

Experimental removal reveals only weak interspecific competition between two coexisting lizards

James E. Paterson, Stacey L. Weiss, and Gabriel Blouin-Demers

Abstract: Competition for resources is an important mechanism that shapes ecological communities. Interspecific competition can affect habitat selection, fitness, and abundance in animals. We used a removal experiment and mark–recapture to test the hypothesis that competition with the larger and more abundant Striped Plateau Lizard (*Sceloporus virgatus* H.M. Smith, 1938) limits habitat selection, fitness, and abundance in Ornate Tree Lizards (*Urosaurus ornatus* (Baird in Baird and Girard, 1852)). Ornate Tree Lizards in the plots where Striped Plateau Lizards were removed switched between habitat types more frequently and moved farther than Ornate Tree Lizards in control plots. However, there were no significant changes in the relative densities of Ornate Tree Lizards in each habitat type or in microhabitat use. We also found no changes in growth rates, survival, or abundance of Ornate Tree Lizards in response to the removal of Striped Plateau Lizards. Our results suggest that interspecific competition was not strong enough to limit habitat use or abundance of Ornate Tree Lizards. Perhaps interspecific competition is 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.

Key words: abundance, habitat selection, interspecific competition, Ornate Tree Lizard, *Sceloporus virgatus*, Striped Plateau Lizard, *Urosaurus ornatus*.

Résumé : La compétition pour les ressources est un important mécanisme qui module les communautés écologiques. La compétition interspécifique peut avoir une incidence sur la sélection d'habitats, l'aptitude et l'abondance chez les animaux. Nous avons eu recours à une expérience de retrait et au marquage–recapture pour vérifier l'hypothèse selon laquelle la compétition avec les lézards des plateaux rayé (*Sceloporus virgatus* H.M. Smith, 1938), plus gros et plus abondants, limite la sélection d'habitats, l'aptitude et l'abondance des lézards arboricole orné (*Urosaurus ornatus* (Baird in Baird and Girard, 1852)). Les *U. ornatus* dans les parcelles dont les *S. virgatus* avaient été retirés changeaient de types d'habitats plus fréquemment et se déplaçaient sur de plus grandes distances que les *U. ornatus* dans les parcelles témoins. Cependant, aucun changement significatif des densités relatives d'*U. ornatus* dans chacun des types d'habitats ou de l'utilisation de microhabitats n'a été décelé. Nous n'avons également noté aucun changement des taux de croissance, des taux de survie ou de l'abondance d'*U. ornatus* en réponse au retrait de *S. virgatus*. Nos résultats donnent à penser que la compétition interspécifique n'était pas suffisamment forte pour limiter l'utilisation des habitats ou l'abondance des *U. ornatus*. Il se peut que la compétition interspécifique soit faible entre des espèces coexistantes quand l'abondance des ressources n'est pas fortement réduite. Il est donc important de tenir compte des conditions environnementales au moment d'évaluer l'importance de la compétition interspécifique. [Traduit par la Rédaction]

Mots-clés : abondance, sélection d'habitats, compétition interspécifique, lézard arboricole orné, *Sceloporus virgatus*, lézard des plateaux rayé, *Urosaurus ornatus*.

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 with 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 con-

tinues to be a major factor explaining patterns in occurrence and abundance in communities (Laiolo 2013; Steen et al. 2014; Tarjuelo et al. 2017). Support for 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. For example, Little Bustard (*Tetrax tetrax* (Linnaeus, 1758)) habitat selection depends on the density of a dominant competitor, the Great Bustard (*Otis tarda* Linnaeus, 1758) (Tarjuelo et al. 2017). Habitat selection based on the density of competitors has also been observed in dragonflies (Suhling 1996) and lizards (Pacala and Roughgarden 1982; Salzburg 1984; Rummel and Roughgarden 1985). Moreover, species that are not currently competing may demonstrate evidence of the “ghost of competition past” because their habitat preferences have di-

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verged as a result of past interspecific competition (Connell 1980; Rosenzweig 1991). For example, the preferred habitats of two lemming species (collared lemmings (*Dicrostonyx groenlandicus* (Traill, 1823)) and Nearctic brown lemmings (*Lemmus trimucronatus* (Richardson, 1825))) do not overlap, and they now experience competition only when high population sizes force some individuals into less-preferred habitats (Morris et al. 2000).

Interspecific competition can affect fitness proxies, such as survival, growth rates, or reproductive rates. For example, Collared Flycatcher (*Ficedula albicollis* (Temminck, 1815)) recruitment increased when the density of two competing species was experimentally reduced (Gustafsson 1987). Competition between species can decrease fitness because of reduced resource availability (Birch 1957; Connell 1983), through behavioural interference (Downes and Bauwens 2002; Melville 2002; Berger and Gese 2007; Lailvaux et al. 2012) or through indirect effects mediated by other species (Tilman 1987). Competition for resources can depress fitness below levels that could be achieved if the competitor were absent, but 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).

