

## Niche Partitioning between Two Sympatric Lizards in the Chiricahua Mountains of Arizona

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**Competition for resources between sympatric species can result in reduced fitness. Resource partitioning allows the minimization of competitive pressures, consequently promoting the coexistence of a diversity of species. We tested the hypothesis that the Striped Plateau Lizard (*Sceloporus virgatus*) and the Ornate Tree Lizard (*Urosaurus ornatus*) that occur in sympatry in the Chiricahua mountains of Arizona, USA have distinct ecological niches to minimize interspecific competition. We compared the activity times, perch microhabitat characteristics, and diet of these insectivorous lizards to test the prediction that they partition resources. Although we found no difference between the two species in the time at which lizards become active in the morning nor in the composition of their diets, the two species used different structural perch microhabitats. The Ornate Tree Lizard selected higher and narrower perches with more closed canopy than the Striped Plateau Lizard, and males generally occupied higher perches than females. These differences in perch microhabitat use may reduce interspecific competition and allow these two sympatric species to cohabitate.**

MANY hypotheses have been proposed to explain how natural selection has led to astonishing evolutionary diversification. Amongst the earlier hypotheses is that of ecological opportunity, according to which the environment consists of various ecological niches, the availability of which determines the expected number of species (Lack, 1944; Dobzhansky, 1951). Several concepts of an ecological niche have been proposed, notably the Grinnellian niche, defined as the habitat in which a species lives and its accompanying behavioral adaptations (Grinnell, 1917), and the Eltonian niche, described as the function performed by a species in the community of which it is a member (Elton, 1927). While the former emphasized a species' "address," the latter highlighted its "profession" (Miller, 1967). In our study, we consider Hutchinson's niche concept, which interprets an ecological niche as a region in a multidimensional space of environmental factors required for a population to persist (Hutchinson, 1957), thus focusing more on a species' "address," as Grinnell did, but in an explicitly multidimensional space. Well supported by early research (Elton, 1933; Crombie, 1946; MacArthur, 1964), the ecological opportunity hypothesis eventually led to the competitive exclusion principle, which dictates that no two species possessing the same ecological niche can stably coexist (Volterra, 1928; Hardin, 1960; MacArthur and Levins, 1964). As such, the more similar two species are in their use of available resources, the more intensely they compete, and the more likely it is that one will be excluded by the other (Hardin, 1960; Pianka, 1974; Day and Young, 2004). Because the competitive exclusion principle relied on an idealized relationship between the number of niches and the number of species, however, the principle of limiting similarity was then described (MacArthur and Levins, 1967; May and MacArthur, 1972; May, 1974). This principle postulates that species can be somewhat similar and still coexist; species may partition resources along certain axes of a multidimensional niche space (Hutchinson, 1959) while still competing over other axes. Together, niche dimensionality, competitive exclusion, and limiting similarity suggest that if two sympatric species compete for resources, they should evolve

a certain divergence in resource use to decrease the intensity of competition (Day and Young, 2004).

Interspecific competition is potentially harmful to individual fitness and, consequently, can decrease population abundance (Schoener, 1983). For example, the number and mass of Collared Flycatcher fledglings increased when densities of Blue and Great Tits (natural competitors of the Collared Flycatcher) were experimentally reduced (Gustafsson, 1987). Thus, competition for resources (in this case food, particularly for the young during both the nestling and postfledging periods) can result in decreased fitness.

Resource partitioning allows the minimization of competitive pressures, reducing the negative effects potential competitors may have on individual fitness, consequently promoting the coexistence of a diversity of species (Dufour et al., 2018). Although the impact of interspecific competition on ecological communities relative to that of other factors such as intraspecific competition, predation, and parasitism has been debated (Connell, 1983; Person et al., 1986; Jackson et al., 2001; Boulangeat et al., 2012), interspecific competition can be a key factor dictating the relative abundance of species (Schoener, 1983) and their distribution between habitats (Laiolo, 2013). The ecological character displacement hypothesis was explicitly developed to explain the specific mechanism through which interspecific competition for resources may drive evolutionary diversification (Schluter, 2000): initially ecologically similar species tend to shift resource use in sympatry to minimize competitive pressure (Schluter, 2000; Kolbe et al., 2008; Losos, 2009; Dufour et al., 2018). Each species influences the relative abundance of available consumable resources and, consequently, impacts the evolutionary trajectory of competing species (Day and Young, 2004).

