95% CI: -42.57 – -1.24) habitats. The top-ranking model did not fit the data better than the model without any differences in growth between habitats ($\Delta AIC_c = 0.06$; F = 2.12, df = 2, 215, $P = 0.12$). Using bootstrapped estimates of the growth curve coefficients in the top-ranked model to generate 95% confidence intervals 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% confidence intervals of predicted SVL in the wash and upland overlapped for the whole range of ages that I sampled (Figure 2-4B).

Discussion

My 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. Density-dependent growth is common in other ectotherms, such as fish (Post et al. 1999, Lorenzen and Enberg 2002, Imre et al. 2005) and some lizards (Massot et al. 1992, Mugabo et al. 2013). However, density-dependence has not previously been linked to habitat selection in wild lizard populations. I found a negative effect of population density on maximum body size in females, but was the effect biologically relevant? The predicted change in asymptotic SVL from the minimum to maximum observed densities per habitat (0.27 cm) represents 15% of the total variation in female SVL (3.93 cm to 5.65 cm). In tree lizards, clutch size is directly related to female body size (Landwer 1994). An increase in body size of 0.27 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 confidence interval overlapped zero. The differences between 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 (Stearns 1989, Roff 2000). 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 1995a). Therefore, the relationship between body size and fitness is different in males and females due to the timing of reproductive demands. Alternatively, I 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 I did not sample populations in the fall after hatchlings emerged. Finally, there may simply be no 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 my hypothesis that habitat selection is density-dependent due to growth being limited by intraspecific competition for resources and habitat quality. I 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 et al. 2007), fishes (Sogard 1992, Phelan et al. 2000), lizards (Dunham 1978), and turtles (Brown et al. 1994). The growth curve with the lowest AIC_c for females included separate estimates of *g* and *K* 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 more support than the model without 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 my 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, I could have failed to detect a difference in growth between habitats in males because I did not have enough observations or because I lacked body size data during the initial two months of life after hatching when growth rates are the highest (Tinkle and Dunham 1983). My 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 to 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.

My data 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. 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 I 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 my 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.

I observed large variation in body size and growth between individuals of ornate tree lizards. I 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. I 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.

Table 2-1. The model results for von Bertalanffy growth curves of female ornate tree lizard (*Urosaurus ornatus*) snout-vent length comparing growth in the upland (n = 89) and wash (n = 109) habitats from six sites in the Chiricahua Mountains of Arizona, USA. AIC_c = Akaike's information criterion for a model; ΔAIC_c = difference in AIC_c between a model and the top-ranked model; k = number of parameters in a model; ω = Akaike weight for a model.

Model	**AIC_c**	**ΔAIC_c**	**k**	**ω**
L_∞(~1)g(~hab)K(~hab)t_0(~1)	26.47		6	0.29
L_∞(~1)g(~hab)K(~hab)t_0(~hab)	26.69	0.22	7	0.26
L_∞(~1)g(~hab)K(~1)t_0(~hab)	27.55	1.08	6	0.17
L_∞(~hab)g(~hab)K(~hab)$t0$(~1)	28.62	2.15	7	0.10
L_∞(~hab)g(~hab)K(~hab)t_0(~hab)	28.85	2.38	8	0.09
L_∞(~hab)g(~1)K(~hab)t_0(~hab)	30.69	4.22	7	0.03
L_∞(~hab)g(~1)K(~hab)t_0(~1)	30.79	4.32	6	0.03
L_∞(~hab)g(~1)K(~1)t_0(~hab)	31.89	5.42	6	0.02
L_∞(~1)g(~hab)K(~1)t_0(~1)	34.48	8.01	5	0.01
L_∞(~hab)g(~hab)K(~1)t_0(~1)	35.19	8.72	6	0.00
L_∞(~1)g(~1)K(~1)t_0(~hab)	37.12	10.65	5	0.00
L_∞(~1)g(~1)K(hab)t_0(~1)	37.30	10.84	5	0.00
L_∞(~hab)g(~1)K(~1)t_0(~1)	37.77	11.30	5	0.00
L_∞(~1)g(~1)K(~hab)t_0(~hab)	38.02	11.56	6	0.00
L_∞(~1)g(~1)K(~1)t_0(~1)	38.06	11.60	4	0.00

L_∞ is the mean maximum body size before density dependent effects, g is the effect of density on maximum body size, K is the rate at which lizards approach the asymptotic body size, t_0 is the age when average length is zero

~hab denotes different estimates for the wash and upland habitat

~1 denotes one estimate for all female lizards

Table 2-2. The model results for von Bertalanffy growth curves of male ornate tree lizard (*Urosaurus ornatus*) snout-vent length comparing growth in the upland (n = 92) and wash (n = 127) habitats from six sites in the Chiricahua Mountains of Arizona, USA. AIC_c = Akaike's information criterion for a model; ΔAIC_c = difference in AIC_c between a model and the top-ranked model; k = number of parameters in a model; ω = Akaike weight for a model.

Model	**AICc**	**ΔAICc**	**k**	**ω**
L_∞(~1)g(~1)K(~hab)t_0(~hab)	3.45		6	0.12
L_∞(~1)g(~1)K(~1)t_0(~1)	3.51	0.06	4	0.11
L_∞(~hab)g(~1)K(~1)t_0(~hab)	3.59	0.15	6	0.11
L_∞(~1)g(~hab)K(~1)t_0(~hab)	3.73	0.28	6	0.10
L_∞(~hab)g(~1)K(~hab)t_0(~1)	3.88	0.43	6	0.09
L_∞(~1)g(~hab)K(~hab)t_0(~1)	4.13	0.69	6	0.08
L_∞(~1)g(~hab)K(~1)t_0(~1)	4.56	1.11	5	0.07
L_∞(~hab)g(~1)K(~1)t_0(~1)	4.90	1.46	5	0.06
L_∞(~1)g(~hab)K(~hab)t_0(~hab)	5.09	1.64	7	0.05
L_∞(~1)g(~1)K(~1)t_0(~hab)	5.27	1.83	5	0.05
L_∞(~hab)g(~1)K(~hab)t_0(~hab)	5.44	1.99	7	0.04
L_∞(~hab)g(~hab)K(~hab)t_0(~1)	5.48	2.04	7	0.04
L_∞(~1)g(~1)K(hab)t_0(~1)	5.50	2.05	5	0.04
L_∞(~hab)g(~hab)K(~1)t_0(~1)	6.69	3.24	6	0.02
L_∞(~hab)g(~hab)K(~hab)t_0(~hab)	7.21	3.77	8	0.02

L_∞ is the mean maximum body size before density dependent effects, g is the effect of density on maximum body size, K is the rate at which lizards approach the asymptotic body size, t_0 is the age when average length is zero

~hab denotes different estimates for the wash and upland habitat

~1 denotes one estimate for all male lizards

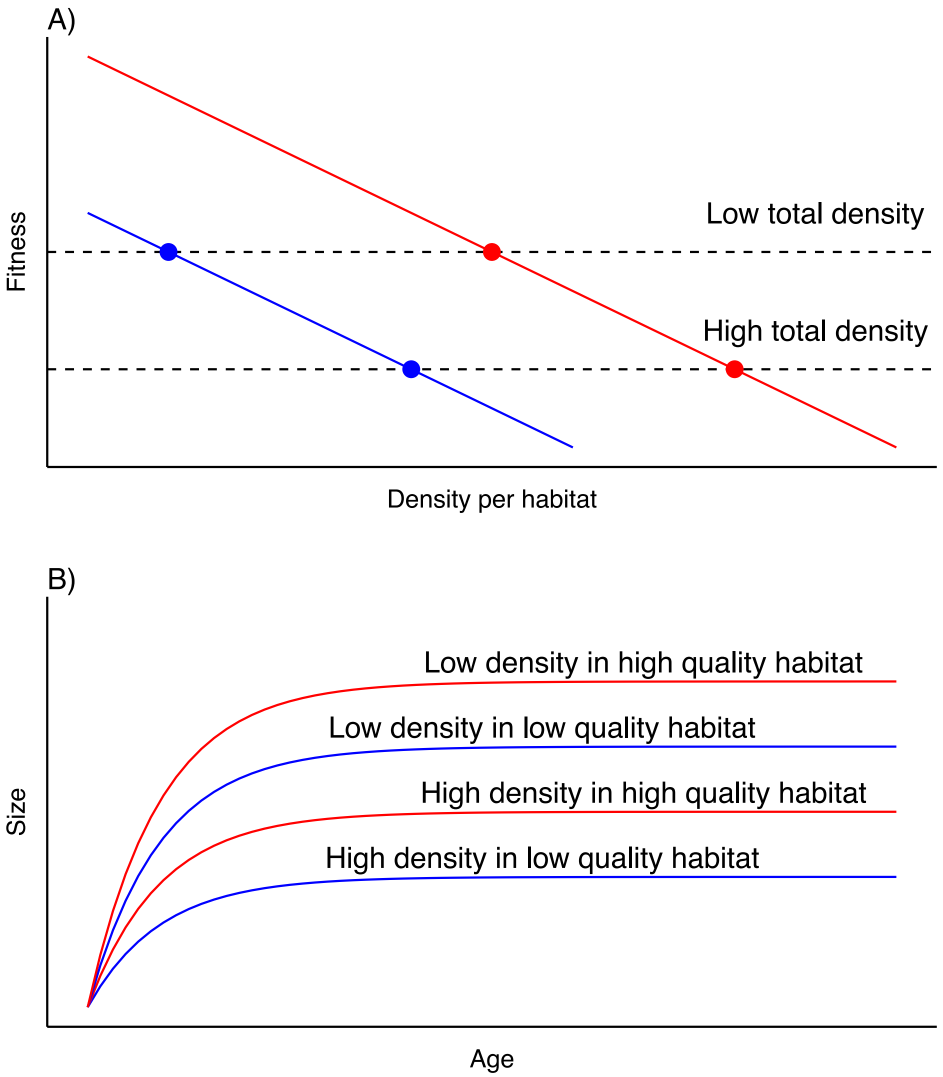

Figure 2-1. A) The predicted decline in fitness as density in a habitat increases for a low quality (blue) and high quality (red) habitat. The horizontal dashed lines represent two total population densities where individuals are in an Ideal Free Distribution with equal fitness in both habitats. Note 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.

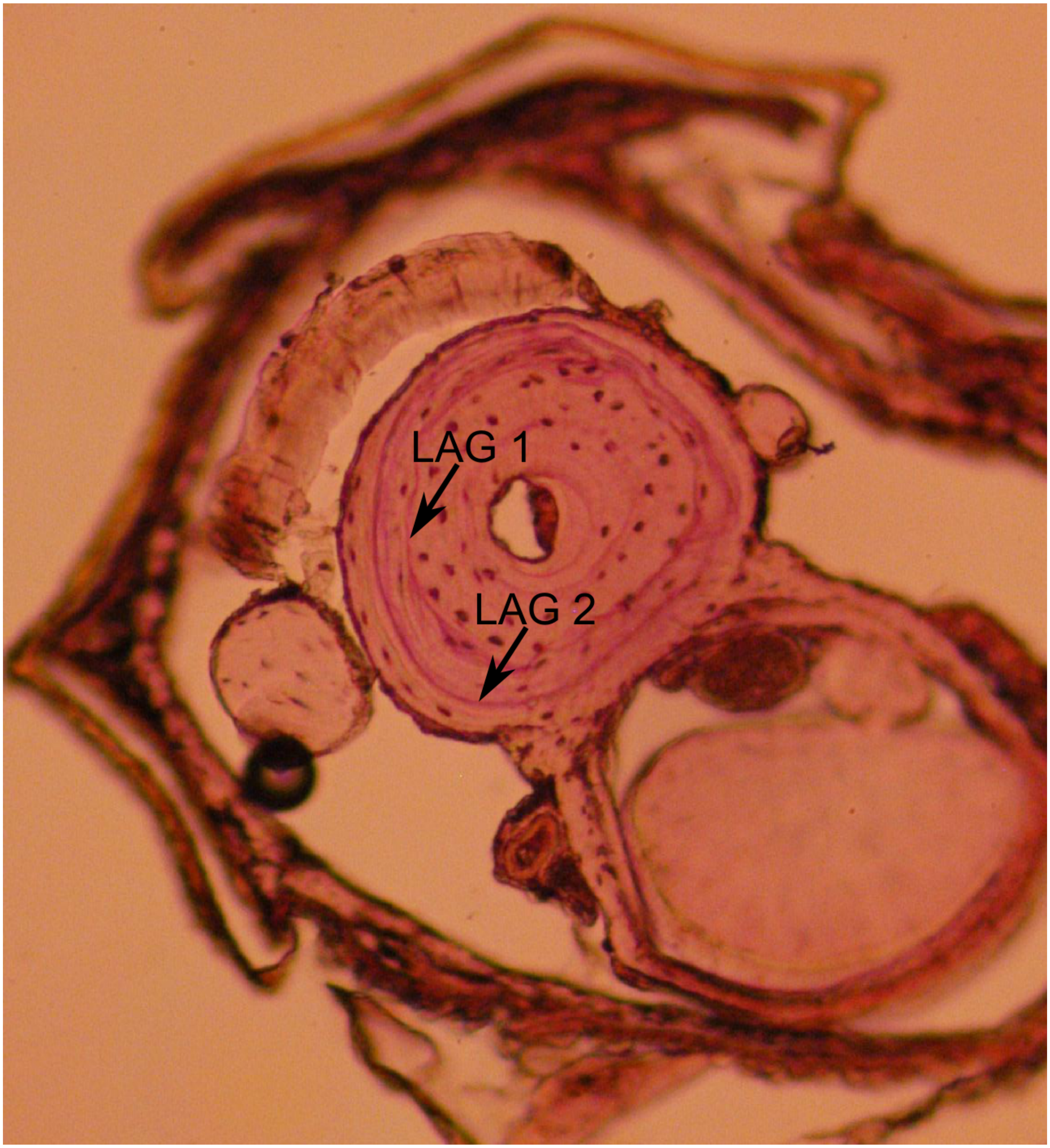

Figure 2-2. A cross section of an ornate tree lizard's (*Urosaurus ornatus*) third phalange showing two lines of arrested growth (LAGs; arrows).

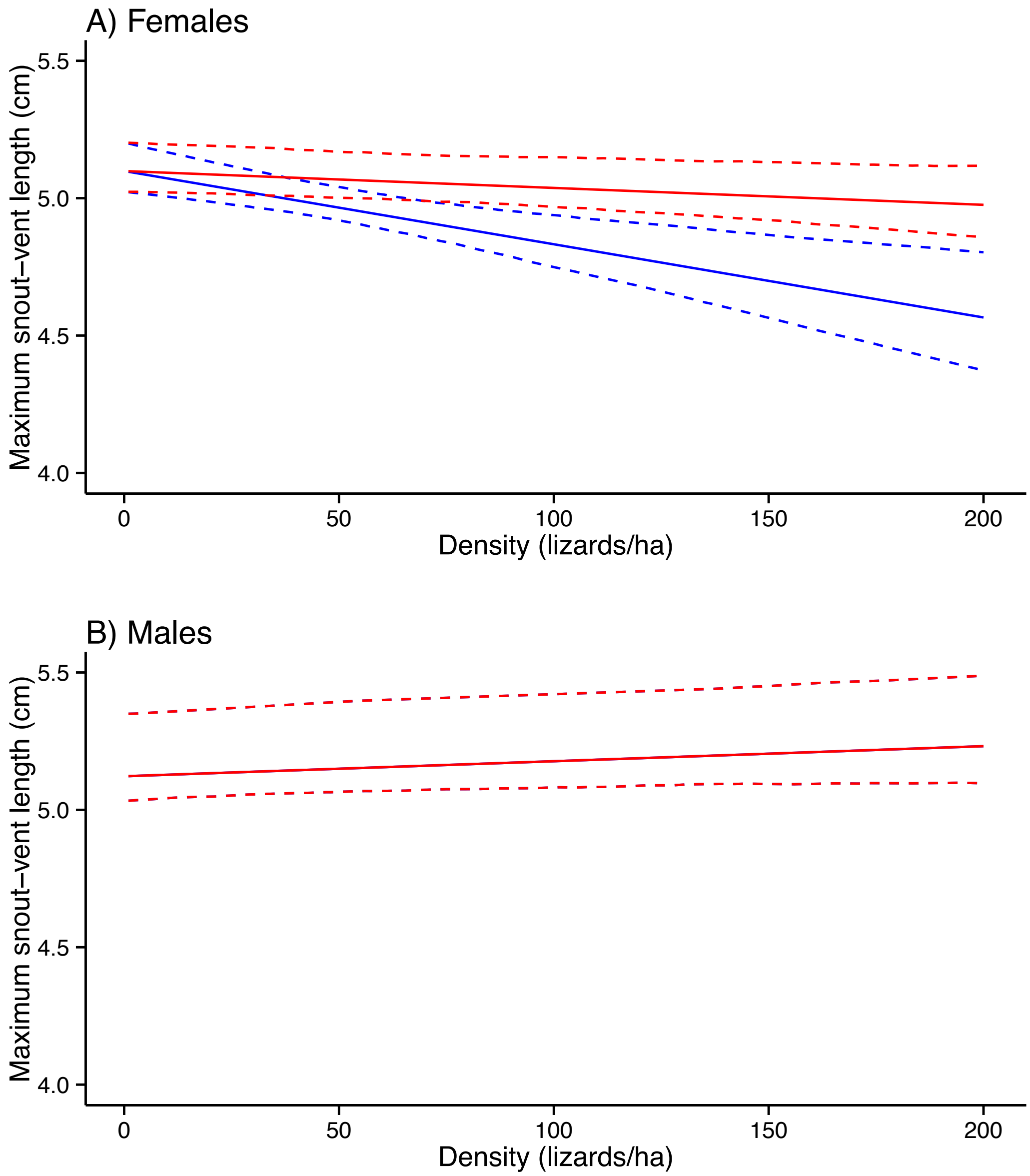

Figure 2-3. The relationship between density per habitat and maximum snout-vent length (L_∞ – (g x d) for ornate tree lizards (*Urosaurus ornatus*) using the top-ranked von Bertalanffy growth curve with a density-dependent term for A) females and B) males in the upland (low quality, blue) and wash (high quality, red) habitats. The top-ranked model for males completely overlaps in both habitats. Dashed lines represent 95% confidence intervals of predicted maximum lengths using bootstrapping.

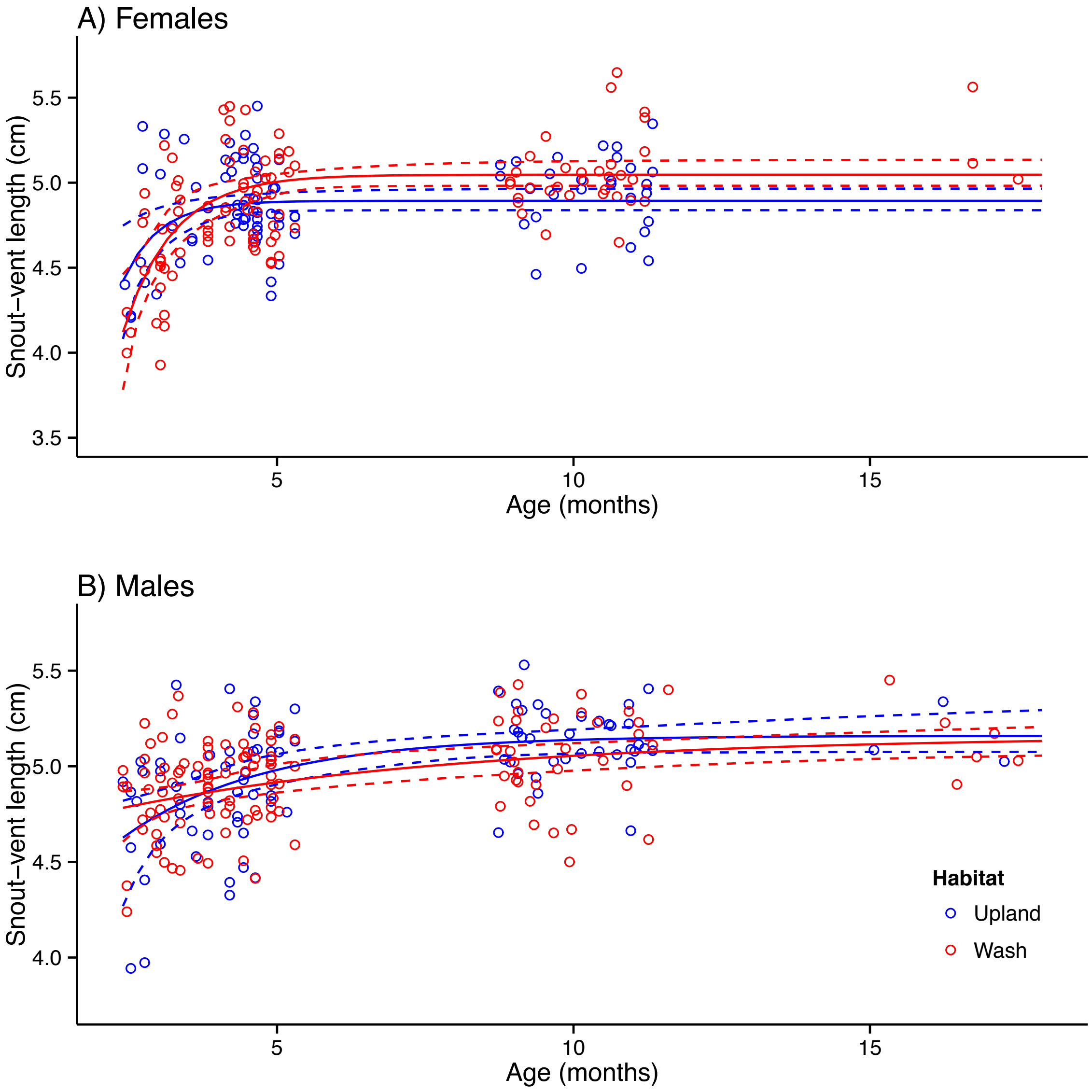

Figure 2-4. Von Bertalanffy growth curves using the top ranked models for habitat differences in ornate tree lizard (*Urosaurus ornatus*) snout-vent length (SVL) over time in the upland (low quality, blue) and wash (high quality, red) at the mean density per habitat (76 lizards/ha). A) Females in the 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% confidence intervals of predicted lengths using bootstrapping.