One 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 exploitation competition) and the decrease in behavioural interference (Birch 1957; Connell 1983; Tilman 1987). For example, removing a large territorial reef fish caused large increases in the abundance of several subordinate species (Robertson 1996). The increase in abundance of subordinate species can be explained by increased birth rates, decreased mortality rates, or increased immigration rates in areas with less interspecific competition.

We previously documented density-dependent habitat selection in Ornate Tree Lizards (*Urosaurus ornatus* (Baird in Baird and Girard, 1852)) between two habitats varying in suitability (Paterson and Blouin-Demers 2017). However, it is possible the habitat selection patterns that we observed could be explained more fully by also considering the effects of interspecific competition, in addition to the effects of intraspecific competition. At our study site, Ornate Tree Lizards occupy the same habitat as Striped Plateau Lizards (*Sceloporus virgatus* H.M. Smith, 1938). 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 habitat selection, fitness, and local abundance of Ornate Tree Lizards is driven by competition with Striped Plateau Lizards, we conducted a removal experiment and mark-recapture study. First, we tested the prediction that interspecific competition influences habitat selection by examining changes in the distribution of Ornate Tree Lizards in response to the removal of Striped Plateau Lizards. We predicted that Ornate Tree Lizards would increase their use of high-quality habitats after the removal of Striped Plateau Lizards. We next tested the prediction that interspecific competition decreases the fitness of Ornate Tree Lizards by examining changes in survival and growth rate of Ornate Tree Lizards in response to the removal of Striped Plateau Lizards. Finally, we tested whether removing Striped Plateau Lizards increased the abundance of Ornate Tree Lizards. We focused on the effects of competition on Ornate Tree Lizards because Striped Plateau Lizards are larger and more abundant than Ornate Tree Lizards at our study sites.

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 with 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). Explaining spatial and temporal patterns in abundance is one of the major challenges in ecology (Elith and Leathwick 2009), and measuring the effects of interspecific competition on habitat selection can improve predictions about variation in abundance.

Materials and methods

Study species and study sites

Ornate Tree Lizards and Striped Plateau Lizards (Supplementary Figs. S1a, S1b)¹ occur sympatrically along canyon bottoms in the Chiricahua Mountains of Arizona, USA, and are the two most abundant lizard species where they occur. We used a removal experiment to test for competitive effects on habitat selection, fitness, and abundance of Ornate Tree Lizards. We studied eight unfenced 50 m × 50 m plots along three creeks within the Middle Fork drainage of Cave Creek; all plots were at least 50 m apart and we did not observe lizards switching plots (Supplementary Fig. S2).¹ Each control plot was paired to a neighbouring removal plot in which we experimentally reduced the abundance of Striped Plateau Lizards. Each plot straddled rocky wash habitat with open canopy and upland habitat consisting of pine-oak woodlands. The wash has more prey and allows Ornate Tree Lizards to be active at their preferred body temperature for longer than the upland habitat; Ornate Tree Lizards prefer and occur at higher densities in the wash habitat (M'Closkey et al. 1990; Paterson and Blouin-Demers 2017; this study).

We surveyed each plot 10 times between May 2015 and July 2016. During each survey, we searched the entire plot at least three times and captured all encountered Ornate Tree Lizards and Striped Plateau Lizards. We recorded the location of each lizard with a handheld GPS unit (accuracy ±3 m), and we measured perch height (±5 cm) and noted habitat type (wash or upland) where lizards were initially located. Within 4 h of capture, we 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, we released all lizards at their capture location the same day. In removal plots, we released all lizards at their capture location the same day for the first three surveys (before removal; 1 May to 20 June 2015); then for the next seven surveys (23 June to 5 August 2015 and 8 May to 27 July 2016), we released all Striped Plateau Lizards 300–500 m away on the same day. We did not recapture any displaced Striped Plateau Lizards in any of the plots. Animal use was approved by the University of Ottawa Animal Care Committee (protocols BL286 and BL-2300-R1) and by Coronado National Forest. Lizards were collected under Arizona Fish and Game Department Scientific Collector's Permits SP713940 and SP740592.

Striped Plateau Lizard abundance and habitat selection

To confirm the removal treatment actually reduced the abundance of Striped Plateau Lizards, we 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 2017). We 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

¹Supplementary figures and tables are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2017-0279>.

probability of new individuals from \hat{N} entering the population (*pent*). We 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 1, between breeding seasons, and after removal year 2; Supplementary Fig. S3¹). Although there were no surveys between the breeding seasons, monthly survival could have differed between the first breeding season (May to August) and the period between the two breeding seasons (September to April); therefore, we 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. We 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; Cooch and White 2012; 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, we adjusted \hat{c} to be the highest estimate of the three methods. We fit all possible subsets of the general model and compared models with QAIC_c (Burnham and Anderson 2002). We model-averaged parameter predictions across the most-supported models ($\Delta\text{QAIC}_c < 4$, compared with the most-supported model) based on their relative support to account for model uncertainty (Burnham and Anderson 2002; Cade 2015).