Several studies on *Anolis* have focused on interspecific competition, resource partitioning (Kolbe et al., 2008), and ecological character displacement (Schluter, 2000; Dufour et al., 2018). Indeed, rather than being randomly distributed across available habitats, lizard species within a community often occupy distinct ecological niches, avoiding overlap in resource use (Murray et al., 2016). These ecological niches

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tend to differ along three main dimensions: spatial, temporal, and dietary, though niche complementarity dictates that species can be similar along some niche axes while differing along others (Kolbe et al., 2008). Ecological niches are often defined by indicators of structural microhabitat, thermal microhabitat (but see Paterson and Blouin-Demers, 2017), and prey size (Losos, 2009). For example, Kolbe et al. (2008) evaluated perch height, substrate type, thermal microhabitat, body size, head length, daily activity, and abundance of three diurnal lizards to characterize their ecological niches. *Ameiva griseivulva* was more similar to *Anolis leachii* in size and daily activity, but more similar to *Anolis wattsi* in perch height, whilst the latter two were more similar in thermal microhabitat, a pattern consistent with niche complementarity. Murray et al. (2016) used similar indicators to compare the ecological niches of two sympatric lizards in the Namib Desert, *Peioplanis husabensis* and *Rhoptropus bradfieldi*, while also characterizing each species' diet using fecal pellets. *Peioplanis husabensis* weighed less, had a higher active body temperature and often was found on warmer substrates than *R. bradfieldi*, and specialized on a termite diet, whilst *R. bradfieldi* specialized on ants.

We studied two sympatric lizards found in the Chiricahua mountains of Arizona, USA, the Ornate Tree Lizard (*Urosaurus ornatus*) and the Striped Plateau Lizard (*Sceloporus virgatus*). Smith (1981) found that although these two species overlap in body size, perch sites, and habitat use, there is evidence of competition in yearling females. Paterson et al. (2018) found no effect of removal of the Striped Plateau Lizard on the fitness and abundance of the Ornate Tree Lizard. In both cases, however, a limited number of niche axes were considered. Here we provide a more stringent test of niche differentiation in the face of interspecific competition by estimating the niches more completely. We test the hypothesis that the sympatric Striped Plateau Lizard and Ornate Tree Lizard have distinct ecological niches to minimize interspecific competition. We characterize and compare their ecological niches to test the prediction that these species partition resources.

## MATERIALS AND METHODS

**Study species and study sites.**—The Ornate Tree Lizard and Striped Plateau Lizard are abundant and occur in sympatry along canyon bottoms in the Chiricahua mountains of Arizona, USA. We studied ten 300 by 50 m plots located along three creeks within the Middle Fork drainage of Cave Creek from 1 May to 21 July 2018. Each site was centered along a creek bed (wash habitat), where the ground was covered with boulders, vegetation was sparse and mainly herbaceous, and extended 50 m into the neighboring wooded area (upland habitat), which consisted of pine-oak woodlands where the ground was mostly covered with leaf litter and scattered boulders. We included both habitats because they differ in prey density and in thermal quality, and thus in lizard density (Paterson and Blouin-Demers, 2018). For details of the study sites, please see Paterson and Blouin-Demers (2018).

We visited each plot between three and ten times during the active season. At every visit, we searched each plot throughout the active period of the lizards (from dawn until it became too hot and lizards retreated into refuges; more specifically when we ceased capturing lizards for an hour).

We captured every encountered tree or plateau lizard by lasso, and we recorded its location with a handheld GPS unit (accuracy  $\pm 3$  m). We gave each lizard a unique marking on its head with a felt-tip marker and determined its sex according to throat color and size of the post-anal scales. We released all captured lizards within a few hours at the location where they were first found. Our work was conducted with a State of Arizona Scientific Collection Permit (SP771492), permission from the U.S. National Forest Service Douglas Ranger District (Douglas Ruppel), and approved by the University of Ottawa Animal Care Committee (BL-2812).