Supplementary information for Chapter 2

Determining the length of the growing season

I calculated the age of lizards in months when growth was possible because tree lizards do not grow during the winter (Dunham 1982). To determine the limits of the growing season, I assumed that lizards could grow on days when they could reach T_{set}. I set out temperature loggers on tree trunks (at 1.5 m height) at random locations within sites. The temperature loggers measured environmental temperatures (T_e) that thermoconforming lizards would experience. Tree trunks were the most common tree lizard perch microhabitat (52% of observed perch locations, n = 529). For each Julian day, I calculated the number of hours that lizards could reach T_{set}. I used weather station data (station: USC00026716) to compare daily maximum temperatures (Menne et al. 2012) to the number of hours lizards could achieve $T_{set.}$ The linear model predicted lizards could not reach T_{set} when daily maximum temperatures were below 23.8 °C (Figure 2-S1A, $R^2 = 0.13$, F = 158.3, df = 1, 1039, $P < 0.001$). Next, I used a loess curve predicting daily maximum temperature from the day of the year to find the earliest and latest days of the year where mean daily maximum temperature was above 23.8 °C (Figure 2-S1B). Therefore, I assumed lizards could grow from 12 April to 18 October. When calculating age, I assumed all individuals hatched on 1 September (Dunham 1982).

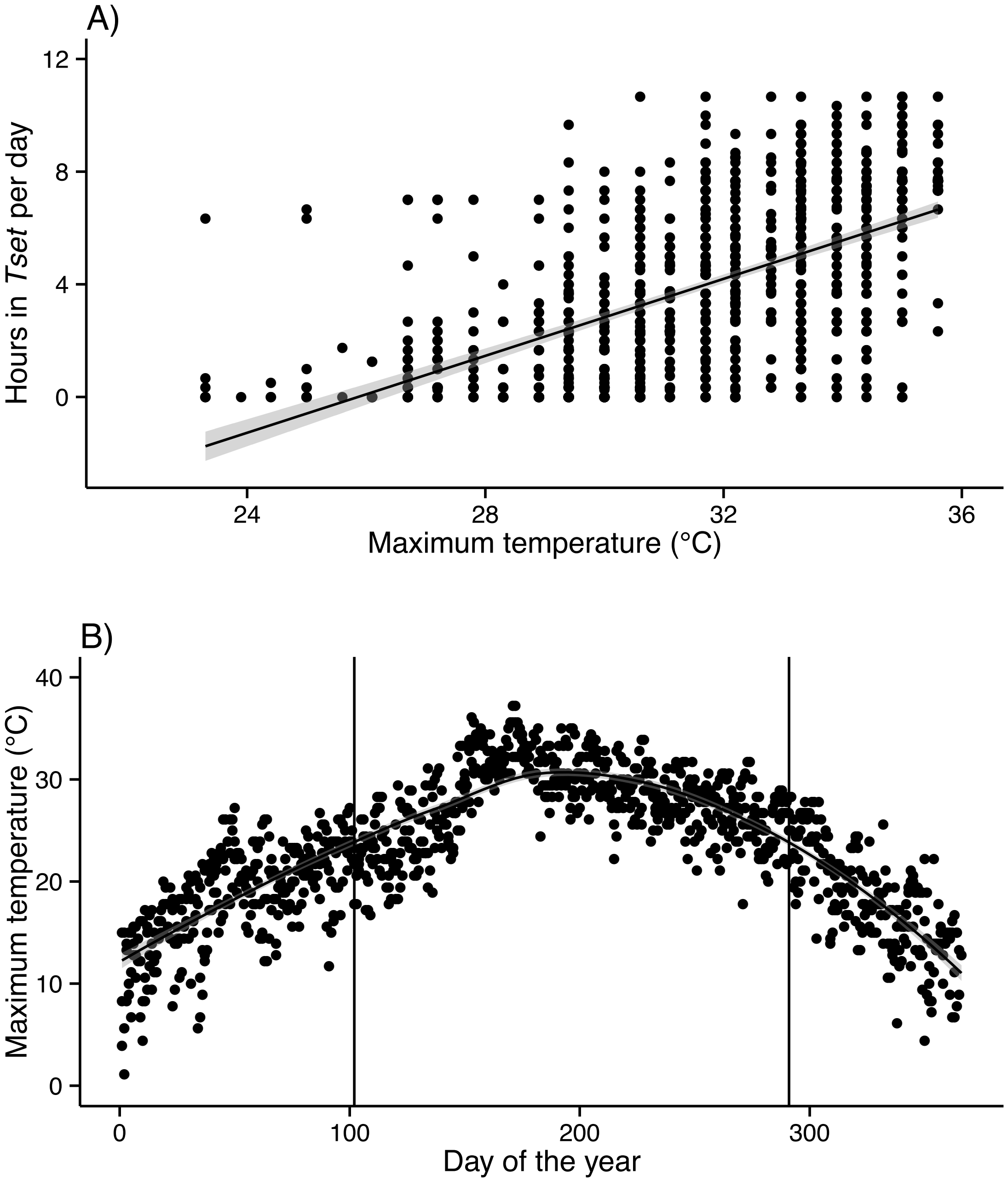

Figure 2-S1. A) The relationship between maximum daily temperature and the number of hours that ornate tree lizards (*Urosaurus ornatus*) could reach their preferred temperature range (T_{set}). B) The growing season where maximum daily temperatures allowed lizards to reach T_{set} was between 12 April and 18 October (vertical lines). The black line is a loess curve fit to the data and the grey ribbon represents the 95% confidence interval for the loess curve.

Chapter 3

Male throat colour polymorphism is linked to differences in space use and habitat selection in tree lizards, *Urosaurus ornatus*

Abstract

Habitat selection is the disproportionate use of some habitats relative to their availability, and is a behaviour organisms use to maximize fitness. Habitat selection has been a key framework for predicting the spatial distribution of organisms between habitat patches, but different habitat selection strategies can occur within a population when there are differences in behaviour or morphology between individuals. Colour polymorphism, the presence of multiple discrete colour phenotypes in a population, is often related to other behavioural and morphological traits and may therefore affect habitat selection strategy. Male ornate tree lizards (*Urosaurus ornatus*) have a throat colour polymorphism associated with differences in behaviour and reproductive strategy. Blue-throated males are dominant and defend home ranges containing several females. Orange-throated males are either nomadic or sedentary and do not defend territories. Yellow or green-throated males are reproductive parasites that sneak copulations with females. I tested whether throat colour in tree lizards affects habitat selection and space use with mark-recapture data collected from 10 sites in the Chiricahua Mountains of southern Arizona, USA. I found that males with green throats moved more than males with blue throats, and that males with orange throats were sedentary with small home ranges. Male ornate tree lizards were closer to the highest quality habitat than if their distribution was random, and green-throated males had a more marked preference for the highest quality habitat than blue-throated males, which may be linked to a reproductive parasite strategy in green-throated males. I found no difference in microhabitat use and in the accuracy of body temperatures compared to the preferred body temperature range between males of different throat colours. I demonstrated that colour polymorphism in tree lizards affects habitat selection strategy and this may help maintain the colour polymorphism.

Introduction

Habitat selection, the disproportionate use of some habitats compared to their availability (Johnson 1980), is one of the most important frameworks in ecology for predicting the distribution of organisms in space. Organisms can maximize fitness by occupying certain habitat patches (Huey 1991). The predictive ability of habitat selection was greatly improved by considering population density in the Ideal Free Distribution (IFD; Fretwell and Lucas 1969). The IFD predicts that organisms should settle in habitat patches that maximize their fitness based on patch suitability (resources) and the population density in the patch. The IFD predicts that organisms should distribute themselves so that mean fitness is equal in each habitat patch. The IFD assumes that competitors are equal, have perfect knowledge of habitat suitability, and are free to colonize any patch. Despite these unrealistic assumptions (Matsumura et al. 2010), the IFD has been very powerful for predicting animal distributions among habitats (Milinski 1979, Walhström and Kjellander 1995, Haché and Bayne 2013). However, the IFD assumes organisms in a population have the same strategy for habitat selection.

Multiple strategies of habitat selection can occur within a population when there are differences in morphology and behaviour between individuals. For example, males and females often differ in body size, nutritional requirements, and other characteristics that cause optimal habitat selection to be different. Female and male American kestrels (*Falco sparverius*) occupy different habitats in the non-breeding season due to size differences and predation risk (Arida and Bildstein 1997). Habitat selection can also be affected by differences in competitive ability, as demonstrated in the Ideal Despotic Distribution where dominant individuals monopolize the highest quality habitat (Fretwell 1972, Calsbeek and Sinervo 2002). The ideal despotic distribution has a different spatial distribution of individuals than the IFD: density is higher in lower quality habitats once the higher quality habitat is fully occupied because subordinate animals are unable to usurp dominants from territories (Fretwell 1972).

Performance in a habitat strongly depends on morphological and behavioural traits, and the structure of the habitat can impose selection for specific traits. For example, habitat-based polymorphisms are common among fishes with distinct morphological differences evolving in pelagic and littoral habitats in lakes (Skúlason and Smith 1995) and in riffle, run, and pool habitats in streams (Senay et al. 2015). Similar morphology-based differences in habitat are found in different ecomorphs of *Anolis* lizards (Losos et al. 1998) and among individuals of the same species of *Anolis* (Kamath and Losos 2016). Besides varying among discrete groups within a population, habitat selection strategy can vary on a continuous scale with individuals specializing on different resources, which may reduce competition with conspecifics (Bolnick et al. 2002, 2003, Kamath and Losos 2016). For example, generalist species of turtles (Paterson et al. 2012) and lizards (Kamath and Losos 2016) display considerable habitat niche differences with low overlap between individuals in the same population. Multiple strategies of habitat selection within a population may also occur when species are polymorphic for other traits, such as colour or reproductive strategy, that lead to differences in morphology and behaviour.

Colour polymorphism, the presence of multiple discrete colour types in a population, is common in many animals, such as birds, fish, insects, and lizards (Ford 1945, Roulin 2004, Forsman et al. 2008). The occurrence of colour polymorphism is puzzling because phenotypes with a fitness advantage should become fixed in a population (Roulin 2004, Gray and McKinnon 2007). However, colour polymorphism can be maintained by frequency-dependent selection, heterosis, or spatial variation in selection (Roulin 2004). Frequency-dependent selection maintains colour polymorphism because rare phenotypes have a fitness advantage that causes the relative frequency of morphs to cycle through time (Ayala and Campbell 1974). Heterosis, or hybrid vigour, can maintain genetic variation when homozygotes have lower fitness than heterozygotes, but the fitness differences required between homozygotes and heterozygotes to maintain genetic variation suggests this mechanism is not common (Levins 1962, Lewontin et al. 1978). Finally, spatial variation in selection can maintain polymorphism when phenotype fitness depends on habitat (Skúlason and Smith 1995, Roulin 2004, Chunco et al. 2007). Often, colour polymorphism is correlated with other traits, such as behaviour, diet, body size, and immune function (McKinnon and Pierotti 2010) that can affect performance in different habitat types. Therefore, differences in habitat selection is a likely mechanism for the maintenance of colour polymorphism within populations (Skúlason and Smith 1995, Chunco et al. 2007). For example, it is likely responsible for maintaining polymorphism in several bird species (Roulin 2004) and in lizard species of the white sands ecotone where background matching and gene flow between populations maintains genetic variation (Rosenblum 2006). Thus, testing for differences in habitat selection in colour polymorphic species can help reveal the mechanism maintaining colour polymorphism.

The ornate tree lizard (*Urosaurus ornatus*) is a widespread small lizard from western North America that displays a complicated throat colour polymorphism linked to reproductive strategy in males (Moore et al. 1998). Although there is significant continuous variation within and between male throat colour categories (Paterson and Blouin-Demers 2017b), males with blue throat patches are aggressive and have been inferred to defend home ranges that contain several females (Moore et al. 1998). Orange throated males are likely nomadic or sedentary, depending on resource levels (Moore et al. 1998), do not defend territories (Thompson et al. 1993, Moore et al. 1998), and grow faster than blue throated males (Thompson et al. 1993). Males with yellow or green throats are assumed to demonstrate a satellite or reproductive parasite breeding strategy and live in between the home ranges of blue-throated males where they sneak copulations with females (Lattanzio et al. 2016, Taylor and Lattanzio 2016). Blue-throated males are more aggressive than yellow-throated males in staged contests, but yellow-throated males are more bold than blue-throated males (Taylor and Lattanzio 2016). Male throat colour is also correlated with differences in diet (Lattanzio et al. 2016) and in microhabitat use (Lattanzio and Miles 2014). The frequency of different morphs is stable through time (Moore et al. 1998), which suggests frequency-dependent selection does not maintain the colour polymorphism. However, it is possible that polymorphism is maintained by frequency-dependent selection without noticeable cycles in morph frequencies. Thus, testing for differences in habitat selection strategy between male throat colour phenotypes will improve our predictive ability of space use in this species and test whether habitat selection can maintain the throat colour polymorphism within populations.

I tested the hypothesis that ornate tree lizard male throat colour affects space use and habitat selection because of differences in morphology and behaviour between males of distinct throat colours. First, I tested whether morphology is correlated with throat colour because body size and colour polymorphism are often genetically linked through pleiotropy or physical linkage (McKinnon and Pierotti 2010) and morphology can affect habitat use (Calsbeek and Irschick 2007, Senay et al. 2015). I then tested four predictions of this hypothesis related to differences in space use and habitat selection. First, I tested the prediction that blue-throated males should have smaller home ranges and move shorter distances than orange or green-throated males because blue-throated males are territory defenders and the other phenotypes do not actively defend against intruders. The second prediction I tested was that dominant blue-throated males should disproportionately occupy higher quality habitat to monopolize areas with high densities of females. I predicted orange and green-throated males should not disproportionately occupy the higher quality habitat because their reproductive strategy involves finding many females, compared to the resource defending strategy of blue-throated males. Third, I predicted blue-throated males should have smaller deviations of body temperature (T_b) from the species' preferred temperature range (T_{set}) if they occupy higher quality habitat. Fourth, I tested the prediction that dominant blue-throated males should perch higher than males with other throat colours because perch height is an indication of dominance (Zucker 1986, Delaney and Warner 2017) and would allow males to survey for territory intruders better than lower perch heights.

Methods

Study site and species

I studied habitat selection of male ornate tree lizards at 10 sites in the Chiricahua Mountains of southeastern Arizona, USA from 2014 to 2016. Each site was centered along a creek bed (wash habitat) and extended 50 m into the adjacent wooded area (upland habitat). Vegetation in the wash was sparse and mostly herbaceous; the upland habitat consisted of pine-oak woodlands. I studied six sites for three years (12 capture events) that were 300 m by 50 m. I studied four sites for one year (two capture events) that were 50 m by 50 m. Ornate tree lizards prefer the wash habitat (Chapter 1) and the wash has more prey items and allows lizards to achieve T_{set} for a longer period in a day than the upland habitat (Chapter 1).

During each capture event, I walked through the site and caught lizards with a noose and pole. I searched sites at least three times during each capture event. Before handling lizards, I measured T_b with an infrared thermometer (± 0.1°C) placed against the lizard's cloaca. Skin temperature is an accurate measure of internal T_b for small lizards like ornate tree lizards

(Herczeg et al. 2006, Carretero 2012, Bouazza et al. 2016). I only measured T_b on lizards that were captured at the exact location they were detected. I measured perch height (± 5 cm) to quantify microhabitat use. I measured the lizards' snout-vent-length (SVL; ± 0.1 mm) and head length (± 0.1 mm) with digital calipers, then I gave lizards a unique mark with a medical cauterizer (Winne et al. 2006, Ekner et al. 2011) and photographed their ventral side to quantify variation in throat colouration.

To quantify variation in throat colour, I used my previously described methods for analyzing photographs of throat patches (Paterson and Blouin-Demers 2017b). Briefly, I linearized and equalized photographs to account for uneven colour scores between the camera's red, green, and blue sensors using photographs of standardized grey scale colour cards (Stevens et al. 2007). Next, I measured the colour intensity in the centre (three variables for red, green, and blue colour scores) and on the periphery (three variables for red, green, and blue colour scores) of the throat in 0.25 cm^2 patches. Finally, I used threshold limits to measure the proportion of the throat that was blue, green, orange, and yellow (four variables). Therefore, I had 10 numerical variables to describe throat colour variation. I summarized throat colour variation with a principal component analysis (PCA) and used the first two components in further analyses.

The throat colour polymorphism in tree lizards is complex, and it is possible that reproductive strategy and habitat selection vary along a continuum or in discrete groups (Paterson and Blouin-Demers 2017b). Therefore, I tested my predictions about variation in morphology, space use, and habitat selection with three methods to describe male throat colour. First, I used PC1 and PC2 from the PCA on the 10 measurements of throat colour (described above). Second, I used five throat colour categories that I assigned to male lizards in the field:

blue, green, orange-blue, orange-green, and orange. Orange-blue and orange-green males had an orange ring on the periphery of their throat patch. These five categories are distinguishable using discriminant function analyses (DFA) on the 10 quantitative variables describing throat colour (85% correct classification; Supplementary information). However, it is possible bi-coloured throats (orange-blue and orange-green) are not separate phenotypes from blue and green throat patches and the amount of orange on the edge of the throat may be related to size or condition. For example, juvenile male tree lizards have orange throats that gradually turn into their adult colour (Carpenter 1995b). Grouping orange-blue throated males with blue-throated males and grouping orange-green throated males with green-throated males may be more representative of alternative phenotypes. Distinguishing between blue, green, and orange males with this reduced group assignment is highly accurate using a DFA (97% correct classification; Supplementary information). Therefore, I also tested my predictions about morphology, space use, and habitat selection using three throat colour categories (blue, green, and orange) that are consistent with previous descriptions of throat colour polymorphism in this species (Lattanzio and Miles 2014). For all analyses, I used throat colour as fixed effects in three separate models. First, I used PC1 and PC2 as continuous predictors. Next I used male throat colour as a discrete predictor with either five or three categories. To rule out frequency-dependent selection in maintaining the colour polymorphism, I tested whether the frequency of different throat colour categories (three or five categories) changed between years at the six sites monitored for three years (Supplementary information). However, I cannot rule out frequency-dependent selection maintaining the colour polymorphism if cycles are longer than three years or if frequencies are at a stable equilibrium through time.

Morphology

To test if lizard throat colour was correlated with morphological differences, I used linear mixed-effects models constructed with the R package *lme4* (Bates et al. 2014) with each lizard's mean SVL as the response variable. For all linear mixed-effects models, I used F-tests with Kenward-Rogers approximations for the degrees of freedom (Kenward and Roger 1997). I analyzed differences in body size between males with different throat colours using throat colour as a fixed effect and site as a random effect.