We calculated abundance in each plot with the model-averaged parameter predictions. To ensure that the treatment actually reduced Striped Plateau Lizard abundance, we calculated their abundance at the beginning of the experiment (survey 1; Supplementary Fig. S3),¹ at the end of the first summer (survey 6), and at the end of the second summer at each plot (survey 10). We fit linear mixed-effects models with the lme4 package (Bates et al. 2015) where we used abundance as the response variable and time (before removal, after removal year 1, and after removal year 2), treatment (control or removal), and the interaction between time and treatment as fixed effects. We included random intercepts for each plot to account for different initial abundances.

We quantified Striped Plateau Lizard habitat selection with isodars (Morris 1988) to confirm that they have the same habitat preference as Ornate Tree Lizards. We 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 us 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. We assigned individual lizards to a habitat based on their mean coordinates before and after removal of Striped Plateau Lizards. This habitat assignment assumes that lizards with home ranges centered in the wash have access to the food and thermal resources in that habitat and that the mean coordinates accurately represent space use. We believe this habitat assignment is reasonable given the short distances moved by each species (see the Results). We calculated density for each plot by dividing the number of Striped Plateau Lizards in a habitat by the area of the habitat.

Ornate Tree Lizard habitat selection

To test the prediction that Ornate Tree Lizard habitat selection changed after removal of Striped Plateau Lizards, we 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. We 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. We compared the 95% confidence intervals of the intercepts and slopes for 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 before and after the removal do not overlap, then habitat selection changed after the removal of Striped Plateau Lizards. We assigned individual Ornate Tree Lizards to a habitat based on their mean coordinates before and after removal of Striped Plateau Lizards. We 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, we used multistate 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, then they would be more likely to switch habitats than lizards in control plots, especially towards the higher quality wash habitat (Paterson and Blouin-Demers 2017). Multistate 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 survey). We used a general model where S was estimated for each treatment and time period (before removal, after removal year 1, between breeding seasons, and after removal year 2); Ψ was estimated for each sex, treatment, time period, and habitat; and p was estimated for each habitat. We compared model-averaged predicted estimates of Ψ based on well-supported models ($\Delta\text{AIC}_c < 4$, compared with 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, we compared the mean distance travelled between captures. We averaged the linear distance between capture locations for lizards caught at least twice, with at least one capture after the removal began ($n = 68$ lizards), 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 ($F_{[1,66]} = 0.005$, $P = 0.98$, $R^2 < 0.01$).