**Ecological niche characterization.**—To characterize each species' ecological niche, we measured multiple indicators of each of their three main niche dimensions (spatial, temporal, and dietary). We recorded the type of habitat where each lizard was initially located (wash or upland), substrate type (log, rock, or tree), perch height, perch width (recorded as the diameter in the case of a log, trunk, or branch, or as the maximum straight width in the case of a rock), and canopy cover (measured with a densiometer). The exact time at which every lizard was first observed was also recorded.

To describe each species' diet, we collected 200 fecal pellets (100 pellets per species, each from different individuals) and preserved them in ethanol. These fecal samples were often found in the cotton bags in which lizards were kept individually. Otherwise, the abdomens of lizards were massaged by hand for approximately 3 minutes in an attempt to induce defecation. Fecal pellets were observed under a dissecting microscope, and arthropod parts were identified to order (Murray et al., 2016).

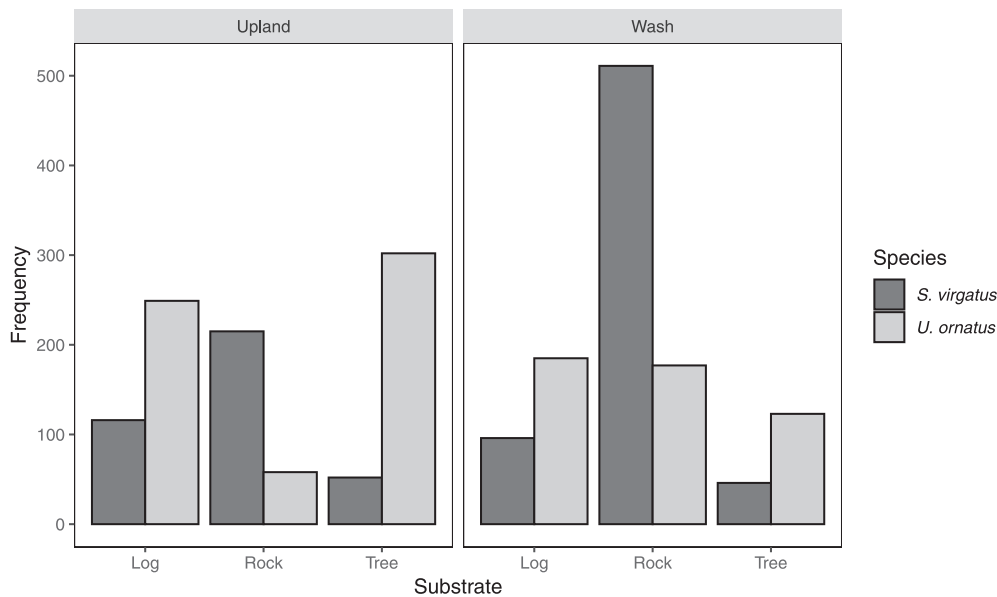
**Statistical analyses.**—We conducted all statistical analyses with R version 3.5.1 (R Core Team, 2018). We compared substrate type, canopy cover (reflected and log-transformed), perch height (log-transformed), and perch width (log-transformed) between species with separate MANOVAs for each habitat (upland and wash) with species, sex, and their interaction as independent variables. We report means  $\pm 1$  standard deviation. We calculated eta-squared values ( $\eta^2$ ) as estimates of effect sizes. These are used specifically in analysis of variance models and are calculated and interpreted the same way as  $R^2$  values.

The times at which every individual of each species were sighted were pooled by week, totaling 12 weeks of data, and the 5<sup>th</sup> percentile of these were calculated, separately for each habitat. These 5<sup>th</sup> percentiles were then compared using mixed ANOVAs, with species and habitat as fixed factors, and week as a random factor. We used the fifth percentile instead of the earliest daily occurrences to minimize the potential effect of outliers.