I tested for differences in head length between males with different throat colours with three linear mixed effects models. Head morphology in lizards affects prey handling (Herrel et al. 2008) and bite strength (Verwaijen et al. 2002) and this can affect resource use and the outcomes of competitive interactions. Since head length was strongly correlated with SVL (F = 716.64, df = 1, 583, $P < 0.0001$, $R^2 = 0.55$), I included SVL as a covariate in the analyses. Each model included site as a random effect and throat colour as a fixed effect.

Mean distance moved

I averaged the linear distance between capture locations for lizards caught at least twice. The mean distance travelled did not increase with the number of captures (F = 0.045, df = 1, 208, $P = 0.83$, $R^2 < 0.01$). I used linear mixed-effects models to compare the mean distance moved between captures of males with different throat colours. I used the mean distance moved by a lizard as the response variable, throat colour as fixed effects, and site as a random effect.

Habitat selection

To compare the habitat selection of male tree lizards with different throat colours, I used a modification of the distance method (Conner et al. 2003). I calculated the mean coordinates of each individual lizard and measured the minimum distance to the wash habitat. I assumed that the mean coordinates are representative of the home range centre of individual lizards. If habitat selection varies between males with different throat colours, then throat colour will affect how close a lizard is to the wash. To test whether male lizards showed a preference for the wash habitat, I compared the distance to the wash of random points to the mean coordinates of individual lizards with a t-test. I generated 580 random points (the same sample size as the number of male lizards) distributed between the 10 sites. Next, I used linear mixed-effects models to test how throat colour is correlated with habitat selection using the distance to the wash for a lizard as the response variable, throat colour as a fixed effect, and site as a random effect in each model.

Habitat selection can be used to maintain a specific T_b and I tested the prediction that more dominant blue-throated males achieve a T_b closer to T_{set} (32.2 °C – 36.0 °C; Chapter 1) using linear mixed-effects models. For each model, I used the accuracy of T_b (d_b), the absolute deviation between T_b and T_{set} (Hertz et al. 1993) as the response variable, lizard throat colour as a fixed effect, and site as a random effect.

To test my prediction that blue-throated males perch higher, I compared the perch height (square root transformed) of male ornate tree lizards with different throat colours using linear mixed-effects models. I used throat colour and habitat (wash or upland) as a fixed effect and site as a random effect.

Results

I captured 580 male tree lizards 907 times. For the PCA on throat colour, I used 720 photographs from 500 males and the first two components cumulatively explained 72% of the variation in throat colour. PC1 had positive loadings for the proportion of the throat that was blue and the blue colour score in the centre of the throat patch (Supplementary information: Table 3-

S1). PC2 had positive loadings for the proportion of the throat that was orange and negative loadings for the proportion of the throat that was green (Supplementary information: Table 3-S1). The intra-class correlation coefficient was 0.75 for PC1 and 0.76 for PC2, indicating both values are highly repeatable for individual males. The frequencies of throat colour categories only differed between years in one site and when throat colours were grouped into three categories (Supplementary information: Table 3-S2, 3-S3, Figure 3-S1, 3-S2).

Morphology

Both PC1 ($\beta = 0.02$, F = 8.97, df = 1, 491, *P* = 0.003) and PC2 ($\beta = -0.03$, F = 14.62, df = 1, 497, *P* = 0.0001) of throat colour were related to the mean SVL of male ornate tree lizards. Males with more blue throats (higher PC1) were larger (Figure 3-1A) and males with more orange throats (higher PC2) were smaller (Figure 3-1B). The five categories of throat colour differed in SVL (F = 3.30, df = 4, 593, *P* = 0.01, Figure 3-2A) with orange-blue and orange-green throated males being smaller than blue-throated males. There was no difference in SVL between the three categories of throat colour (F = 1.29, df = 2, 594, *P* = 0.28; Figure 3-2B).

The mean head length of male ornate tree lizards was not related to PC1 (F = 1.10, df = 1, 338, *P* = 0.30) or PC2 (F = 0.06, df = 1, 342, *P* = 0.80) of throat colour when controlling for SVL (F = 534.32, df = 1, 343, *P* < 0.0001). Head length did not differ between the five throat colour categories (F = 1.26, df = 1, 388, *P* = 0.29) or the three throat colour categories (F = 1.12, df = 1, 391, *P* = 0.33) when controlling for SVL.

Distance moved

The mean distance moved between capture locations was not related to PC1 (F = 1.63, df = 1, 193, *P* = 0.20) or PC2 (F = 3.19, df = 1, 196, *P* = 0.08) of throat colour. Using five throat colour categories, there was an effect of throat colour on the mean distance moved between captures (F = 3.57, df = 4, 201, $P = 0.008$). Males with orange-green throats moved the most, and males with orange throats moved the least (Figure 3-3A). Using three discrete colour categories, there was an effect of throat colour on the mean distance moved between captures (F = 6.8, df = 2, 203, $P = 0.001$). Orange-throated males moved the least and green-throated males moved the most (Figure 3-3B).

Habitat selection

Male tree lizards preferred the wash habitat and were closer to the wash than random points generated within each study site (t = 6.64, df = 1125, $P < 0.001$). There was a marginal effect of PC1 ($\beta = 0.07$, F = 3.84, df = 1, 492, $P = 0.05$) and no effect of PC2 (F = 0.24, df = 1, 496, $P = 0.63$) on how close male tree lizards were to the wash habitat. There was no difference between the five throat colour categories in how close they were to the wash (F = 2.56, df = 4, 570, $P = 0.06$), but there was a difference when comparing the three throat colour categories (F = 3.96, df = 2, 573, $P = 0.02$). Males with green throats were closer to the wash than males with blue throats (Figure 3-4).

Lizard d_b was not related to PC1 (F = 0.36, df = 1, 122, $P = 0.55$) or PC2 (F = 3.48, df = 1, 124, $P = 0.06$) of throat colour. Using five colour categories, there was a marginal effect of throat colour on d_b (F = 2.40, df = 4, 137, $P = 0.05$; Figure 3-5) where males with orange-blue throats had slightly lower d_b than blue-throated males. However, the estimated difference in d_b was very small (0.8 °C). Using three colour categories, there was no effect of throat colour on d_b (F = 0.53, df = 2, 139, $P = 0.59$). Therefore, throat colour did not affect how close lizard T_b was to T_{set}.

Perch height did not change with PC1 (F = 0.06, df = 1, 169, $P = 0.80$) or PC2 (F = 0.83, df = 1, 175, $P = 0.36$) of throat colour. Perch height did not differ between the five throat colour categories (F = 0.62, df = 4, 151, *P* = 0.65) or the three throat colour categories (F = 0.14, df = 2, 134, *P* = 0.87). Lizard perch height did not differ between the upland and wash habitats in any of the mixed-effects models (all *P* > 0.05).

Discussion

My data partially support the hypothesis that male ornate tree lizard throat colour affects habitat selection because of differences in behaviour and morphology. I found evidence that throat colour differences in male ornate tree lizards are correlated with body size, mean distance moved between captures, and use of the highest quality habitat.

Male ornate tree lizard body size was correlated with throat colour and bigger lizards had higher PC1 scores, indicating that blueness was positively related to size. This is consistent with other lizard species where the size or intensity of a male's blue throat patch increased with size or age (Cox et al. 2005, 2008). In addition, there was a negative relationship between PC2 and size: lizards with more orange on their throat were smaller. Juvenile male ornate tree lizards have orange throats that change as they reach sexual maturity (Carpenter 1995b). Thus, the observed continuous variation in the proportion of the throat that was orange may be due to hormonal changes as lizards reach maturity, rather than orange-blue and orange-green throats representing discrete morphs. It is possible that orange-blue and blue-throated males represent the same phenotype, but vary continuously in body size. The same is possible for differences between orange-green and green-throated males. Some males maintain all orange throats as adults, but this phenotype was rare at all of my study sites (ca. 1% of individuals). This hypothesis is further supported by the differences in SVL between males with different throat colour categories because orange-blue and orange-green-throated males were smaller than blue-throated males.

I found evidence that throat colour was correlated with space use in male tree lizards because male throat colour was correlated with the mean distance travelled between captures. Although PC1 and PC2 were not related to the mean distance moved, throat colour category was a strong predictor of distance moved. Green-throated males moved more than blue-throated males, consistent with the hypothesis that green-throated males (often categorized as yellow-throated males in other studies) exhibit a reproductive parasite strategy and blue-throated males defend small territories (Thompson and Moore 1991b, Lattanzio and Miles 2014). The lack of a difference in mean distance moved between blue and orange-blue, and green and orange-green throat patches is consistent with my hypothesis that the orange ring around the throat is related to body size or age and does not represent a different male reproductive strategy. Orange-throated males moved significantly less than green or blue-throated males, contrary to the hypothesis that this morph is nomadic (Moore et al. 1998). However, previous studies have found males with all orange throats to be nomadic in drought years and sedentary in wet years (Moore et al. 1998, Knapp et al. 2003) so resource depletion may not have been extreme enough to cause males with orange throats to become nomadic during my study. However, I cannot draw strong conclusions about space use in orange-throated males because they were very rare (8 individuals spread between 10 sites over three years, or 1% of individuals).

I found evidence that habitat selection differed between throat colour morphs: green-throated males were closer to the wash than blue-throated males. In general, tree lizards prefer the wash habitat (Chapter 1; this chapter) and I found evidence that green-throated males were closer to the wash than blue-throated males. Since population density is higher in the wash habitat than in the upland (Chapter 1), green-throated males displaying a reproductive parasite strategy (Alonzo and Calsbeek 2010, Lattanzio and Miles 2014) may be more successful in crowded areas where female density is highest (Chapter 1).

The d_b of male ornate tree lizards did not change with PC1 and PC2 and there were no differences between throat colour categories. Therefore, ornate tree lizard throat colour did not affect how close lizards were to T_{set}. The majority of T_b measurements (56%) were within the preferred body temperature range of this species (32.2 – 36 °C; Figure 3-5) and lizards were close to T_{set} when we caught them (80% of T_b measurements were within 2°C of T_{set}). Therefore, this result may be an artefact of my capturing only active individuals, likely engaged in thermoregulation.

There were no differences in perch height based on throat colour. Other lizard communities, species (Losos et al. 1998), life stages (Delaney and Warner 2016, 2017), or individuals (Kamath and Losos 2016) partition perch height and use different sections of trees. Species that overlap more in perch habitat have a higher overlap in trophic niche (Schoener 1968) and I predicted that trophic differences between ornate tree lizards with different throat colours (Lattanzio et al. 2016) were a result of partitioning perch heights. However, throat colour was not correlated with perch height in male tree lizards and this niche axis did not spatially segregate throat colour phenotypes.

Different space use and habitat selection based on throat colours can maintain polymorphism within populations. Two commonly proposed mechanisms for the maintenance of polymorphism are frequency-dependent selection (Ford 1945, Pryke et al. 2007) and niche specialization or partitioning (Ford 1945, Skúlason and Smith 1995). In frequency-dependent selection, a phenotype's fitness depends on the frequency of other phenotypes. For example, side-blotched lizards (*Uta stansburiana*) have a throat colour polymorphism where three phenotypes play a rock-paper-scissors game (Sinervo and Lively 1996). Rare morphs have a fitness advantage and this causes population frequencies of morphs to cycle. Although I only have three years of data, the frequencies of different throat colours in male ornate tree lizards did not appear to cycle. The frequencies of throat colour categories only differed between years in one site and grouping throat colours into three categories (Supplementary information: Table 3-S2, 3-S3, Figure 3-S1, 3-S2). Side-blotched lizard morph frequency differed every year over six years (Sinervo and Lively 1996), but it is possible I could not detect changes in frequency between male tree lizard throat colours because there was little variation in throat colour frequency during those three years.

Polymorphism can also be maintained if morphs partition niches and pleiotropic effects link colour to behavioural or physiological traits that affect performance in different habitats (Skúlason and Smith 1995, Roulin 2004). My data partially support the hypothesis that male tree lizard throat colour polymorphism affects habitat selection because of differences in behaviour and morphology. In addition, throat colour frequency did not cycle through years at my study sites and throat colours show differences in trophic niche (Lattanzio et al. 2016). Thus, the colour polymorphism in male ornate tree lizards may be maintained by niche partitioning among phenotypes rather than a similar frequency-dependent selection to side-blotched lizards. Future work should further test this hypothesis through experimental manipulations of phenotype frequency, density, and habitat. Researchers have made significant progress determining the mechanisms that create and maintain colour polymorphisms in different species, such as resource partitioning, frequency-dependent correlational selection, and divergent natural selection with gene flow (Gray and McKinnon 2007). However, the relative frequencies at which these mechanisms occur are still unknown and require more well studied systems with colour polymorphisms. Testing for differences in habitat selection between phenotypes within a population will increase our ability to predict the spatial distribution of organisms between habitats.

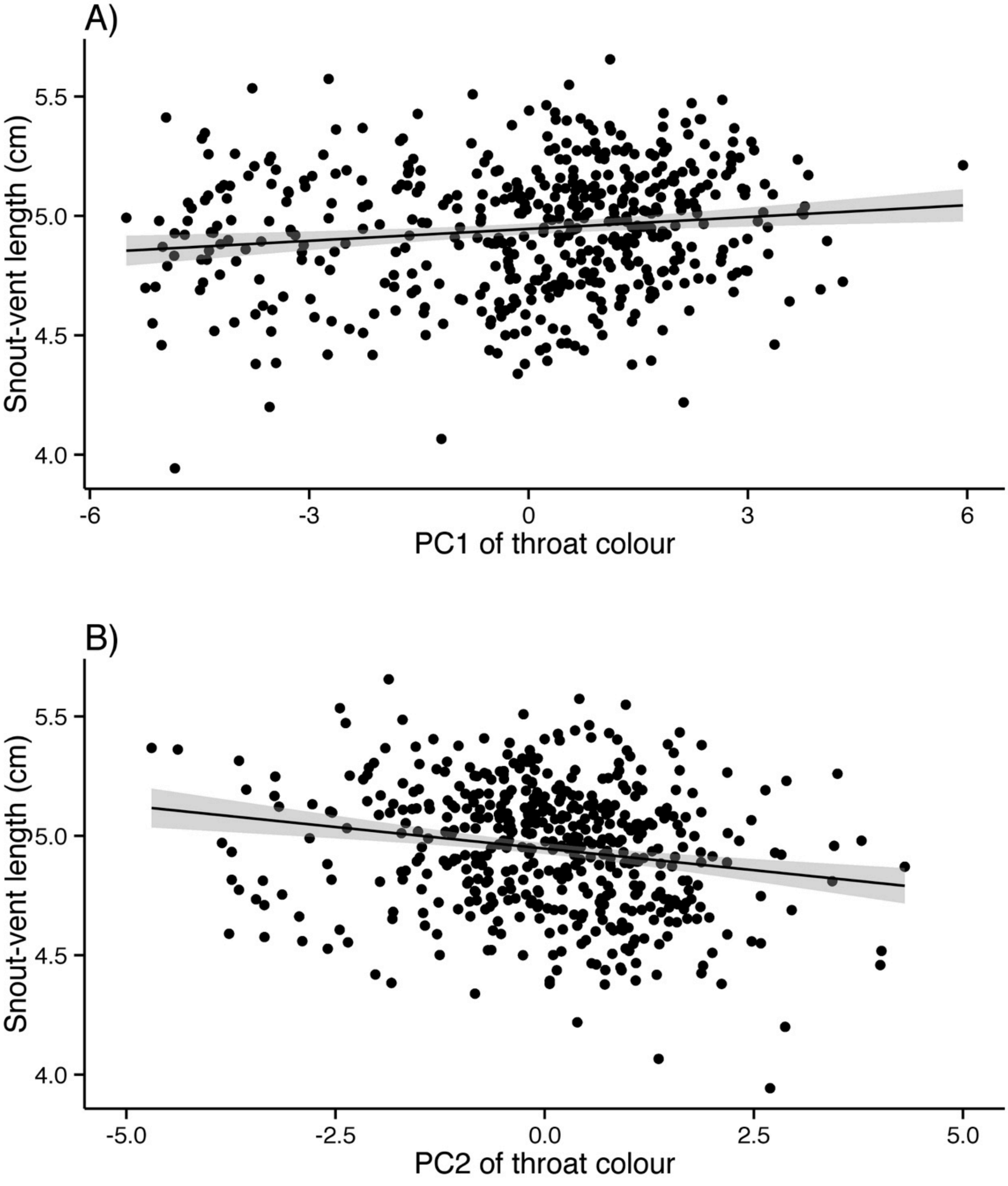

Figure 3-1. The mean snout-vent length (cm) of male ornate tree lizards (*Urosaurus ornatus,* n = 500) in the Chiricahua Mountains of Arizona, USA was positively related to A) PC1 of throat colour, and negatively related to B) PC2 of throat colour.

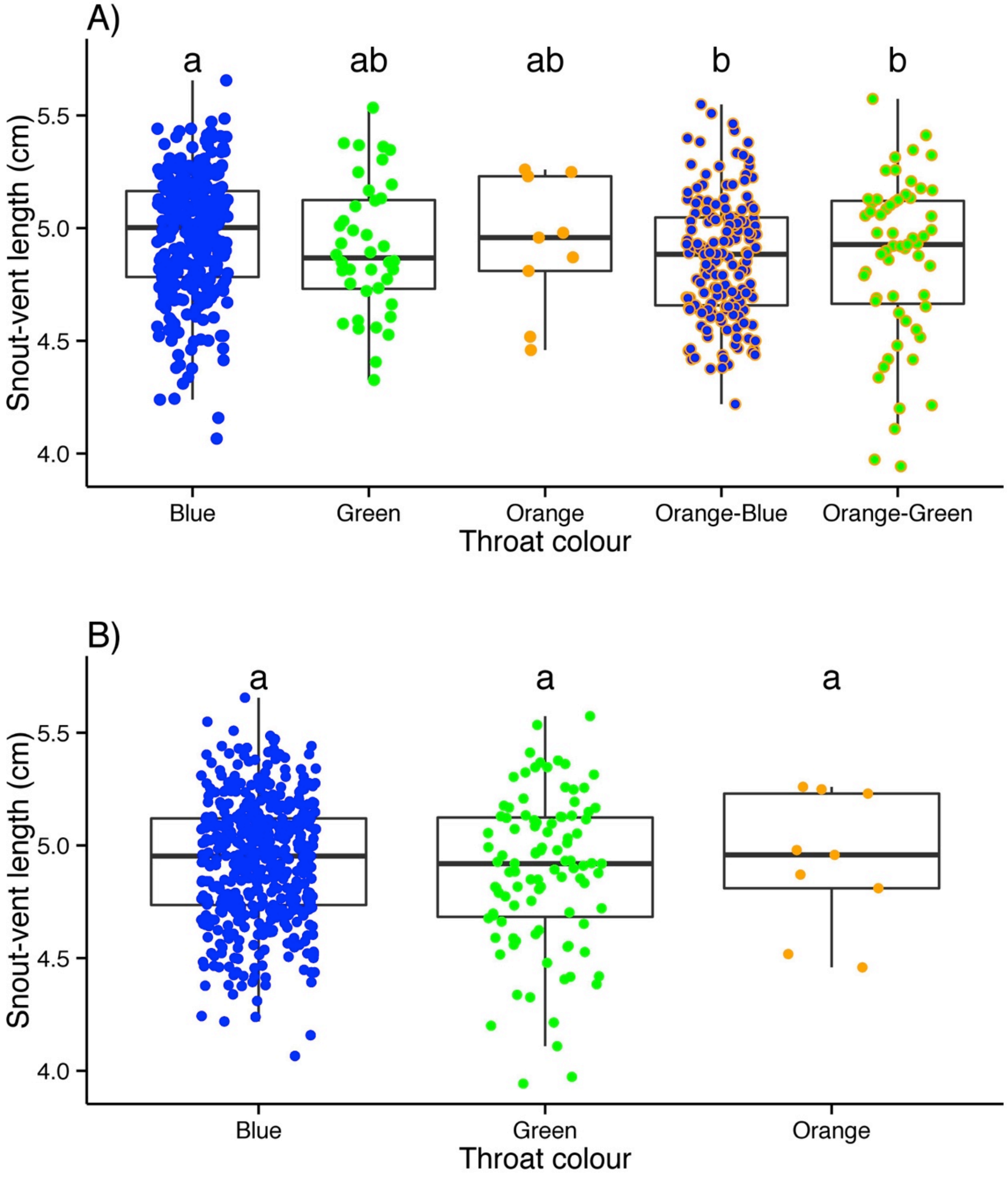

Figure 3-2. The snout-vent length (cm) male ornate tree lizards (*Urosaurus ornatus,* n = 580) in the Chiricahua Mountains of Arizona, USA differed between A) five categories for throat colour, but not between B) three categories for throat colour.