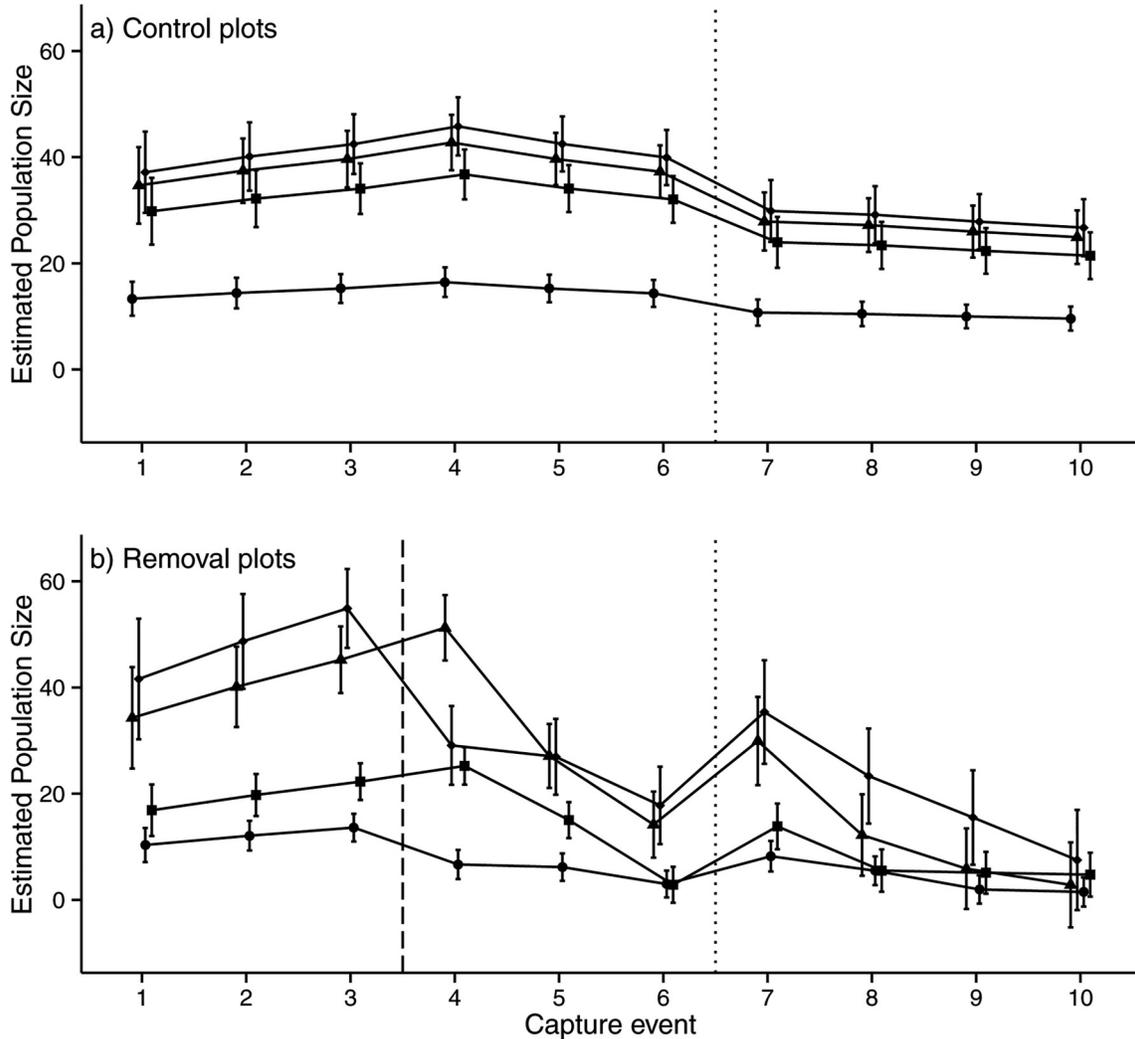
To test whether microhabitat use was affected by interspecific competition, we analyzed perch heights using a linear mixed-effects model fit with the lme4 package (Bates et al. 2015). Perch height (log-transformed) was the response variable and sex, treatment (control or removal), time period (before, after removal in year 1, and after removal in year 2), and the interaction between treatment and time period were fixed effects. We 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.

Ornate Tree Lizard fitness proxies

To test the prediction that removing Striped Plateau Lizards should increase the fitness of Ornate Tree Lizards, we used apparent survival and individual growth rate. To estimate survival, we fit Jolly–Seber mark–recapture models to Ornate Tree Lizard capture histories with the same general model used for Striped Plateau Lizards (Supplementary Fig. S3).¹ We compared model-averaged apparent monthly survival estimates between control and removal plots after removal of Striped Plateau Lizards during the first year and second year of the experiment.

To calculate growth rate, we divided the difference in SVL by the number of days elapsed since the lizard was last captured. We adjusted time elapsed to remove winter days when lizards were unlikely to grow (1 November to 1 April; Dunham 1982). Most Ornate Tree Lizard growth occurs in the first year after birth, thus we restricted growth analyses to yearlings. We 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

Fig. 1. Estimated (± 1 SE) abundance of Striped Plateau Lizards (*Sceloporus virgatus*) in the Chiricahua Mountains of Arizona, USA, based on Jolly–Seber mark–recapture models that (a) remained stable in four control plots and (b) decreased in four experimental plots where lizards were removed after the third survey. The vertical broken line represents the start of the removal of Striped Plateau Lizards and the vertical dotted lines represent the winter. All plots were 50 m \times 50 m. Symbols correspond to paired control–removal plots.



rates were only used when the interval between captures was greater than 14 days. We compared growth rates using ANOVA with sex, treatment, and the interaction between sex and treatment as fixed effects.

Ornate Tree Lizard abundance

To test the prediction that removing Striped Plateau Lizards increased the abundance of Ornate Tree Lizards, we analyzed the estimated abundance of Ornate Tree Lizards using linear mixed-effects models fit with the lme4 package (Bates et al. 2015). Abundances were derived from Jolly–Seber POPAN mark–recapture models, as described above. The fixed effects were time (before removal, after removal year 1, and after removal year 2), treatment (control or removal), and the interaction between time and treatment. We included random intercepts for each plot to account for different initial abundances.

Results

Striped Plateau Lizard abundance and habitat selection

We 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 sum-

marized in the Supplementary Table S1.¹ Plots varied in their initial abundance of Striped Plateau Lizards, but abundance was significantly reduced on experimental plots after removal (Figs. 1a, 1b) as indicated by the fixed effect of time ($F_{[2,12]} = 4.84, P = 0.03$), treatment ($F_{[1,8]} = 9.43, P = 0.01$), and the interaction between time and treatment ($F_{[2,12]} = 7.65, P = 0.01$).