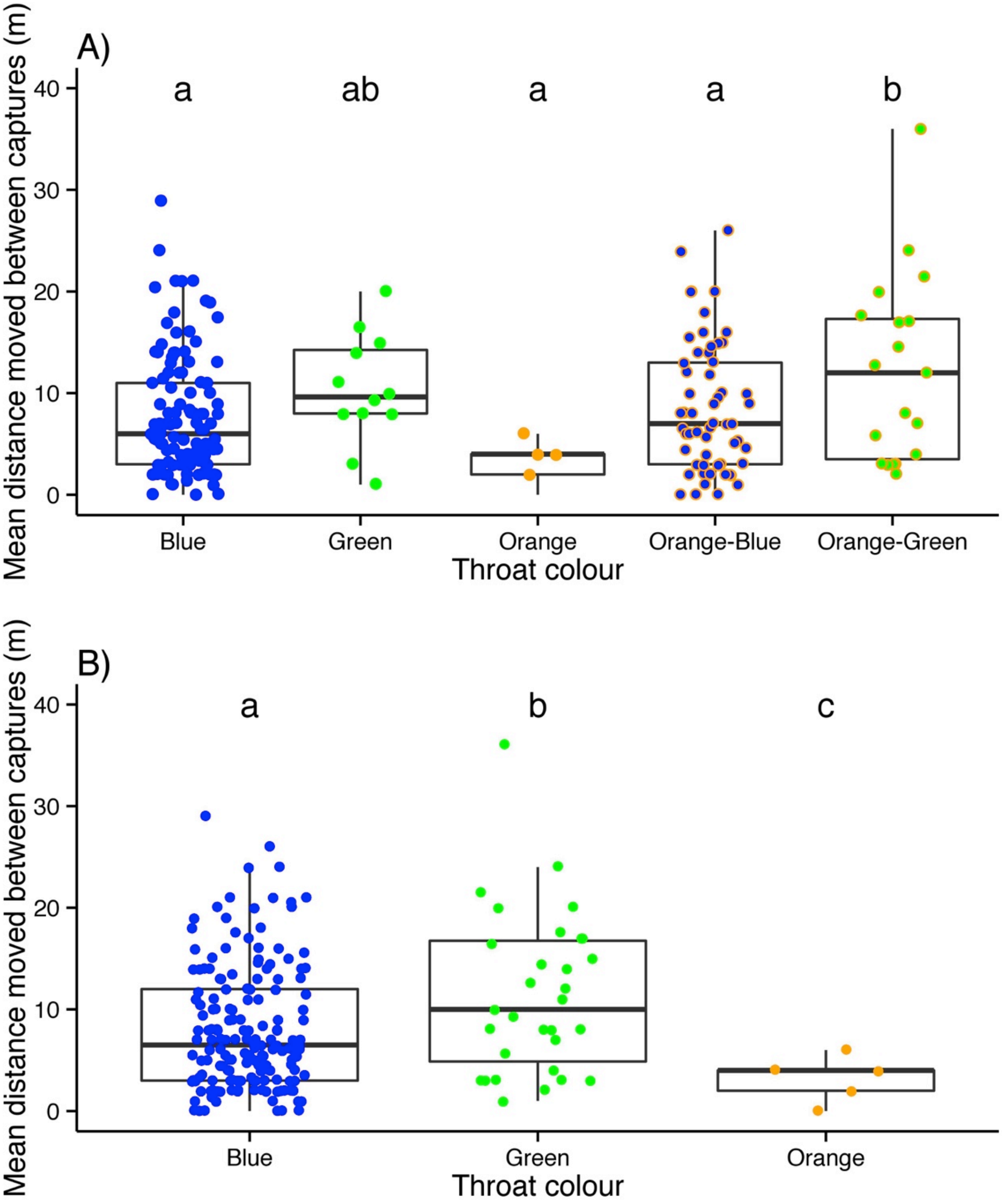

Figure 3-3. The mean distance moved between captures by male ornate tree lizards (*Urosaurus ornatus,* n = 209) in the Chiricahua Mountains of Arizona, USA differed between A) five categories for throat colour, and B) three categories for throat colour.

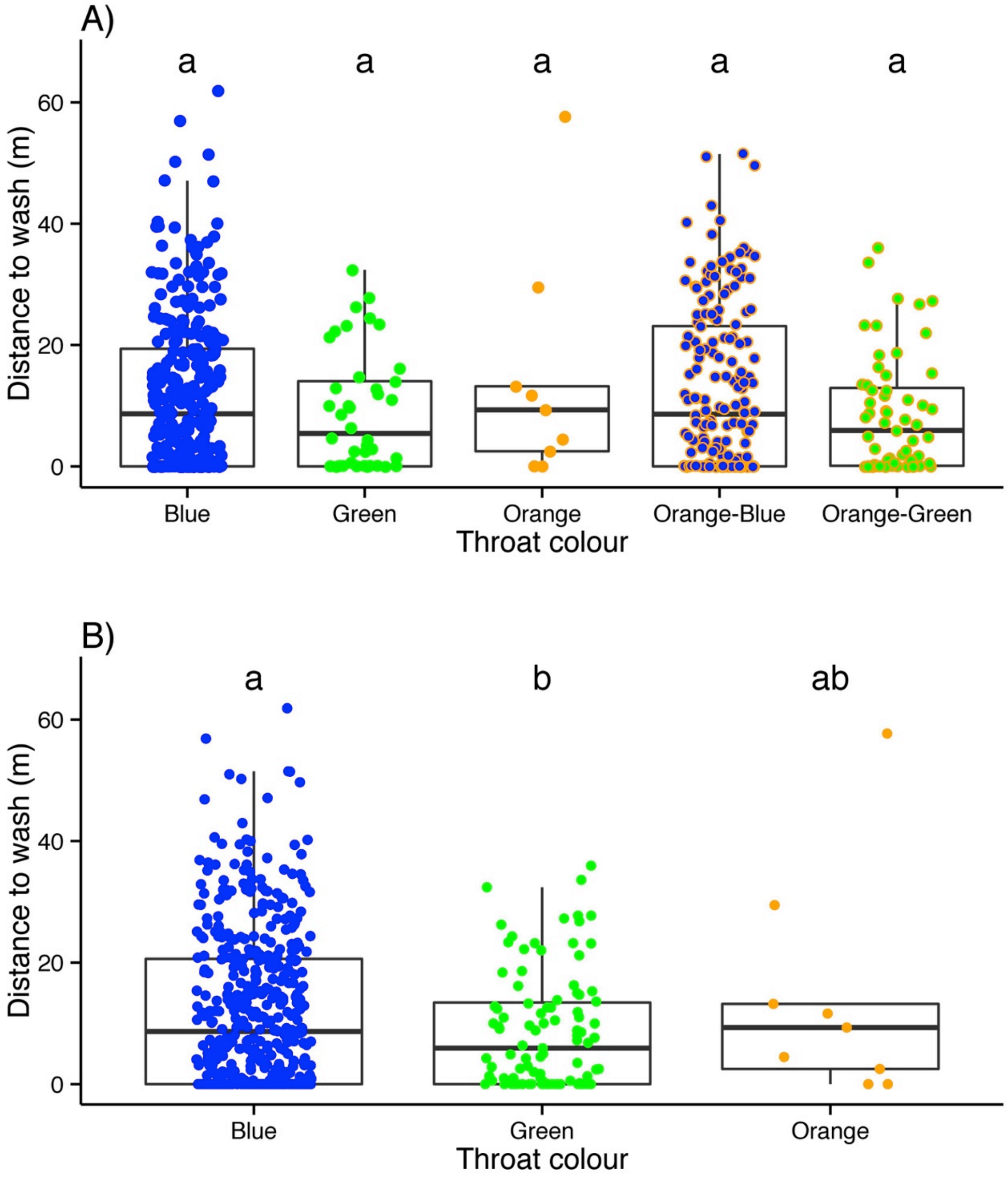

Figure 3-4. The mean distance to the wash of male ornate tree lizards (*Urosaurus ornatus,* n = 578) in the Chiricahua Mountains of Arizona, USA A) did not differ between five throat colour categories, but B) was lower for green than blue or orange males when using three throat colour categories.

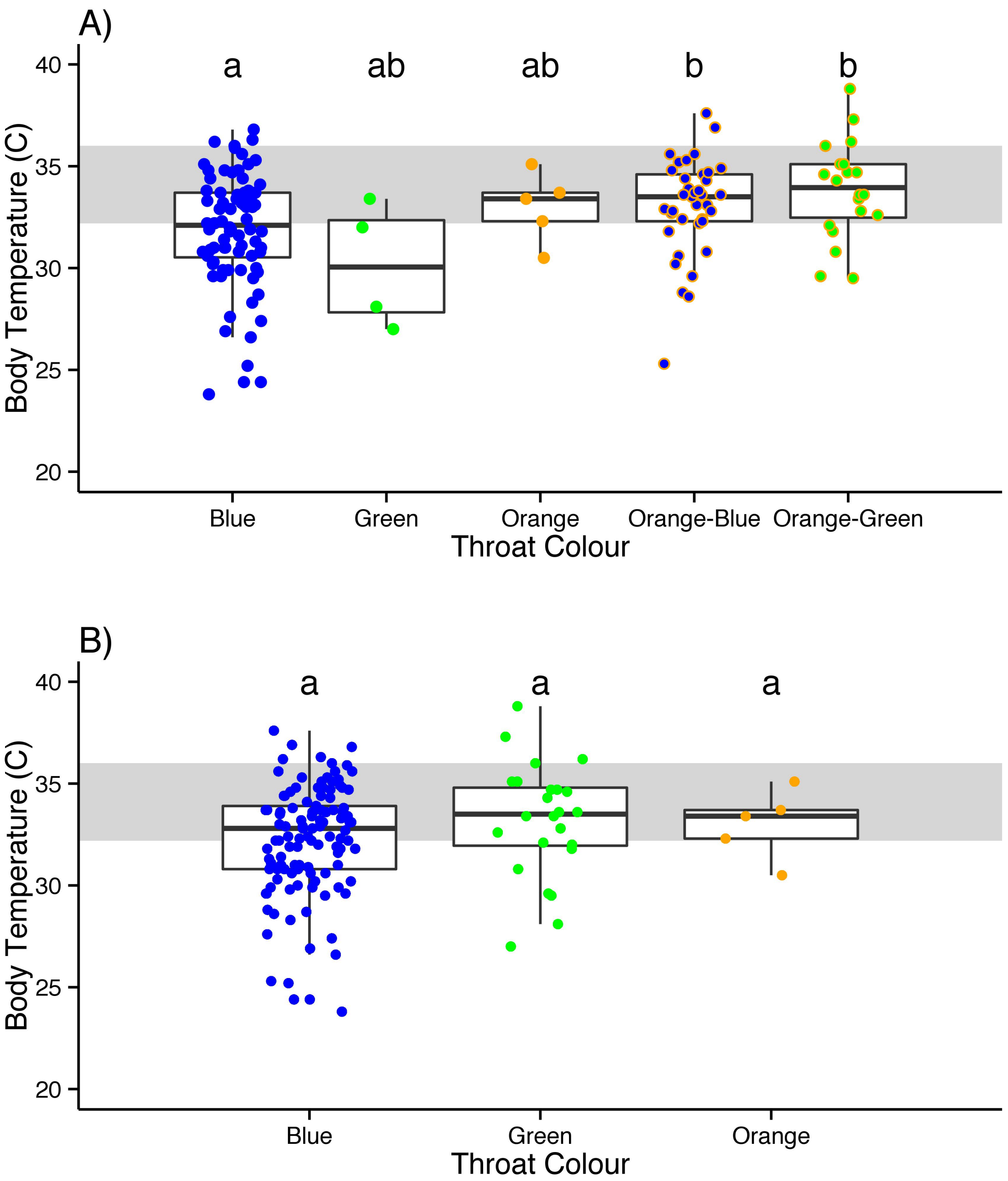

Figure 3-5. The body temperature (°C) of male ornate tree lizards (*Urosaurus ornatus,* n = 146) in relation to the species' preferred body temperature (T_{set}, shaded areas) in the Chiricahua Mountains of Arizona, USA grouped into A) five categories, or B) three categories for throat colour.

Supplementary information for Chapter 3

Table 3-S1. The variable loadings for PC1 and PC2 in a principal component analysis with 10 variables describing throat colour of male ornate tree lizards (*Urosaurus ornatus,* n = 720 photographs) in the Chiricahua Mountains of Arizona, USA.

Variable	**PC1**	**PC2**
Proportion blue	0.397	0.112
Proportion green	-0.276	-0.384
Proportion orange	-0.294	0.351
Proportion yellow	-0.305	-0.355
Centre red score	-0.357	0.467
Centre green score	-0.116	-0.328
Centre blue score	0.385	0.221
Periphery red score	-0.343	0.348
Periphery green score	0.221	-0.528
Periphery blue score	0.361	-0.178

Discriminant function analyses on throat colour categories

To determine whether male tree lizard throat colour categories identified in the field were distinguishable based on 10 quantitative variables of photographs, I conducted discriminant function analyses (DFA). Using the category assigned in the field (blue, green, orange, orange-blue, and orange-green), the DFA correctly classified 85% of 720 photographs. Therefore, the five categories of throat colour were distinguishable based on colour measurements of photographs, but there is some overlap between categories. The amount of orange in orange-blue and orange-green males decreased with body size, so I also conducted a DFA with three throat colour categories (blue, green, and orange) and assigned orange-blue males to the blue category and orange-green males to the green category. Using three categories, the DFA correctly classified 97% of 720 photographs. Therefore, the three categories of throat colour were highly distinguishable based on colour measurements of photographs.

Changes in frequency of throat colour categories

I used χ^2 tests of independence to test if the frequencies of throat colours changed between years at the same site. I used six tests at sites I monitored for all three years of the study (one test per site). I used separate analyses with five and three throat colour categories. For analyses with five throat colour categories, throat colour category frequencies did not change through time at a site (Table 3-S2). For analyses using three throat colour categories, one site (site 1) showed evidence of change in the relative frequencies of throat colours (Table 3-S3).

Table 3-S2. The results of χ^2 tests comparing the relative frequencies of five throat colour categories (blue, green, orange, orange-blue, and orange-green) in male ornate tree lizards (*Urosaurus ornatus*) between three years at six sites in the Chiricahua Mountains of Arizona, USA. Sample sizes (n) are the total number of males captured during a year at each site. Site 5 had too few individuals to compare throat colour frequencies between years.

Site	**n (2014)**	**n (2015)**	**n (2016)**	**χ2**	***P***
1	42	25	37	2.8	0.65
2	60	48	49	2.61	0.77
3	31	21	14	4.91	0.31
4	50	49	40	6.05	0.13
5	13	16	17	NA	NA
6	38	27	21	2.52	0.71

Table 3-S3. The results of χ^2 tests comparing the relative frequencies of three throat colour categories (blue, green, and orange) in male ornate tree lizards (*Urosaurus ornatus*) between three years at six sites in the Chiricahua Mountains of Arizona, USA. Sample sizes (n) are the total number of males captured during a year at each site. Site 5 had too few individuals to compare frequencies of throat colours between years.

Site	**n (2014)**	**n (2015)**	**n (2016)**	**χ2**	***P***
1	42	25	37	9.83	0.01
2	60	48	49	3.78	0.4
3	31	21	14	3.92	0.44
4	50	49	40	2.53	0.82
5	13	16	17	NA	NA
6	38	27	21	3.3	0.59

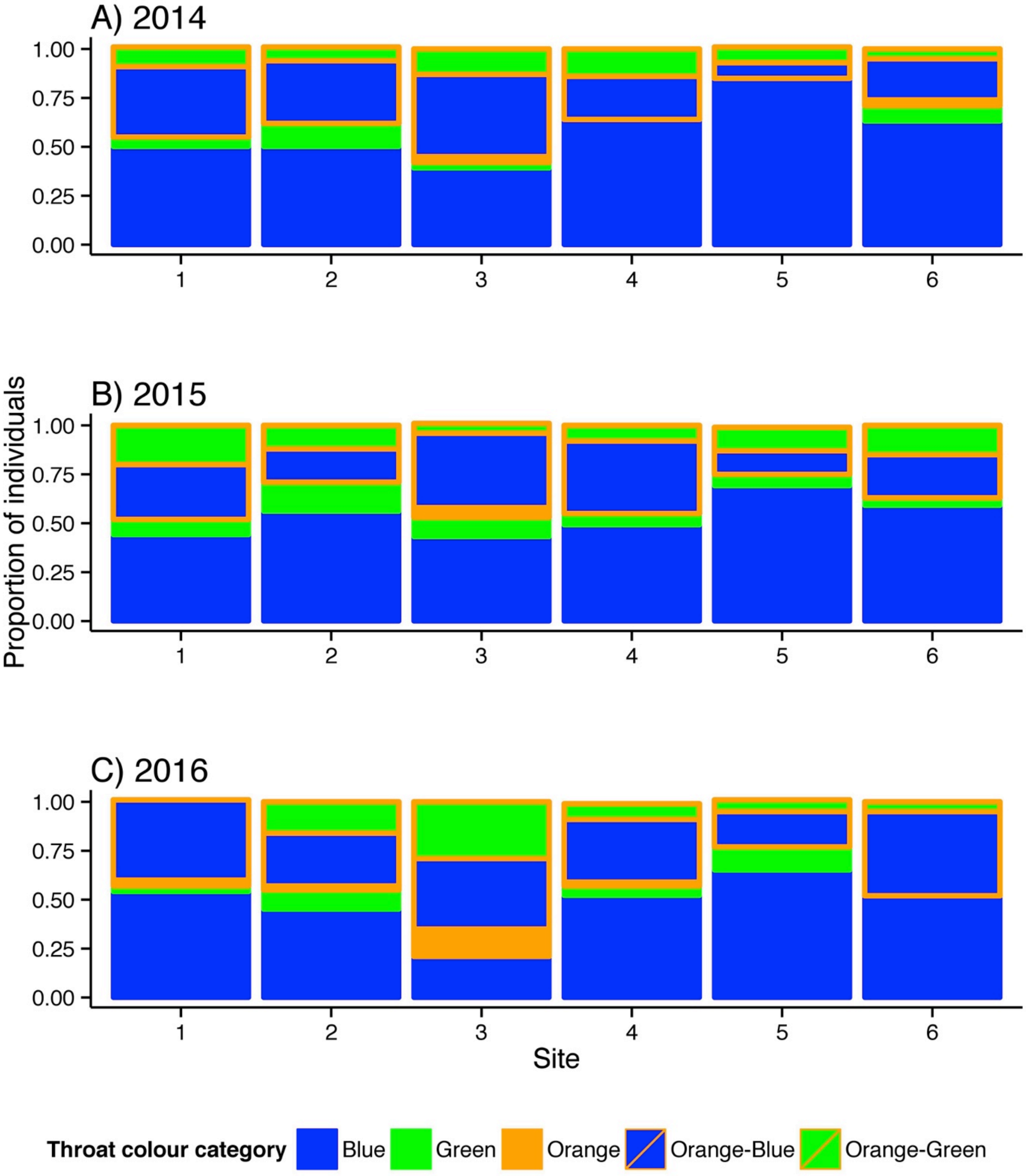

Figure 3-S1. The relative frequency of five throat colour categories (blue, green, orange, orange-blue, and orange-green) over three years in male ornate tree lizards (*Urosaurus ornatus,* n = 580) at six sites in the Chiricahua Mountains of Arizona, USA.