The isodars for Striped Plateau Lizards in control plots did not change during the experiment (Supplementary Fig. S4 and Table S2).¹ Striped Plateau Lizards preferred the wash habitat, and density was higher in the wash than the upland habitat.

Ornate Tree Lizard habitat selection

We captured 98 Ornate Tree Lizards 171 times in control plots and 93 Ornate Tree Lizards 164 times in removal plots. The isodars for Ornate Tree Lizards in removal plots before and after the removal of Striped Plateau Lizards overlapped in intercepts and in slopes (Table 1; Supplementary Fig. S5¹). 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. Ornate Tree Lizard isodars in the control plots before and after the removal also overlapped in confidence intervals (Supplementary

Table 1. Parameter estimates and confidence intervals for isodars of Ornate Tree Lizards (*Urosaurus ornatus*) in the Chiricahua Mountains, Arizona, USA.

Parameter	Type	Estimate	Confidence interval	
			2.5%	97.5%
Intercept	Before removal	-82.6	340.66	17.15
	After removal	-143.74	73.39	40.38
Slope	Before removal	6.09	2.22	-10.3
	After removal	14.41	1.03	-1.37

Note: 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 the confidence interval lower bound line passes through quadrant three or when the upper bound confidence interval line passes through quadrant two (Jolicœur 1973).

Table S3),¹ indicating habitat selection did not change during the experiment.

All the well-supported multistate mark–recapture models (Supplementary Table S4)¹ had higher transition probabilities for Ornate Tree Lizards in removal plots compared with control plots. Ornate 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 habitat and from upland habitat to wash habitat (Fig. 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 (14 m) than in females (8 m; $F_{[1,65]} = 11.67$, $P = 0.001$) and higher in removal plots (14 m) than in control plots (10 m; $F_{[1,65]} = 6.10$, $P = 0.016$; Fig. 3). There was no interaction between sex and treatment ($F_{[1,65]} = 2.15$, $P = 0.15$). 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 $P < 0.05$).

Ornate Tree Lizard perch height increased by a mean of 18 cm in the second period of the experiment (after removal year 1; $F_{[2,278]} = 3.57$, $P = 0.03$), but did not differ between control and removal plots ($F_{[1,6]} = 0.53$, $P = 0.49$), and was unaffected by the interaction between time period and treatment ($F_{[1,275]} = 0.14$, $P = 0.87$; Figs. 4a, 4b). Males perched an estimated 15 cm higher than females ($F_{[1,117]} = 7.04$, $P = 0.009$).

Ornate Tree Lizard fitness proxies

During the first year of the experiment, Ornate Tree Lizard monthly survival probabilities were similar in control (0.76 ± 0.12) and removal (0.74 ± 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 removal (0.87 ± 0.08) plots where Striped Plateau Lizards were removed. Twelve of the top 20 most-supported Jolly–Seber models (cumulative QAIC_c weight = 0.70; Supplementary Table S5¹) did not include differences in survival between removal and control plots.

There was no effect of treatment ($F_{[1,6]} = 0.36$, $P = 0.57$) or the interaction between treatment and sex ($F_{[1,10]} = 0.52$, $P = 0.49$) on yearling Ornate Tree Lizard growth rates. Yearling female Ornate Tree Lizards grew faster than males ($F_{[1,11]} = 21.42$, $P < 0.001$). Including growth rates of all individuals did not change our conclusions regarding the effect of treatment ($F_{[1,5]} = 0.31$, $P = 0.60$) or of the interaction between treatment and sex ($F_{[1,72]} = 2.51$, $P = 0.12$) on growth rate. Therefore, Ornate Tree Lizards grew at similar rates in control plots and in plots where Striped Plateau Lizards were removed.

Fig. 2. Female and 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 $\Psi \pm 1$ SE) in plots where Striped Plateau Lizards (*Sceloporus virgatus*) were removed than in control plots.