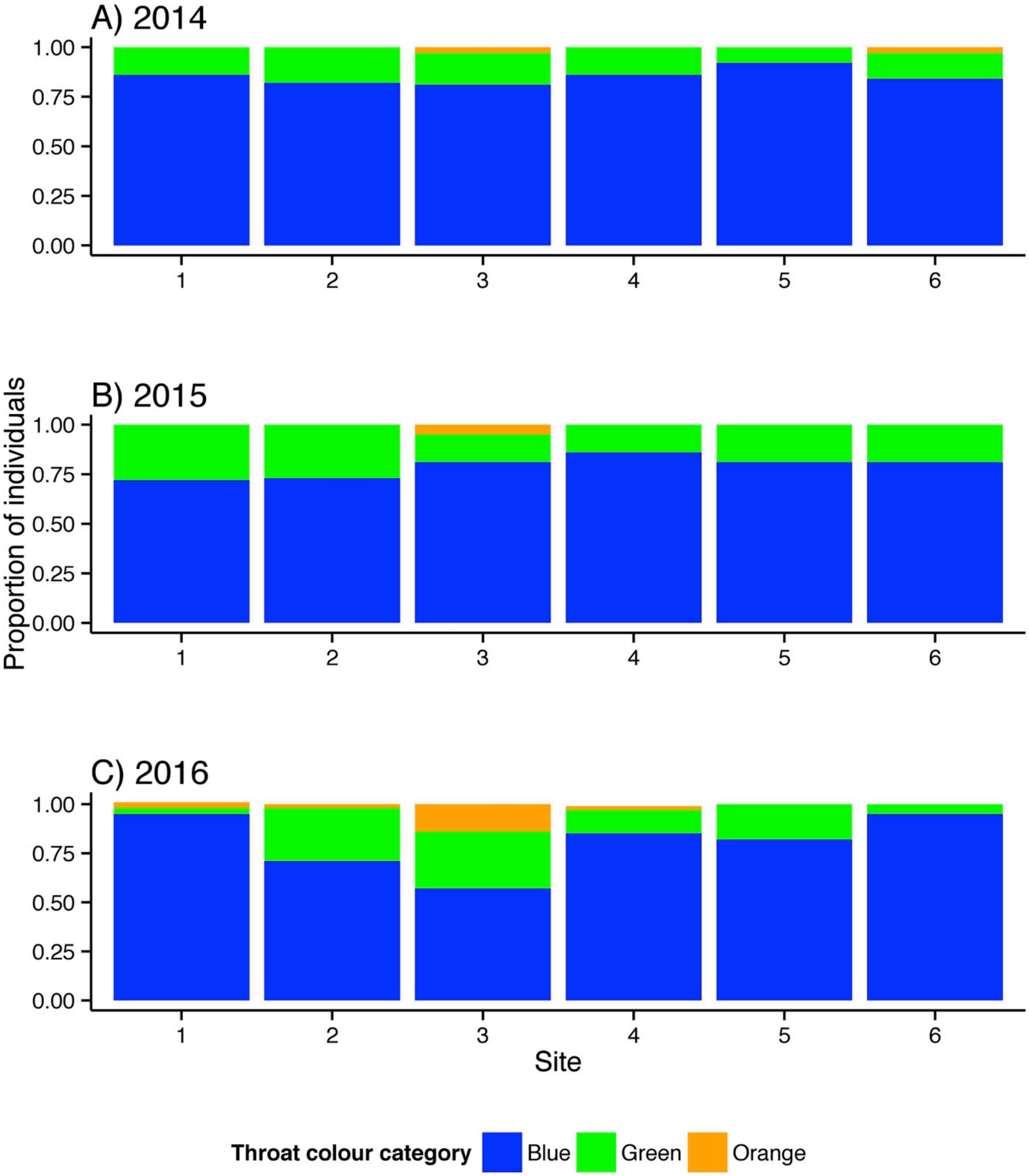

Figure 3-S2. The relative frequency of three throat colour categories (blue, green, and orange) over three years in male ornate tree lizards (*Urosaurus ornatus,* n = 580) at six sites in the Chiricahua Mountains of Arizona, USA.

Chapter 4

Experimental removal reveals that competition between two lizard species affects space use but not habitat selection, fitness, or abundance

This chapter formed the basis for the following publication:

Paterson, J.E., Weiss, S.L., and Blouin-Demers, G. 2017. Experimental removal reveals weak competition between two lizard species. *In review.*

Abstract

Competition for food, space or other resources is an important mechanism that shapes ecological communities. Interspecific competition can affect habitat selection, fitness, and abundance in animals. I used a removal experiment and mark-recapture to test the hypothesis that competition with the larger and more abundant striped plateau lizard (*Sceloporus virgatus*) limits habitat selection, fitness, and abundance in ornate tree lizards (*Urosaurus ornatus*). The removal treatment was successful in significantly reducing striped plateau lizard populations. Tree lizards in the plots where plateau lizards were removed switched between habitat types more frequently and moved further than tree lizards in control plots. However, there were no significant changes in the relative densities of tree lizards in each habitat type or in microhabitat use. I also found no changes in growth rates, survival, or abundance of tree lizards in response to the removal of plateau lizards. My results suggest that interspecific competition with striped plateau lizards was not strong enough to limit habitat use or abundance of tree lizards. The variation in abundance and habitat use between tree lizard populations is more likely due to other factors, such as intraspecific competition, predation pressure, or abiotic conditions. Considering my results and those of previous studies, it appears interspecific competition is likely to be weak between coexisting species when resource levels are not severely depleted. Therefore, it is important to consider environmental conditions when assessing the importance of interspecific competition in communities.

Introduction

Competition is a primary force that shapes ecological communities and drives evolutionary diversification (Day and Young 2004). Intraspecific competition for food, space, or other resources affects population dynamics (Brook and Bradshaw 2006), habitat use (Fretwell and Lucas 1969), and niche breadth (Bolnick 2001). Interspecific competition also plays a major role in dictating the relative abundance of species (Schoener 1983) and their distribution between habitats (Laiolo 2013). Although interspecific competition is frequently detected through field experiments (Schoener 1983), its relative importance in shaping ecological communities compared to other factors, such as intraspecific competition, parasitism, and predation has been debated (Connell 1983, Ferson et al. 1986, Jackson et al. 2001, Boulangeat et al. 2012). Regardless, interspecific competition continues to be a major factor explaining patterns in occurrence and abundance in communities (Laiolo 2013, Steen et al. 2014, Tarjuelo et al. 2016). Evidence of interspecific competition can be found by examining changes in habitat selection, fitness, or abundance in response to a manipulation of abundance of other species.

Interspecific competition can affect habitat selection if there is a cost to settling in a habitat occupied by another species sharing the same resources. Competing species may select habitat based on the density of their competitor in different patches. For example, little bustard habitat selection depends on the density of a dominant competitor, the great bustard (Tarjuelo et al. 2016). Habitat selection based on the presence or density of competitors has also been observed in dragonflies (Suhling 1996) and lizards (Pacala and Roughgarden 1982, Salzburg 1984, Rummel and Roughgarden 1985). Therefore, interspecific competition can influence the distribution of individuals between habitats. Even species that are not currently competing may demonstrate evidence of the ‘ghost of competition past’ because their habitat preferences have diverged as a result of past interspecific competition (Connell 1980, Rosenzweig 1991). For example, the preferred habitats of two lemming species do not overlap, and they experience current competition only when high population sizes force some individuals into less-preferred habitats (Morris et al. 2000). Interspecific competition affects the spatial distribution of organisms partially because of its effects on habitat selection.

Interspecific competition can affect fitness proxies, such as survival, growth rates, or reproductive rates. For example, collared flycatcher recruitment increased when the density of two competing species was experimentally reduced (Gustafsson 1987). Thus, competition for resources can depress fitness below levels that could be achieved if the competitor were absent. However, the magnitude of fitness effects induced by competition are often temporally variable and related to resource availability, climatic conditions, predator population size, or parasite prevalence (Smith 1981, Connell 1983). When present, the effects of interspecific competition on demographic parameters, such as survival and reproductive rate, can affect population abundance.

The most commonly explored consequence of interspecific competition is its effect on abundance. Removing a competitor can greatly increase the abundance of a species because of the increase in resource availability (reduced exploitative competition) and the decrease in behavioral interference. For example, removing a large territorial reef fish caused large increases in the abundance of several subordinate species (Robertson 1996). The changes in abundance can result from increased birth rates, decreased mortality rates, or increased immigration rates in areas with less interspecific competition. Explaining spatial and temporal patterns in abundance is one of the major predictive challenges in ecology (Elith and Leathwick 2009), so measuring the effects of interspecific competition on habitat selection can improve predictions about variation in abundance.

I previously documented density-dependent habitat selection in ornate tree lizards (*Urosaurus ornatus*) between two habitats varying in suitability in the Chiricahua Mountains of Arizona, USA (Chapter 1). However, it is possible that the habitat selection patterns I observed could be explained more fully by also considering the effects of interspecific competition, in addition to the effects of intraspecific competition. At my study site, tree lizards occupy the same habitat as striped plateau lizards (*Sceloporus virgatus*). These two species are likely to compete for resources because they overlap in size, perch sites, and habitat use (Smith 1981). Competition between these two species affects juvenile survival during years with low resource availability (Smith 1981).

To test the hypothesis that local abundance of tree lizards is driven by competition with striped plateau lizards, I conducted a removal experiment and mark-recapture study to test three predictions. First, I tested the prediction that interspecific competition influences habitat selection by examining changes in the distribution of tree lizards in response to the removal of striped plateau lizards. I next tested the prediction that interspecific competition decreases the fitness of tree lizards by examining changes in survival and growth rate of tree lizards in response to the removal of striped plateau lizards. Finally, I tested whether removing striped plateau lizards increased the abundance of tree lizards.

Methods

Study species and study sites

I studied interspecific competition between ornate tree lizards and striped plateau lizards (Supplementary information: Figure 4-S1). These species occur sympatrically along canyon bottoms in the Chiricahua Mountains of Arizona, USA and are the two most abundant lizard species where they occur. I used a removal experiment to test for competitive effects on habitat selection, fitness, and abundance. I studied eight 50 m by 50 m plots along three creeks within the Middle Fork drainage of Cave Creek; all plots were at least 50 m apart and I did not observe lizards switching plots. Each control plot was paired to a neighboring removal plot in which I experimentally reduced the abundance of striped plateau lizards (Supplementary information: Table 4-S1; Figure 4-S2). Each plot straddled rocky wash habitat with open canopy and upland habitat consisting of pine-oak woodlands. The wash has higher prey density and allows tree lizards to be active at their preferred body temperature for longer than the upland habitat; tree lizards prefer and occur at higher densities in the wash habitat (M'Closkey et al. 1990, Chapter 1, this study).

I surveyed each plot ten times between 1 May 2015 and 31 July 2016. During each survey, I searched the entire plot at least three times and captured all encountered tree lizards and striped plateau lizards. I recorded the location of each lizard with a handheld GPS unit (accuracy ± 3 m), and measured perch height (± 5 cm) and habitat type (wash or upland) where lizards were initially located. Within four hours of capture, I gave lizards a unique mark on their ventral side with heat-branding by a medical cauterizer (Ekner et al. 2011) and measured snout-vent length (SVL) with calipers (± 0.1 mm). In control plots, I released all lizards at their capture location the same day. In removal plots, I released all lizards at their capture location the same day for the first three surveys (before removal; 01-May-2015 to 20-Jun-2015) and then for the next seven surveys (23-Jun-2015 to 05-Aug-2015 and 08-May-2016 to 27-Jul-2016) I released all striped plateau lizards 300 – 500 m away on the same day. I did not recapture any displaced striped plateau lizards in any of the plots.

Striped plateau lizard abundance

To test whether the removal treatment actually reduced the abundance of striped plateau lizards, I estimated population sizes with open population mark-recapture models using the *RMark* package (Laake 2013) to access the program MARK (White and Burnham 1999) in R (R Core Team 2014). I used the POPAN formulation (Schwarz and Arnason 1996) of the Jolly-Seber model (Jolly 1965, Seber 1965) to estimate four parameters with maximum likelihood on lizard recapture histories: detection probability (p), monthly survival (ϕ), super-population size ($\hat{N}$), and the probability of new individuals from $\hat{N}$ entering the population (*pent*). I started with a general model where p varied with plot, and ϕ varied with treatment (control or removal) and time (before removal, after removal year one, between breeding seasons, and after removal year two; Supplementary information: Figure 4-S3). Although there were no capture events between the breeding seasons, monthly survival could have differed between the first breeding season and the period between the two breeding seasons. Therefore, I included separate estimates of survival during this period. The general model had distinct estimates of $\hat{N}$ for each plot and distinct estimates of *pent* for each treatment and time period. I tested the goodness of fit of the general model with the variance inflation factor ($\hat{c}$) estimated using: bootstrapping, the median $\hat{c}$ method, and the Fletcher method (Lebreton et al. 1992, Fletcher 2012) on the analogous Cormack-Jolly-Seber models (Cormack 1989) estimating survival and detection probability. To be conservative regarding the fit of the general models, I adjusted $\hat{c}$ to be the highest estimate of the three methods used for each site. I fit all possible subsets of the general model and compared models with $QAIC_c$ (Burnham and Anderson 2002). I model-averaged parameter predictions across the most supported models ($\Delta QAIC_c < 4$, compared to the most supported model) based on their relative support to account for model uncertainty (Burnham and Anderson 2002, Cade 2015).

I calculated abundance at each survey with the model-averaged parameter predictions. To ensure that the treatment actually reduced striped plateau lizard abundance, I calculated their abundance at the beginning of the experiment, the end of the first summer, and the end of the second summer at each plot. I fit linear mixed-effects models with the *lme4* package (Bates et al. 2014) where I used abundance as the response variable and time (before removal, after removal year one, and after removal year two), treatment (control or removal), and the interaction between time and treatment as fixed effects. I included random intercepts for each plot to account for different initial abundances.

To quantify habitat selection in striped plateau lizards, I used isodar analyses (Morris 1988). I constructed isodars predicting the density of lizards in the wash habitat based on the density of lizards in the upland habitat with geometric mean regression in the *lmodel2* package (Legendre 2014). Isodars were constructed for striped plateau lizards in control plots before and after the removal. This allowed me to test whether striped plateau lizard habitat selection shifted during the experiment and to test whether striped plateau lizards preferred the same habitat as ornate tree lizards. I assigned lizards to a habitat based on their mean coordinates before and after removal of striped plateau lizards. The mean distance between captures for all lizards was 11 m. Therefore, I assigned individuals to the wash habitat if their mean coordinates were less than 11 m from the wash. I used the same distance (11 m) for habitat assignment in both species because mean distances between captures were similar for ornate tree lizards (10 m) and for striped plateau lizards (12 m) and so that the area of each habitat type was the same for both species. This habitat assignment assumes that lizards with home ranges overlapping the wash have access to the food and thermal resources in that habitat. My habitat assignment also assumes that home ranges are approximately circular and that the mean coordinates accurately represent space use. I calculated density for each plot by dividing the number of striped plateau lizards in a habitat by the area of the habitat. The habitat areas accounted for the buffer distance (11 m) used for habitat assignment.

Habitat selection

To test the prediction that ornate tree lizard habitat selection changed after removal of striped plateau lizards, I used four metrics: the relative density in each habitat analyzed with isodars (Morris 1988), the probability of switching habitats, the distance travelled between captures, and the perch height. I constructed isodars predicting the density of ornate tree lizards in the wash habitat based on the density of ornate tree lizards in the upland habitat with geometric mean regression using the same methods implemented for striped plateau lizards. I compared the 95% confidence intervals of the intercepts and slopes for treatment plot ornate tree lizard isodars before and after the removal of striped plateau lizards. If the confidence intervals for the slope and intercept of the isodars do not overlap, then habitat selection changed after the removal of striped plateau lizards. I assigned ornate tree lizards to a habitat based on their mean coordinates before and after removal of striped plateau lizards with the same distance as above (11 m). I calculated density for each plot by dividing the number of ornate tree lizards in a habitat by the area of the habitat.

To estimate the probability of habitat switching by ornate tree lizards, I used multi-state mark-recapture models (Nichols and Kendall 1995) where lizards could transition between habitats (upland and wash). If ornate tree lizards in removal plots changed their habitat use, they would be more likely to switch habitats than lizards in control plots, especially towards the higher quality wash habitat. Multi-state models estimate three parameters, S (the probability a lizard survives and remains in the same habitat), Ψ (the probability that a lizard transitions between states, in this case habitats), and p (the probability that a lizard is detected during a capture event). I used a general model where S was estimated for each treatment and time period (before removal, after removal year one, between breeding seasons, and after removal year two), Ψ was estimated for each sex, treatment, time period, and habitat, and p was estimated for each habitat. I constructed all possible subsets of the general model and ranked them based on AIC_c to determine the most supported model (Burnham and Anderson 2002). I compared model-averaged predicted estimates of Ψ based on well-supported models ($\Delta AIC_c < 4$, compared to the most supported model) to test whether Ψ was higher in removal plots.

As another metric of how removal of striped plateau lizards affected ornate tree lizard space use, I compared the mean distance travelled between captures. I averaged the linear distance between capture locations for lizards caught at least twice, with at least one capture after the removal began (n = 68), and used an ANOVA with sex, treatment, and their interaction as predictor variables. The mean distance between capture locations did not increase with the number of captures ($F = 0.005$, df = 1, 66, $P = 0.98$, $R^2 < 0.01$).

To test whether microhabitat use was affected by interspecific competition, I analyzed perch heights using a linear mixed-effects model. Perch height (log-transformed) was the response variable and sex, treatment (control or removal), time period (before, after removal in year one, and after removal in year two), and the interaction between treatment and time period were fixed effects. I included lizard identity, nested within plot, as a random effect because of possible differences in the height of perch sites between plots and repeated captures of lizards.

Fitness proxies

To test the prediction that removing striped plateau lizards should increase the fitness of ornate tree lizards, I used apparent survival and individual growth rate. To estimate survival, I fit

Jolly-Seber mark-recapture models to ornate tree lizard capture histories with the same general model used for striped plateau lizards (Supplementary information: Figure 4-S3). I compared model-averaged apparent monthly survival estimates between control and removal plots after removal of striped plateau lizards during the first and second year of the experiment.

To calculate growth rate, I divided the difference in SVL by the number of days elapsed since the lizard was last captured. I adjusted time elapsed to remove winter days when lizards were unlikely to grow (1-Nov-2015 to 1-Apr-2016; Dunham 1982). Most ornate tree lizard growth occurs in the first year after birth, thus I restricted growth analyses to yearlings. I classified lizards as yearlings when their initial SVL was smaller than the minimum size of a lizard found in 2016 that was known to have been alive in 2015 (4.58 cm for females, 4.75 cm for males). Individuals recaptured several times were assigned one growth rate, and growth rates were only used when the interval between captures was greater than 14 days. I compared growth rates using ANOVA with sex, treatment, and the interaction between sex and treatment as fixed effects.

Abundance

To test the prediction that removing striped plateau lizards increased the abundance of ornate tree lizards, I analyzed the estimated abundance of tree lizards using linear mixed-effects models. Abundances were derived from Jolly-Seber POPAN mark-recapture models, as described above. The fixed effects were time (before removal, after removal year one, and after removal year two), treatment (control or removal), and the interaction between time and treatment. I included random intercepts for each plot to account for different initial abundances.

Results

Striped plateau lizard abundance

I captured 193 striped plateau lizards 434 times in control plots and 235 striped plateau lizards 333 times in removal plots. The most-supported Jolly-Seber mark-recapture models are summarized in Table 4-S2 (Supplementary information). Plots varied in their initial abundance of striped plateau lizards, but abundance was significantly reduced on experimental plots after removal (Figure 4-1) as indicated by the fixed effect of time (F = 5.02, df = 1, 12, $P = 0.026$), treatment (F = 9.29, df = 1, 8, $P = 0.01$), and the interaction between time and treatment (F = 7.94, df = 1, 12, $P = 0.006$).

The isodars for striped plateau lizards in control plots did not change during the experiment (Supplementary information: Table 4-S3, Figure 4-S4). Striped plateau lizards preferred the wash habitat and density was higher in the wash than the upland habitat.

Ornate tree lizard habitat selection

I captured 98 ornate tree lizards 171 times in control plots and 93 ornate tree lizards 164 times in removal plots. The isodars for tree lizards in removal plots before and after the removal of striped plateau lizards overlapped in intercepts and in slopes (Table 4-1; Supplementary information: Figure 4-S5). Therefore, the relative density of lizards in the wash habitat and in the upland habitat did not change after the removal of striped plateau lizards. Tree lizard isodars in the control plots before and after the removal also overlapped in confidence intervals (Supplementary information: Table 4-S4).

All the well-supported mark-recapture models (Supplementary information: Table 4-S5) had higher transition probabilities for tree lizards in removal plots compared to control plots. Tree lizards were more likely to switch habitats in removal plots than in control plots, although transition probabilities were similar for lizards moving from wash habitat to upland and from upland habitat to wash habitat (Figure 4-2). Therefore, ornate tree lizards moved between habitats more in plots where striped plateau lizards were removed than in control plots, but movement was not more frequent towards the preferred wash habitat.

Mean distance between capture locations was higher in males than in females (F = 11.67, df = 1, 65, $P = 0.001$) and higher in removal plots than in control plots (F = 6.10, df = 1, 65, $P = 0.016$; Figure 4-3). There was no interaction between sex and treatment (F = 2.15, df = 1, 65, $P = 0.15$). Based on Tukey's pairwise comparisons, males in removal plots moved more than males in control plots and than females in control and in removal plots (all $P < 0.05$). Therefore, the increased probability of ornate tree lizards switching habitats after the removal of striped plateau lizards likely arose because males moved longer distances in removal plots.

Ornate tree lizard perch height increased by a mean of 18 cm in the second period of the experiment (after removal year one; F = 3.57, df = 2, 278, $P = 0.03$), but did not differ between control and removal plots (F = 0.53, df = 1, 6, $P = 0.49$) and was unaffected by the interaction between time-period and treatment (F = 0.14, df = 1, 275, $P = 0.87$; Figure 4-4). Males perched an estimated 15 cm higher than females (F = 7.04, df = 1, 117, $P = 0.009$).

Ornate tree lizard fitness proxies

During the first year of the experiment, ornate tree lizard monthly survival probabilities were similar in control (0.77 ± 0.12) and in removal (0.75 ± 0.13) plots after striped plateau lizards were removed. During the second year of the experiment, ornate tree lizard monthly survival probabilities were also similar in control (0.88 ± 0.07) and in removal (0.87 ± 0.08) plots where striped plateau lizards were removed. The nine most-supported Jolly-Seber models (cumulative weight = 0.56; Supplementary information: Table 4-S6) did not include differences in survival between removal and control plots.

There was no effect of treatment (F = 0.36, df = 1, 6, $P = 0.57$) or the interaction between treatment and sex (F = 0.52, df = 1, 10, $P = 0.49$) on yearling ornate tree lizard growth rates. Yearling female ornate tree lizards grew faster than males (F = 21.42, df = 1, 11, $P < 0.001$). Including growth rates of all individuals did not change my conclusions regarding the effect of treatment (F = 0.31, df = 1, 5, $P = 0.60$) or of the interaction between treatment and sex (F = 2.51, df = 1, 72, $P = 0.12$) on growth rate. Therefore, ornate tree lizards grew at similar rates in control plots and in plots where striped plateau lizards were removed.

Ornate tree lizard abundance

The well-supported Jolly-Seber models for ornate tree lizards are presented in Table 4-S6 (Supplementary information). Ornate tree lizard abundance did not differ between control and removal plots (F = 0.16, df = 1, 6, $P = 0.70$). Ornate tree lizard abundance decreased during the experiment in all plots (F = 7.61, df = 2, 12, $P = 0.007$) with an estimated decrease in abundance of 2 lizards in year two compared to year one ($P = 0.002$). There was an interaction between time and treatment (F = 13.78, df = 2, 12, $P < 0.001$, Figure 4-5) on ornate tree lizard abundance, but the effect was not in the predicted direction of increased abundance in plots where striped plateau lizards were removed. Ornate tree lizard abundance in removal plots decreased after removal of striped plateau lizards more than in control plots during the second year of the experiment, but the effect size was small (estimated decrease of 3 individuals more than in control plots). The abundance of ornate tree lizards did not increase in plots where striped plateau lizards were removed.

Discussion

I successfully depressed the density of striped plateau lizards to almost zero in both summers (Figure 4-1). Therefore, the treatment created the desired effect of reducing potential interspecific competition between ornate tree lizards and striped plateau lizards. Depressing density in wild populations is useful for testing hypotheses about the effects of competition because it preserves natural variation in abundance and in environmental conditions of the focal species, compared to enclosure experiments that often have unnatural densities or resource levels. Furthermore, competitive effects are typically stronger in enclosures than in free-ranging organisms (Schoener 1983, Gurevitch et al. 1992).

Ornate tree lizard habitat selection did not shift after removal of striped plateau lizards because isodars before and after the removal were the same. The isodars for striped plateau lizards suggest they also prefer the wash habitat, but ornate tree lizard habitat density did not respond to a reduction in striped plateau lizard density. While some species adjust habitat selection based on the density of other species (Mönkkönen et al. 1999, Tarjuelo et al. 2016), other species select habitat based on food abundance (Kielty et al. 1996), conspecific density (Stamps 1991), or predator cues (Downes and Shine 1998). The cues used by ornate tree lizards for habitat selection are unknown, but they did not respond to the decreased density of striped plateau lizards, possibly because there is no large fitness cost associated with being in the same habitat.

Ornate tree lizard habitat selection was similar after the removal of a potential competitor, but space use changed. Male ornate tree lizards from removal plots moved longer distances between captures than individuals from control plots. The change in space use was also evident from the increased probability that ornate tree lizards transition between wash and upland habitats in removal plots compared to control plots. The increase in distance moved by male ornate tree lizards after the removal of striped plateau lizards is likely because the cost of defending an area had decreased after the removal (Trombulak 1985), and provides some evidence that these two species are competing, at least for space. Both ornate tree lizards and striped plateau lizards defend territories against intruders (Rose 1981, M'Closkey et al. 1987b), so the cost of defending an area should increase with the density of lizards. The relative densities of ornate tree lizards in the wash habitat and in the upland habitat did not change following the removal of the competitor, but there is some evidence that ornate tree lizards and striped plateau lizards compete for resources because ornate tree lizards moved further between captures (for males only) and switched habitats more frequently in plots where striped plateau lizards were removed.

The removal of striped plateau lizards did not cause an increase in ornate tree lizard survival, growth rate, or abundance. Since I successfully reduced the abundance of striped plateau lizards in removal plots, the lack of fitness response by ornate tree lizards could be because the experiment did not last long enough to observe changes in abundance and fitness, or because competition between the two species is not strong. It seems unlikely that my experiment was too short because striped plateau lizard abundance rebounded between years and because there was a large pool of potential immigrants outside my experimental plots. The recovery of striped plateau lizard populations between years indicates that populations had sufficient time to increase from recruitment and immigration during the experiment. Thus, it would have been possible for large differences in abundance of ornate tree lizards to occur during the experiment if competition with striped plateau lizards was strong. Therefore, it is more likely that the lack of a response in ornate tree lizard fitness and abundance is because competition with striped plateau lizards was weak during my experiment.

Factors such as predation, parasitism, intraspecific competition, and abiotic conditions can modify the strength of interspecific competition (Connell 1983, Sinclair 1985, Dunson and Travis 1991) because they can depress the abundance of potentially competing species to levels where there is no longer strong competition. Although I did not directly measure predation pressure, annual survival was low (approximately 0.15 by extrapolating monthly survival rates to a year) in ornate tree lizards and this could be because of high predation, high disease risk, or low resource levels. It is plausible that there was some compensatory effect of increased predation on ornate tree lizards in plots where I removed striped plateau lizards, but the data I collected do not allow me to test this hypothesis. Quantifying predation risk is challenging because predation events are rare and some types of lizard predators (e.g., snakes such as *Masticophis bilineatus* and *Crotalus lepidus*) are difficult to detect.

Environmental conditions, such as precipitation, likely have a strong effect on lizard populations because insect biomass increases with precipitation (Janzen and Schoener 1968). Also, lizard survival rates are frequently lower during drought years (Smith and Ballinger 1994b). For example, Smith (1981) only detected effects of competition between ornate tree lizards and striped plateau lizards in an extreme drought year when arthropod prey were very limited. The two years of my experiment had annual precipitation (69 cm and 55 cm) above the 30-year average (51 cm ± 2.6 cm) for the area so insect prey abundance was unlikely to be depressed (National Oceanic and Atmospheric Administration weather station USC00026716 available at http://www.ncdc.noaa.gov/oa/climate/stationlocator.html). Interspecific competition is predicted to be high during times of either very high or very low resources (Goldberg and

Novoplansky 1997). Therefore, it is possible that in most years competition between ornate tree lizards and striped plateau lizards is not strong enough to have detectable effects on the fitness and abundance of ornate tree lizards.

The lack of evidence for competitive effects on fitness and abundance of ornate tree lizards could also be explained by the partitioning of resources. Species that compete for resources can diverge through ecological character displacement and eventually this reduces competition (Schluter and McPhail 1992, Stuart and Losos 2013). Therefore, it is possible that ornate tree lizards and striped plateau lizards have diverged in resource use enough that they no longer compete strongly with one another. It would be useful to compare diets between these species to determine if there is significant prey overlap, as observed between striped plateau lizards and Yarrow’s spiny lizard (*Sceloporus jarrovii*) in the same region (Watters 2008). My experiment, however, was designed to measure the effect of interspecific competition on habitat selection, fitness, and abundance, not to test whether species had undergone ecological character displacement.

Competition between species may not have large effects on the fitness and abundance of many lizard communities. Several field experiments have manipulated density of one or more lizard species and found negligible or no effects of interspecific competition on density and fitness of other lizard species (Dunham 1980, Smith 1981, Tinkle 1982). Furthermore, environmental gradients, not interspecific competition, explain patterns in lizard species richness in Australia (Powney et al. 2010). However, field experiments with arboreal lizard communities have found strong support for the role of competition in habitat use (Pacala and Roughgarden 1982, Harmon et al. 2007) and abundance (Leal et al. 1998). It appears that interspecific competition plays a minor role in dictating the habitat selection and abundance of terrestrial lizard communities in North America, but most field experiments have examined only a handful of potentially competing species.

I found evidence that competition between ornate tree lizards and striped plateau lizards affected the distance moved by male ornate tree lizards and the rate at which ornate tree lizards switched between two habitats. However, there was no evidence that interspecific competition decreased the fitness and abundance of ornate tree lizards over a period of one year. Therefore, environmental conditions, intraspecific competition, or other factors are likely more important in dictating the distribution of ornate tree lizards between habitats. For instance, it is possible that abiotic factors keep the abundances of both species below levels at which interspecific competition becomes strong enough to affect fitness and abundance.

Table 4-1. Parameter estimates and confidence intervals for isodars of ornate tree lizards (*Urosaurus ornatus*) in the Chiricahua Mountains, Arizona, USA. Isodars predicted density in the wash habitat based on density in the upland habitat and separate isodars were constructed for removal plots before and after the removal of striped plateau lizards (*Sceloporus virgatus*). Major axis regression model parameters can have inverted confidence intervals when confidence interval lower bound line passes through quadrant three or when the upper bound confidence interval line passes through quadrant two (Jolicoeur 1973).

Parameter	**Type**	**Estimate**	**2.50%**	**97.5%**
Intercept	Before removal	2.59	-152.2	26.9
	After removal	49.2	34.6	16.43
Slope	Before removal	1.8	0.81	8.13
	After removal	-1.8	2.02	-0.09

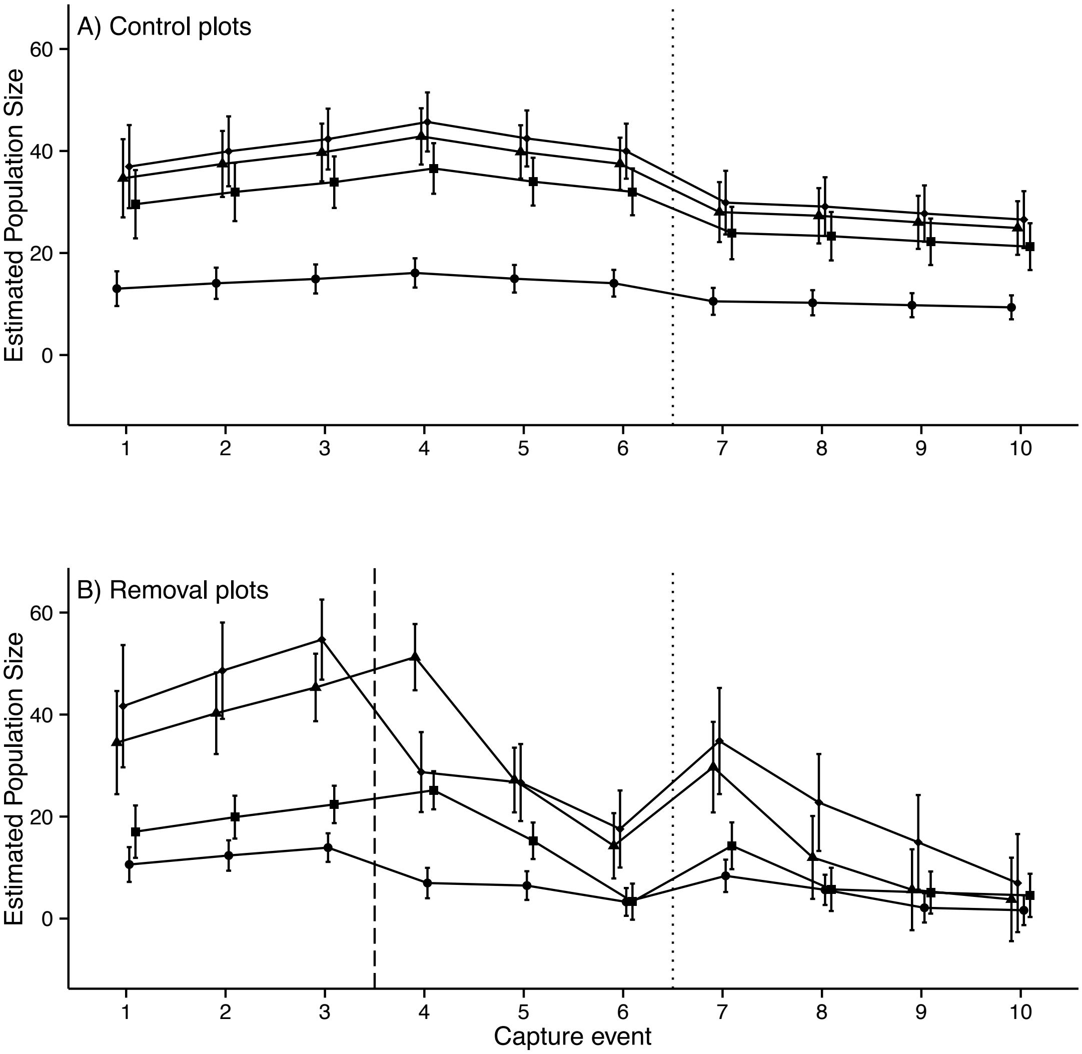

Figure 4-1. Estimated abundance (± 1 SE) of striped plateau lizards (*Sceloporus virgatus*) in the Chiricahua Mountains of Arizona, USA, based on Jolly-Seber mark-recapture models remained stable in A) four control plots and decreased in B) four experimental plots where lizards were removed after the third capture event. The vertical dashed line represents the start of the removal of striped plateau lizards and the vertical dotted lines represent the winter. All plots were 50 m by 50 m. Symbols (diamonds, triangles, squares, circles) correspond to paired control-removal plots.

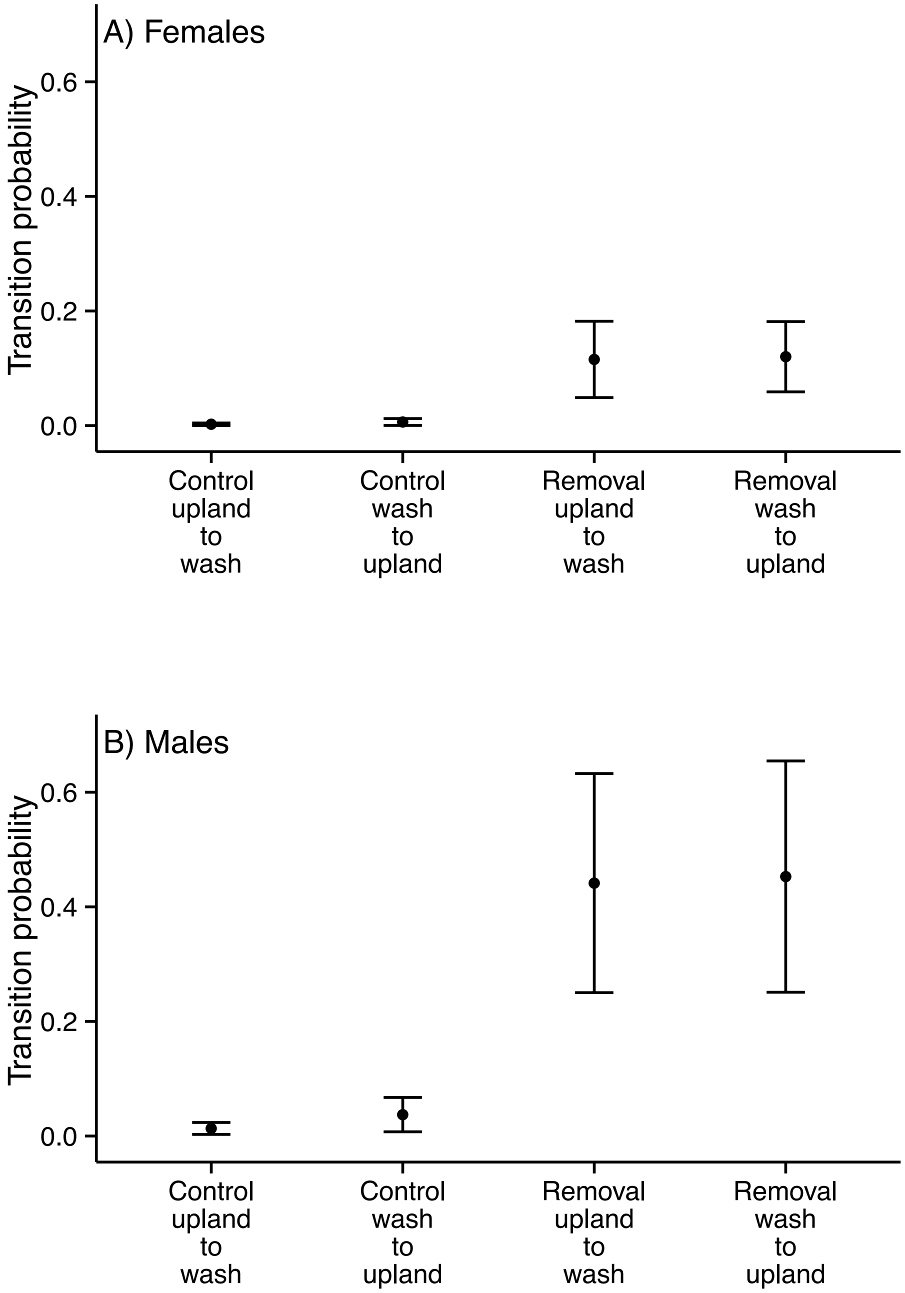

Figure 4-2. A) Female and B) male ornate tree lizards (*Urosaurus ornatus*) in the Chiricahua Mountains of Arizona, USA were more likely to transition between wash and upland habitats (model averaged Ψ ±1 SE) in plots where striped plateau lizards were removed (n = 4) than in control plots (n = 4).