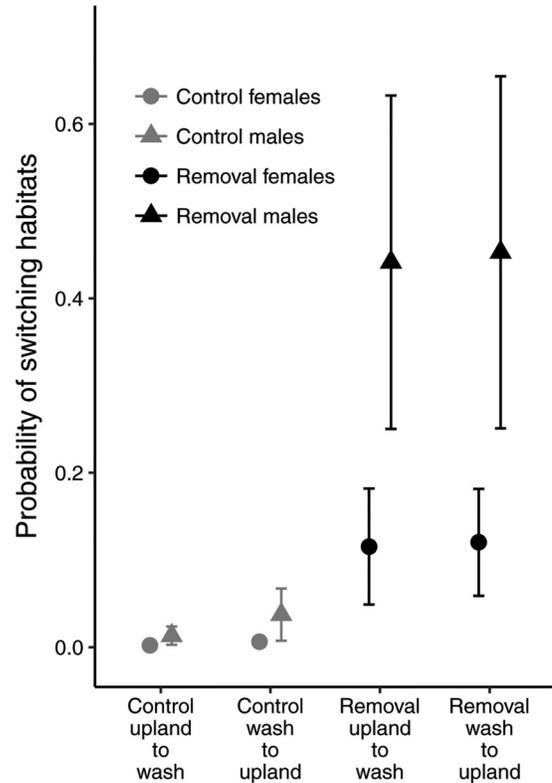


Fig. 3. Male Ornate Tree Lizards (*Urosaurus ornatus*) from plots where Striped Plateau Lizards (*Sceloporus virgatus*) were removed ($n = 20$ individuals) moved longer mean distances between capture locations than males from control plots ($n = 21$ individuals) and than females ($n = 15$ individuals in control plots, $n = 12$ individuals in removal plots) in the Chiricahua Mountains of Arizona, USA. Horizontal lines represent group medians and box limits represent the interquartile ranges.

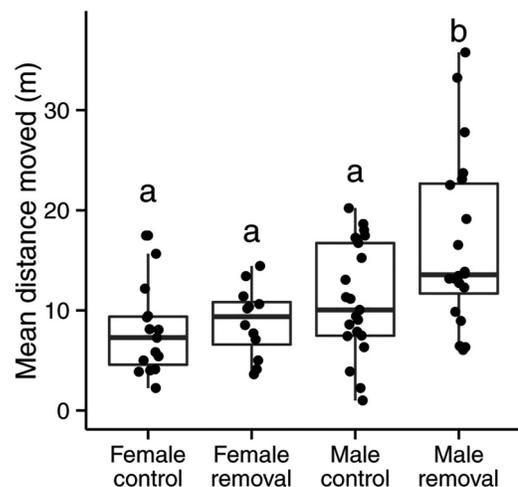
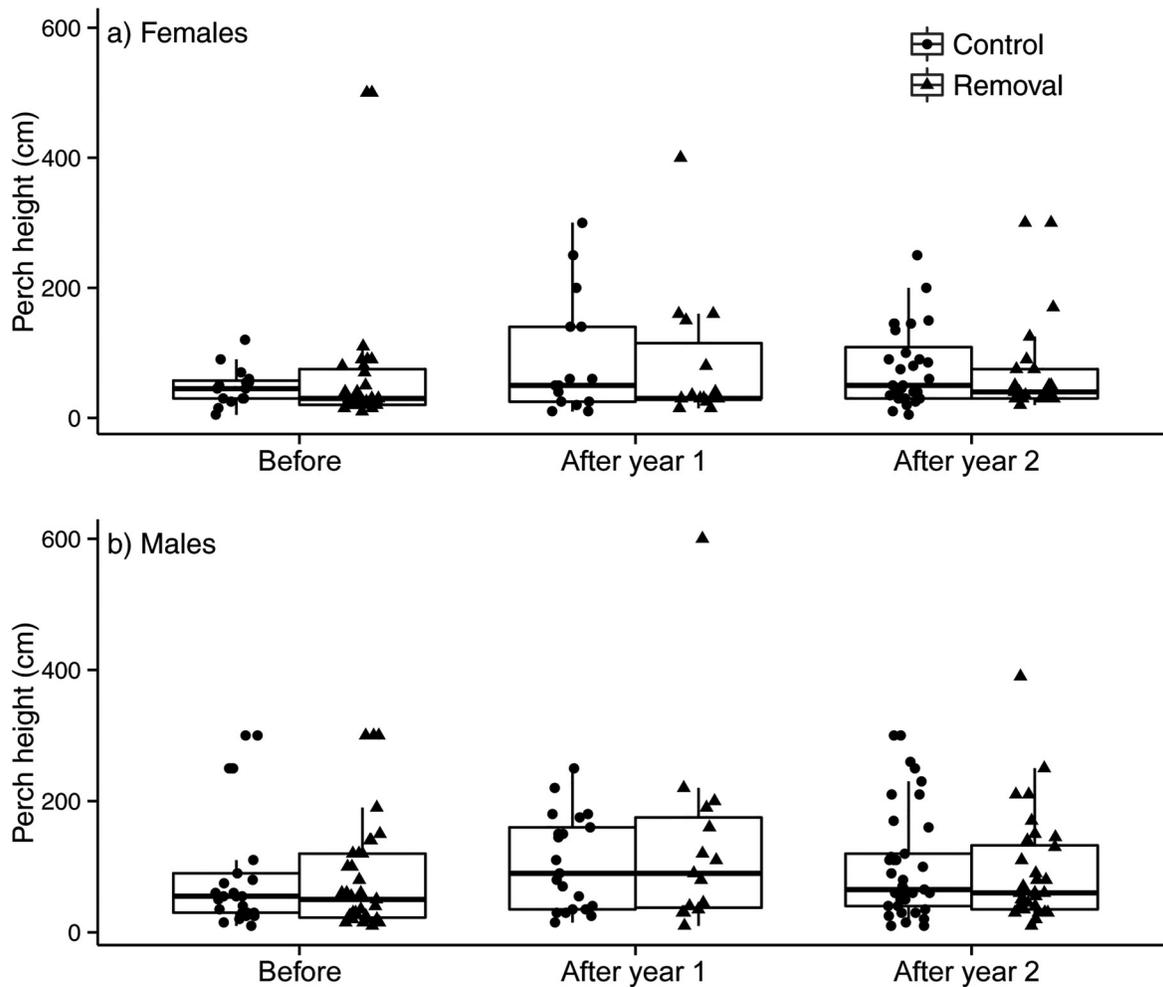