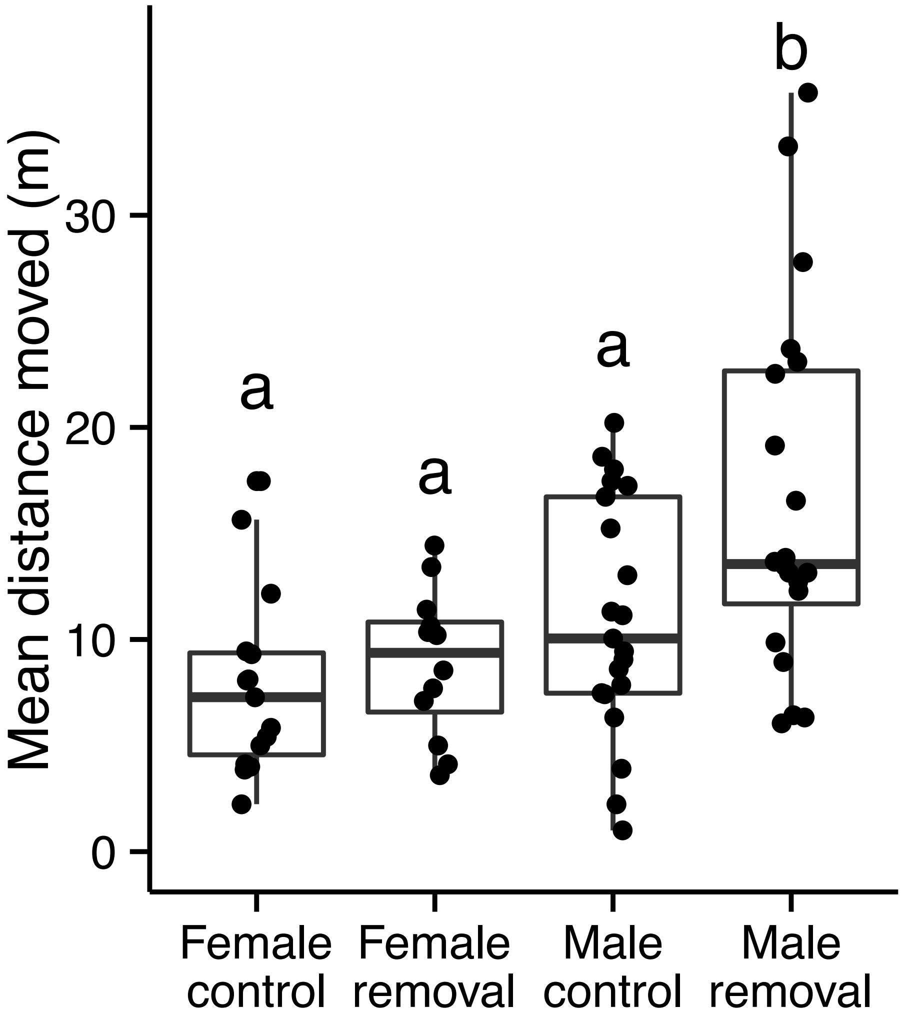

Figure 4-3. Male ornate tree lizards from plots where striped plateau lizards were removed moved longer mean distances between capture locations than males from control plots and than females in the Chiricahua Mountains of Arizona, USA ($n = 68$). Horizontal lines represent group medians, and the box limits represent the interquartile ranges. Letters (a, b) correspond to differences between groups in Tukey's pairwise comparisons ($P < 0.05$).

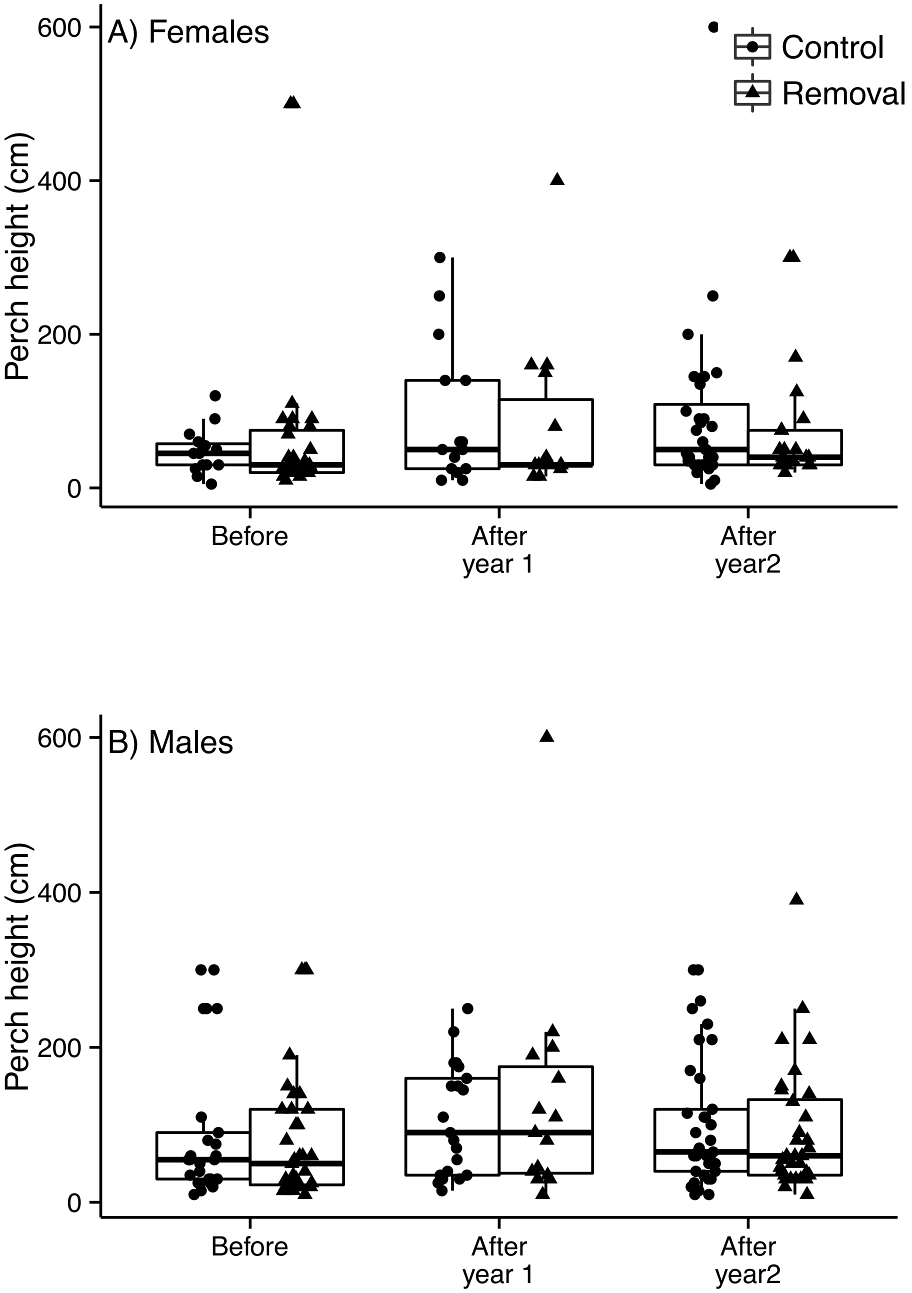

Figure 4-4. Perch heights of A) female (n = 130) and B) male (n = 165) ornate tree lizards in the Chiricahua Mountains of Arizona, USA did not differ between control plots (filled circles) and plots where striped plateau lizards were removed (filled triangles). Horizontal lines represent group medians, and the box limits represent the interquartile ranges.

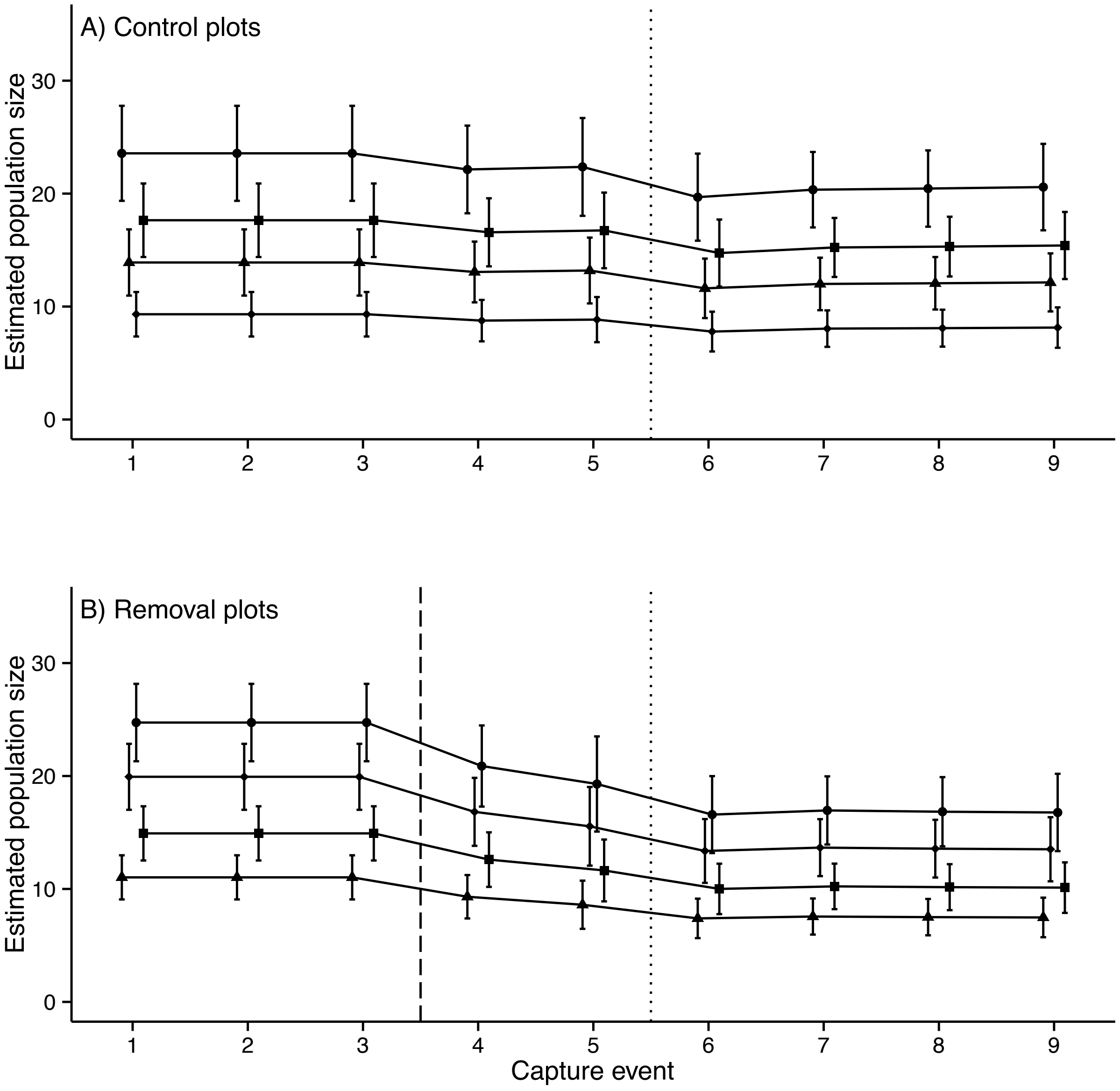

Figure 4-5. Estimated abundance (± 1 SE) of ornate tree lizards in the Chiricahua Mountains of Arizona, USA, based on Jolly-Seber mark-recapture models remained stable in A) four control plots, and B) four experimental plots where striped plateau lizards were removed after the third capture event. The vertical dashed line represents the start of the removal of striped plateau lizards and the vertical dotted lines represent the winter. All plots were 50 m by 50 m. Symbols (diamonds, triangles, squares, circles) correspond to paired control-removal plots.

Supplementary information for Chapter 4

A) Ornate tree lizard

B) Striped plateau lizard

Figure 4-S1. I studied competition between A) ornate tree lizards (*Urosaurus ornatus*) and B) striped plateau lizards (*Sceloporus virgatus*; photo by Stacey Weiss) in the Chiricahua Mountains of Arizona, USA.

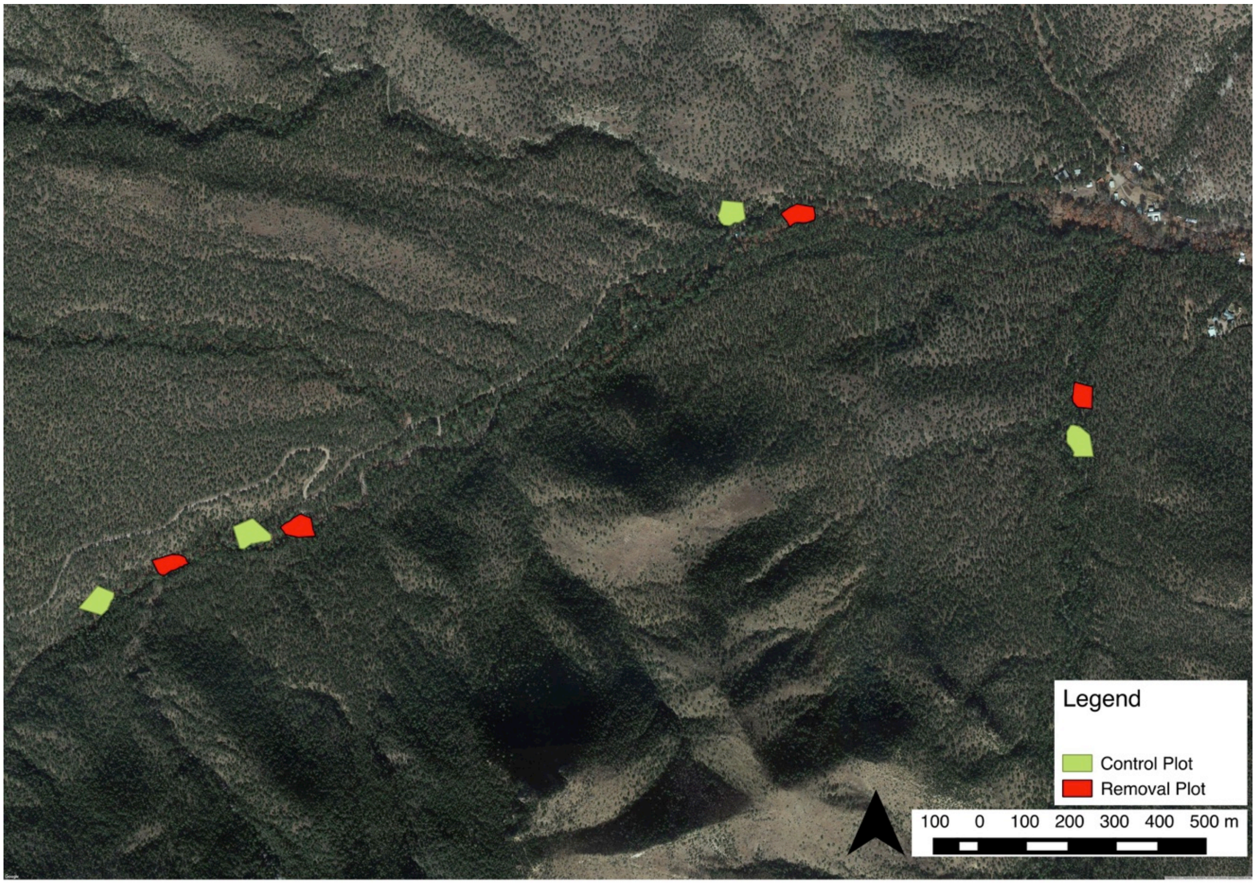

Figure 4-S2. Location of eight plots for studying competition between ornate tree lizards and striped plateau lizards in the Chiricahua Mountains of Arizona, USA.

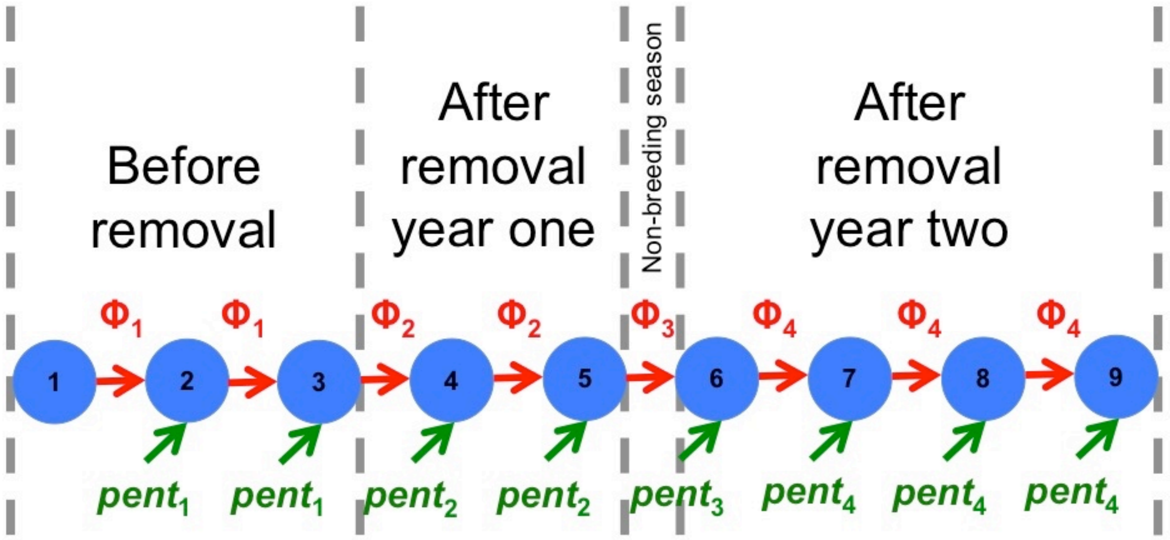

Figure 4-S3. The parameter design of Jolly-Seber mark-recapture models for the abundance of striped plateau lizards and ornate tree lizards. Apparent survival (Φ) and probability of new individuals entering the population by immigration and birth (*pent*) varied by four time periods (divided by gray dashed lines) over the nine capture events (blue circles).

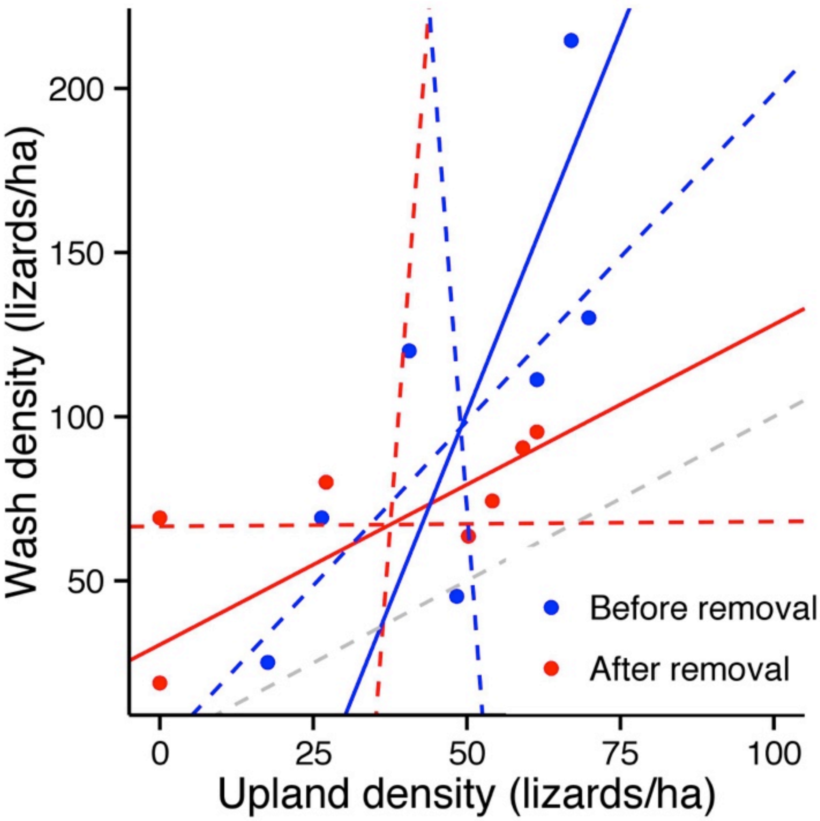

Figure 4-S4. Isodar plot of striped plateau lizard density in the wash and upland habitat in four control plots before and after the treatment began in the Chiricahua Mountains of Arizona, USA. The dashed gray line represents no habitat selection and equal density in both habitats. Solid lines are the geometric regression line for each time period, and the coloured dashed lines represent 95% confidence intervals.

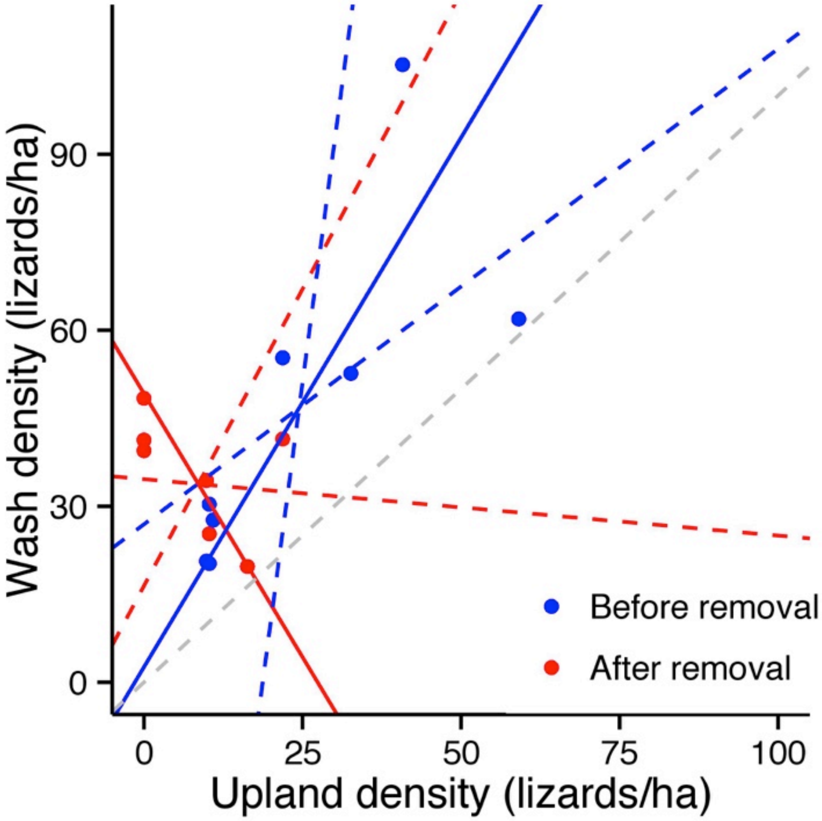

Figure 4-S5. Isodar plot of ornate tree lizard density in the wash and upland habitat in four removal plots before and after the removal of striped plateau lizards in the Chiricahua Mountains of Arizona, USA. The dashed gray line represents no habitat selection and equal density in both habitats. Solid lines are the geometric regression line for each time period, and the coloured dashed lines represent 95% confidence intervals.