Fig. 4. Perch heights of (a) female ($n = 130$) and (b) male ($n = 165$) Ornate Tree Lizards (*Urosaurus ornatus*) in the Chiricahua Mountains of Arizona, USA, did not differ between control plots and plots where Striped Plateau Lizards (*Sceloporus virgatus*) were removed. Horizontal lines represent group medians and box limits represent the interquartile ranges.



Ornate Tree Lizard abundance

The well-supported Jolly–Seber models for Ornate Tree Lizards are presented in the Supplementary Table S3.¹ Ornate Tree Lizard abundance did not differ between control and removal plots ($F_{1,61} = 0.28$, $P = 0.62$), but decreased during the experiment in all plots ($F_{2,121} = 5.82$, $P = 0.02$) with an estimated decrease in abundance of two lizards in year 2 compared with year 1 ($P < 0.01$). There was an interaction between time and treatment ($F_{2,121} = 15.25$, $P < 0.001$; Figs. 5a, 5b) 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 three individuals more than in control plots). The abundance of Ornate Tree Lizards did not increase in plots where Striped Plateau Lizards were removed.

Discussion

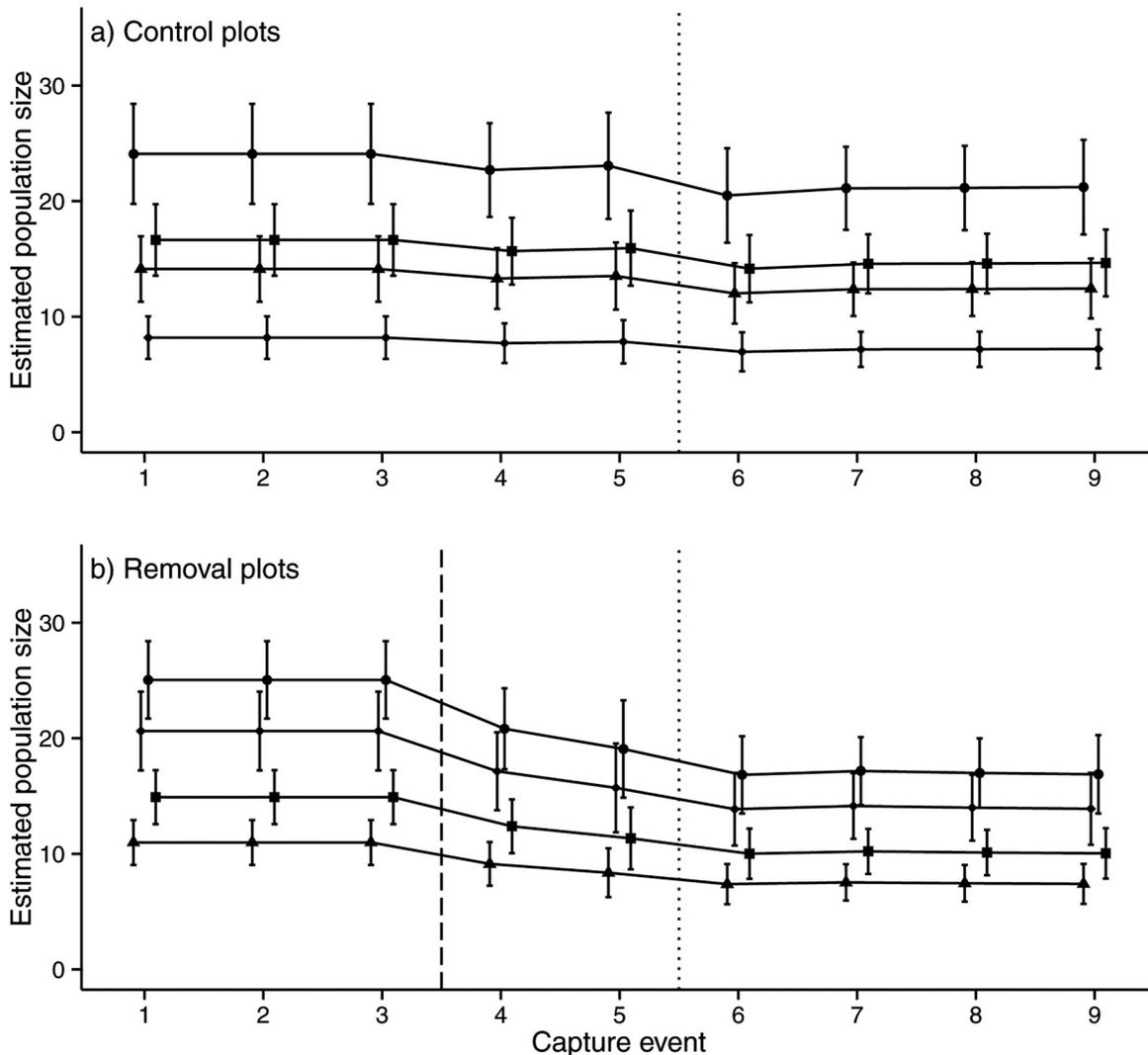
Our results only partially support the hypothesis that habitat selection, fitness, and local abundance of Ornate Tree Lizards is driven by competition with Striped Plateau Lizards. We successfully depressed the density of Striped Plateau Lizards to almost zero in both summers (Fig. 1b). Therefore, the treatment created the desired effect of reducing potential interspecific competition