Table 4-S1. Coordinates of study sites (UTM zone 12R) for measuring competition between ornate tree lizards (*Urosaurus ornatus*) and striped plateau lizards (*Sceloporus virgatus*) in the Chiricahua Mountains of Arizona, USA.

Site	**Treatment**	**E**	**N**
1	Removal	667762	3528146
2	Control	667674	3528092
3	Removal	667504	3528027
4	Control	667326	3527952
5	Removal	668885	3528827
6	Control	668778	3528854
7	Control	669549	3528381
8	Removal	669551	3528479

Table 4-S2. The most supported Jolly-Seber mark-recapture models for abundance of striped plateau lizards in removal and in control plots in the Chiricahua Mountains of Arizona, USA. The variance inflation factor has been set to 3.94. k = number of parameters in a model; QAIC_c = quasi-likelihood Akaike's information criterion for a model; $\Delta\mathrm{QAIC}_c$ = difference in QAIC_c between a model and the top-ranked model; ω = Akaike weight for a model.

Model	**k**	$\mathbf{QAIC_c}$	$\mathbf{\Delta QAIC_c}$	**ω**
Φ(~1)*p*(~1)*pent*(~time + treatment)$\hat{N}$(~plot)	15	492.86	0.00	0.20
Φ(~1)*p*(~1)*pent*(~time)$\hat{N}$(~plot)	14	493.67	0.81	0.13
Φ(~1)*p*(~learn)*pent*(~time + treatment)$\hat{N}$(~plot)	16	493.93	1.07	0.11
Φ(~1)*p*(~hab)*pent*(~time + treatment)$\hat{N}$(~plot)	16	494.24	1.38	0.10
Φ(~1)*p*(~learn)*pent*(~time)$\hat{N}$(~plot)	15	494.65	1.79	0.08
Φ(~1)*p*(~hab)*pent*(~time)$\hat{N}$(~plot)	15	495.09	2.23	0.06
Φ(~1)*p*(~hab + learn)*pent*(~time + treatment)$\hat{N}$(~plot)	17	495.33	2.47	0.06
Φ(~treatment)*p*(~1)*pent*(~time + treatment)$\hat{N}$(~plot)	16	495.69	2.83	0.05
Φ(~treatment)*p*(~1)*pent*(~time)$\hat{N}$(~plot)	15	495.78	2.92	0.05
Φ(~treatment)*p*(~learn)*pent*(~time + treatment)$\hat{N}$(~plot)	17	496.01	3.16	0.04
Φ(~1)*p*(~hab + learn)*pent*(~time)$\hat{N}$(~plot)	16	496.08	3.22	0.04
Φ(~treatment)*p*(~hab)*pent*(~time + treatment)$\hat{N}$(~plot)	17	496.28	3.42	0.04
Φ(~time)*p*(~1)*pent*(~time + treatment)$\hat{N}$(~plot)	18	496.74	3.88	0.03
Φ(~treatment)*p*(~learn)*pent*(~time)$\hat{N}$(~plot)	16	496.77	3.91	0.03

Table 4-S3. Parameter estimates and confidence intervals for isodars of control plot striped plateau lizards in the Chiricahua Mountains, Arizona, USA. Isodars predicted density in the wash habitat based on density in the upland habitat and separate isodars were constructed for control plots before and after the period where striped plateau lizards were removed in treatment plots.

Parameter	**Type**	**Estimate**	**2.50%**	**97.5%**
Intercept	Before removal	-131.41	1311.86	-1.40
	After removal	30.52	-873.65	66.58
Slope	Before removal	4.65	2.00	-24.79
	After removal	0.98	-10.34	49.47

Table 4-S4. Parameter estimates and confidence intervals for isodars of control plot ornate tree lizards in the Chiricahua Mountains, Arizona, USA. Isodars predicted density in the wash habitat based on density in the upland habitat and separate isodars were constructed for control plots before and after the removal of striped plateau lizards.

Parameter	**Type**	**Estimate**	**2.50%**	**97.5%**
Intercept	Before removal	98.95	53.70	-431.59
	After removal	82.27	22.40	0.84
Slope	Before removal	-2.54	16.12	-0.95
	After removal	-1.89	0.96	0.21

Table 4-S5. The most supported multi-state mark-recapture models for ornate tree lizards in removal and in control plots in the Chiricahua Mountains of Arizona, USA. k = number of parameters in a model; AIC$_c$ = Akaike's information criterion for a model; ΔAIC$_c$ = difference in AIC$_c$ between a model and the top-ranked model; ω = Akaike weight for a model.

model	**k**	**AIC$_c$**	**ΔAIC$_c$**	**ω**
S(~time)*p*(~habitat)Ψ(~sex + treatment)	8	820.09	0.00	0.24
S(~time)*p*(~habitat)Ψ(~sex + treatment * habitat)	10	820.43	0.35	0.20
S(~time)*p*(~habitat)Ψ(~sex + treatment + habitat)	9	821.81	1.72	0.10
S(~time + treatment)*p*(~habitat)Ψ(~sex + treatment)	9	822.18	2.09	0.09
S(~time)*p*(~habitat)Ψ(~sex + time + treatment)	10	822.26	2.17	0.08
S(~time + treatment)*p*(~habitat)Ψ(~sex + treatment * habitat)	11	822.59	2.50	0.07
S(~1)*p*(~habitat)Ψ(~sex + treatment)	6	822.70	2.61	0.07
S(~1)*p*(~habitat)Ψ(~sex + treatment * habitat)	8	822.93	2.85	0.06
S(~time)*p*(~habitat)Ψ(~sex + time + treatment * habitat)	12	823.29	3.20	0.05
S(~time + treatment)*p*(~habitat)Ψ(~sex + treatment + habitat)	10	823.83	3.75	0.04

Table 4-S6. The most supported Jolly-Seber mark-recapture models for abundance of ornate tree lizards in removal and in control plots in the Chiricahua Mountains of Arizona, USA. The variance inflation factor has been set to 1.07. k = number of parameters in a model; QAIC_c = quasi-likelihood Akaike's information criterion for a model; ΔQAIC_c = difference in QAIC_c between a model and the top-ranked model; ω = Akaike weight for a model.

model	**k**	**QAIC_c**	**ΔQAICc**	**ω**
Φ(~time)*p*(~1)*pent*(~time * treatment)$\hat{N}$(~plot)	18	1046.39	0.00	0.09
Φ(~time)*p*(~hab)*pent*(~time)$\hat{N}$(~plot)	16	1046.99	0.60	0.07
Φ(~time)*p*(~hab)*pent*(~time * treatment)$\hat{N}$(~plot)	19	1047.08	0.69	0.06
Φ(~1)*p*(~hab)*pent*(~time)$\hat{N}$(~plot)	14	1047.11	0.72	0.06
Φ(~time)*p*(~1)*pent*(~time)$\hat{N}$(~plot)	15	1047.18	0.79	0.06
Φ(~time)*p*(~1)*pent*(~time + treatment)$\hat{N}$(~plot)	16	1047.31	0.92	0.06
Φ(~1)*p*(~1)*pent*(~time)$\hat{N}$(~plot)	13	1047.42	1.03	0.05
Φ(~time)*p*(~hab)*pent*(~time + treatment)$\hat{N}$(~plot)	17	1047.48	1.09	0.05
Φ(~time + treatment)*p*(~hab)*pent*(~time)$\hat{N}$(~plot)	17	1047.86	1.47	0.04
Φ(~treatment)*p*(~hab)*pent*(~time)$\hat{N}$(~plot)	15	1047.96	1.58	0.04
Φ(~time + treatment)*p*(~1)*pent*(~time * treatment)$\hat{N}$(~plot)	19	1048.24	1.85	0.04
Φ(~time + treatment)*p*(~1)*pent*(~time)$\hat{N}$(~plot)	16	1048.46	2.08	0.03
Φ(~treatment)*p*(~1)*pent*(~time)$\hat{N}$(~plot)	14	1048.62	2.23	0.03
Φ(~1)*p*(~1)*pent*(~time * treatment)$\hat{N}$(~plot)	16	1048.64	2.26	0.03
Φ(~time)*p*(~hab)*pent*(~treatment)$\hat{N}$(~plot)	15	1048.66	2.27	0.03
Φ(~time + treatment)*p*(~hab)*pent*(~time * treatment)$\hat{N}$(~plot)	20	1048.70	2.31	0.03
Φ(~1)*p*(~hab)*pent*(~time + treatment)$\hat{N}$(~plot)	15	1048.77	2.38	0.03
Φ(~1)*p*(~1)*pent*(~time + treatment)$\hat{N}$(~plot)	14	1048.87	2.48	0.03
Φ(~time + treatment)*p*(~hab)*pent*(~time + treatment)$\hat{N}$(~plot)	18	1048.95	2.56	0.03
Φ(~time)*p*(~1)*pent*(~treatment)$\hat{N}$(~plot)	14	1049.01	2.62	0.02
Φ(~time + treatment)*p*(~1)*pent*(~time + treatment)$\hat{N}$(~plot)	17	1049.11	2.72	0.02
Φ(~1)*p*(~hab)*pent*(~time * treatment)$\hat{N}$(~plot)	17	1049.15	2.76	0.02
Φ(~treatment)*p*(~hab)*pent*(~time + treatment)$\hat{N}$(~plot)	16	1049.94	3.55	0.02
Φ(~treatment)*p*(~1)*pent*(~time * treatment)$\hat{N}$(~plot)	17	1050.12	3.73	0.01
Φ(~time + treatment)*p*(~hab)*pent*(~treatment)$\hat{N}$(~plot)	16	1050.19	3.80	0.01
Φ(~treatment)*p*(~hab)*pent*(~time * treatment)$\hat{N}$(~plot)	18	1050.35	3.96	0.01

Φ(~treatment)*p*(~1)*pent*(~time + treatment)$\hat{N}$(~plot)	15	1050.38	3.99	0.01

General Conclusion

Overall, I demonstrate in my thesis the importance of intraspecific competition for resources in shaping fitness, abundance, and distribution between habitats in a terrestrial ectotherm, a group in which we may not expect strong density dependence because their populations could be more limited by their ability to process resources rather than their ability to harvest resources. I found that intraspecific competition for resources in ornate tree lizards (*Urosaurus ornatus*) limits mean fitness through its effect on survival (Chapter 1) and, in females, on growth (Chapter 2). Density-dependence is common in population abundance time series data (Brook and Bradshaw 2006), but detecting demographic effects from overcrowding, as I found in tree lizard populations, is stronger evidence of density-dependence (Osenberg et al. 2002). In addition, I found that competition for limited resources causes the habitat selection pattern to be density-dependent and follow the predictions of an ideal free distribution. This is in contradiction to work on snakes, where low thermal quality in one habitat caused habitat selection to be largely density-independent (Halliday and Blouin-Demers 2016). Furthermore, I demonstrate in my thesis that even though interspecific competition does affect how tree lizards use space (Chapter 4), its effect on abundance is small compared to that of intraspecific competition. My field experiment removing striped plateau lizards is one of the strongest tests to date of interspecific competition in lizards. Although I tested my hypotheses about density-dependent habitat selection in one study species, I believe my results have implications for many other species. Considering my results and those of previous studies on the effect of temperature on habitat selection (Halliday et al. 2015, Halliday and Blouin-Demers 2016), I hypothesize that the strength of density-dependent responses to resource limitation and habitat selection in ectotherms increases as environmental temperatures get closer to a species' preferred temperature range.

The evidence I found for density-dependent habitat selection is strong, but there are several limitations. First, I only studied one species and it is possible that ornate tree lizards are unique in some way and that generalizing to other ectotherms is thus inappropriate. Even among lizard species (> 4600 species), however, most species that are less than 100 g in mass are arthropod predators (Pough 1973) like tree lizards. These species are likely to vary in abundance due to differences in arthropod abundance. Therefore, I think my choice of study species is appropriate for generalizing to other lizards at the same trophic level. Second, one limitation of using natural variation in abundance to test for density-dependent responses in fitness proxies is that I cannot tease out the effect of population density from other possible site specific differences that cause a similar response. Because I found a linear effect of density on both survival and growth, however, it seems unlikely that sites varied linearly in some way that was not related to population density. The decline in survival and growth with increasing density could be caused by parasites rather than by competition for resources. Finally, I am limited to making inferences about population abundance and distribution from data collected over three field seasons. I think my conclusions can be generalized for this system at other times for two reasons. First, the three years I studied tree lizard ecology had close to average resource levels, using precipitation levels as a metric for limiting food abundance (Chapter 4). Second, tree lizards have a very short generation time and most individuals only survive to reproduce during one breeding season. Thus, my study covered three largely non-overlapping generations and resulting estimates of density and distribution between habitats. However, it is possible that patterns I detected during these years cannot be generalized to the system more broadly.

Future work could test the hypothesis that the strength of density-dependence in ectotherms depends on environmental temperatures. I propose two ways of doing this. First, by using a wide-ranging species and testing whether the strength of density-dependence within populations declines as temperatures depart from the species preferred temperature range. Second, a meta-analysis of published data on fitness proxies and abundance can test this hypothesis on a whole taxonomic group using environmental data to estimate relative thermal quality. Another fruitful direction of research arising from my thesis is to further investigate how within population variation in habitat selection affects population dynamics. I demonstrated that male tree lizards with different throat colours use space and habitat differently, and future research could investigate how the presence of multiple strategies affects population abundance. For example, studying a much higher number of populations and testing whether population abundance increases with the number of different strategies and throat colours that are present. Polymorphic species are predicted to have a wider niche (Forsman et al. 2008) and this could allow species to reach higher abundances than monomorphic species. The stochastic loss of morphs within populations appears to be common in polymorphic species (Eckert and Barrett 1992, Corl et al. 2010), thus providing an opportunity to study the effect of the number of habitat selection strategies on population dynamics.

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Appendix 1

Abstracts of additional publications completed during my Ph.D. that are not thesis chapters

J.E. Paterson and G. Blouin-Demers. 2017. Do ectotherms partition thermal resources? We still do not know. Oecologia 183: 337-345.

Partitioning of the niche space is a mechanism used to explain the coexistence of similar species. Ectotherms have variable body temperatures and their body temperatures influence performance and, ultimately, fitness. Therefore, many ectotherms use behavioral thermoregulation to avoid reduced capacities associated with body temperatures far from the optimal temperature for performance. Several authors have proposed that thermal niche partitioning in response to interspecific competition is a mechanism that allows the coexistence of similar species of ectotherms. We reviewed studies on thermal resource partitioning to evaluate the evidence for this hypothesis. In almost all studies, there was insufficient evidence to conclude unequivocally that thermal resource partitioning allowed species coexistence. Future studies should include sites where species are sympatric and sites where they are allopatric to rule out alternative mechanisms that cause differences in thermal traits between coexisting species. There is evidence of conservatism in the evolution of most thermal traits across a wide range of taxa, but thermal performance curves and preferred temperatures do respond to strong selection under laboratory conditions. Thus, there is potential for selection to act on thermal traits in response to interspecific competition. Nevertheless, more stringent tests of the thermal resource partitioning hypothesis are required before we can assess whether it is widespread in communities of ectotherms in nature.

J.E. Paterson and G. Blouin-Demers. 2017. Distinguishing discrete polymorphism from continuous variation in throat colour of tree lizards, *Urosaurus ornatus*. Biological Journal of the Linnean Society 121: 72-81.

Within population colour variation in animals is ubiquitous and can range from discrete polymorphism to continuous variation. Distinguishing discrete polymorphism from continuous variation can be challenging, and this hinders our ability to test hypotheses about colour variation. We tested whether throat colour variation in the ornate tree lizard [*Urosaurus ornatus* (*U. ornatus*); Baird & Girard, 1852] is discrete or continuous using photographs of 617 individuals from seven study sites in the Chiricahua Mountains of Arizona, USA. Using principal component analyses on ten colour variables derived from photographs, we found throat colour to be highly repeatable for both males and females. Cluster analyses suggested that there are different groups of individuals based on their throat colours in males and in females, but distinguishing between the groups was difficult due to significant overlap in colour. Therefore, it appears that there is a significant amount of continuous variation in both male and female tree lizard throat colours. We suggest quantifying trait variation before assuming a colour trait is discrete. By using numerical descriptors of colour, more information is retained than by using discrete groups. Quantifying individual variation in colour is important for linking colour with other traits such as reproductive strategy, immune function, and size and for testing hypotheses about the evolution and maintenance of colour polymorphism.

Lennox, R., K. Choi, P.M. Harrison, **J.E. Paterson**, T.B. Peat, T.D. Ward & S.J. Cooke. 2015. Improving science-based invasive species management with physiological knowledge, concepts, and tools. Biological Invasions 17: 2213-2227

Biological invasions are a prominent factor contributing to global biodiversity loss. As a result, managing invasive species is a priority for many conservation scientists and natural resource managers. Invasive species management requires a multidisciplinary approach and there is increasing recognition that physiology can be used to inform conservation efforts because physiological processes underlie an individual's response to its environment. For example, physiological concepts and tools can be used to assess the impacts of invasive animals on their new ecosystems, to predict which animal species are likely to become invasive, to prevent the introduction of non- native animals, and to control incipient or established invasions. To evaluate whether physiology is integrated within invasion science, the journal Biological Invasions was surveyed for a quantitative literature review. To determine how physiology is used to inform invasion science and which subdisciplines of physiology are particularly relevant to invasive animal management, the broader invasion literature was also reviewed to identify examples where physiology has contributed to studying and managing invasive animals. Only 6 % of articles published in Biological Invasions incorporated physiological knowledge or tools, mostly for the purposes of identifying traits associated with species invasiveness (i.e. prediction). However, the broader literature indicated that successful invasive species research and management can be supported by fundamental and applied physiological research for assessing, predicting, preventing, and controlling invasive animals. Development of new techniques and increased availability of equipment for remote or rapid monitoring of physiology in the field will increase opportunities for integrating physiology within invasion science.

Halliday*, W.D., **J.E. Paterson***, L.D. Patterson*, S.J. Cooke, G. Blouin-Demers. 2014. Testosterone, body size, and sexual signals predict parasite load in Yarrow's Spiny Lizards (*Sceloporus jarrovii*). Canadian Journal of Zoology 92: 1075-1082 *contributed equally and considered joint first authors.

Parasite load significantly impacts host health and fitness and may vary substantially among individuals within a population. The immunocompetence handicap hypothesis posits that sexual signals are honest indicators of male quality because they are maintained by testosterone, an immunosuppressant that yields higher parasite loads. Additionally, testosterone may influence parasite load by increasing activity levels. We examined these two hypotheses in a wild population of Yarrow's Spiny Lizards (*Sceloporus jarrovii* Cope, 1875) in Arizona. We (i) compared fecal testosterone levels to ectoparasite and haemoparasite loads, (ii) tested if sexual signals (total coloured area, aggression, and head size), locomotor activity, and body size correlated with testosterone levels, and (iii) compared sexual signals, locomotor activity, and body size to parasite load. Ectoparasite loads increased with total coloured area and tended to increase with testosterone, but this latter relationship was only nearly significant. Parasite loads increased with body size. Thus, we found some support for the immunocompetence handicap hypothesis and none for the activity hypothesis. Our results are consistent with an alternative hypothesis that larger individuals have more parasites because they have more surface area and (or) have had longer to accumulate parasites. Future studies should examine the relative contributions of testosterone and glucocorticoids in driving variation in parasite loads.