between Ornate Tree Lizards and Striped Plateau Lizards. Ornate Tree Lizard space use shifted in response to the removal of Striped Plateau Lizards. However, there was no change in survival, growth rates, or abundance of Ornate Tree Lizards in response to the removal of Striped Plateau Lizards.

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 that 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 competing species (Mönkkönen et al. 1999; Tarjuelo et al. 2017), other species select habitat based on food abundance (Kielty et al. 1996), conspecific density (Stamps 1991), predator cues (Downes and Shine 1998), or other factors. 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.

Although habitat selection by Ornate Tree Lizards was similar after the removal of a potential competitor, their 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 (and vice versa) in removal plots compared with

Fig. 5. Estimated (± 1 SE) abundance of Ornate Tree Lizards (*Urosaurus ornatus*) in the Chiricahua Mountains of Arizona, USA, based on Jolly–Seber mark–recapture models that remained stable in (a) four control plots and (b) four experimental plots where Striped Plateau Lizards (*Sceloporus virgatus*) were removed after the third survey. The vertical broken line represents the start of the removal of Striped Plateau Lizards and the vertical dotted lines represent the winter. All plots were 50 m \times 50 m. Symbols correspond to paired control–removal plots.



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 support 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. 1987), so the cost of defending an area should increase with the density of lizards. Ornate Tree Lizards may have undergone microhabitat shifts that we did not detect. For instance, Ornate Tree Lizards could have increased access to microhabitats for thermoregulation after the removal of Striped Plateau Lizards (Langkilde and Shine 2004; Žagar et al. 2015). 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 farther 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, yearling growth rate, or abundance. 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 our experiment was too short because Striped Plateau Lizard abundance rebounded between years and because there was a large pool of potential immigrants outside our experimental plots. 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 our 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 we 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 (Dunham 1980; Tinkle and Dunham 1983). Other

studies have found low, but very variable annual survival rates (0.08 to 0.24) in Ornate Tree Lizards (Smith 1981; Tinkle and Dunham 1983). Abiotic 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 1994). 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 2 years of our experiment had annual precipitation (69 and 55 cm, respectively) above the 30-year average (51 ± 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 <https://www.ncdc.noaa.gov/cdo-web/datatools/findstation>). 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 interspecific 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 jarrovi* Cope in Yarrow, 1875) in the same region (Watters 2008).

Competition between species may not have large effects on the fitness and abundance of many communities. For example, interspecific competition was weak or undetectable in studies on rodents (Schroder and Rosenzweig 1975), beetles (Wise 1981), and other insects (Shorrocks et al. 1984). In lizards, authors of 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). However, field experiments with arboreal lizard communities have found strong support for the role of interspecific competition in habitat use (Pacala and Roughgarden 1982; Harmon et al. 2007) and abundance (Leal et al. 1998).

In summary, we 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 1 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 predation or abiotic factors keep the abundances of both species below levels at which interspecific competition becomes strong enough to affect fitness and abundance. Our study highlights the importance of considering environmental conditions when assessing the strength of interspecific competition because competition is likely to be weak between coexisting species except during periods with severely depleted resource levels.

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