Symmetrical dietary niche overlap ( $O_{jk}$ ) between the Ornate Tree Lizard and the Striped Plateau Lizard was estimated using Pianka's similarity index (Pianka, 1973):

$$O_{kj} = O_{jk} = \frac{\sum_{i=1}^n P_{ij}P_{ik}}{\sqrt{\sum_{i=1}^n P_{ij}^2 \sum_{i=1}^n P_{ik}^2}}$$

where  $j$  and  $k$  represent the two lizard species for which the overlap is computed, and  $P$  is the proportional utilization of prey type  $i$ . Niche overlap can range from 0 (no dietary overlap) to 1 (complete dietary overlap).



**Fig. 1.** Proportional use of each substrate type (log, rock, and tree) differed between *Urosaurus ornatus* and *Sceloporus virgatus* in the upland habitat, but did not differ in the wash habitat nor between sexes within each species in the Chiricahua Mountains of Arizona, USA.

## RESULTS

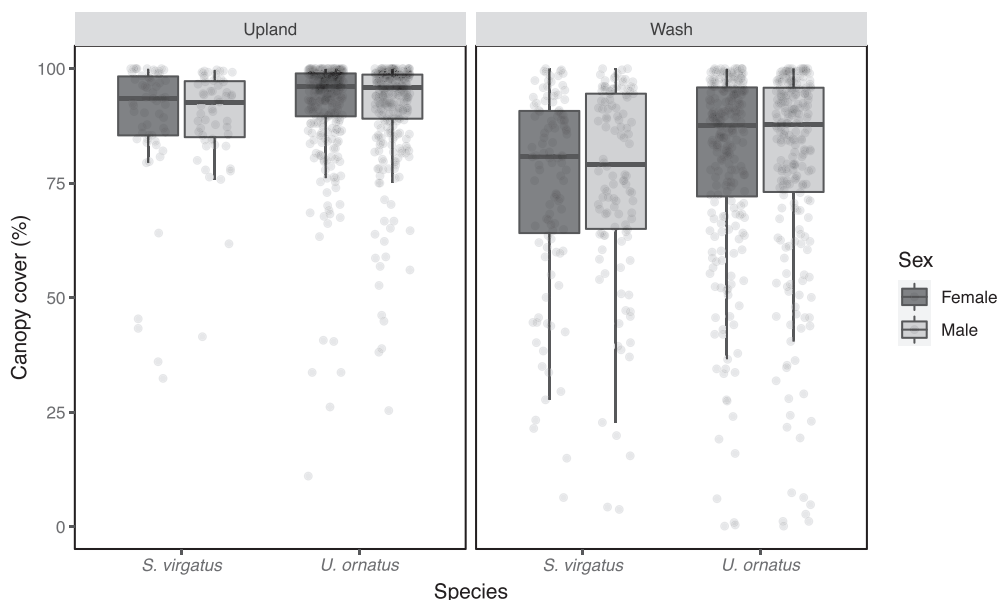
**Microhabitat.**—Although both species perched on logs, rocks, and trees, the frequency with which they used each of these substrates was significantly different within the upland habitat ( $n = 612$ ,  $P < 0.001$ ; Fig. 1). *Urosaurus ornatus* were most often observed on trees and logs, whereas *S. virgatus* tended to perch on rocks (Fig. 1). Within the wash habitat, a much higher proportion of *S. virgatus* were found on rocks than on either of the other substrates, and *U. ornatus* used the three substrates approximately equally, but the difference between the two species was not significant ( $n = 609$ ,  $P = 0.652$ ; Fig. 1). Males and females used the three substrates in the same proportions (upland:  $n = 612$ ,  $P = 0.896$ , wash:  $n = 609$ ,  $P = 0.247$ ).

Canopy cover where lizards were found ranged from 11 to 100%. *Urosaurus ornatus* were found in sites with more closed canopy than *S. virgatus* both in the upland ( $n = 612$ ,  $P = 0.009$ ) and in the wash ( $n = 609$ ,  $P < 0.001$ ; Fig. 2). We found

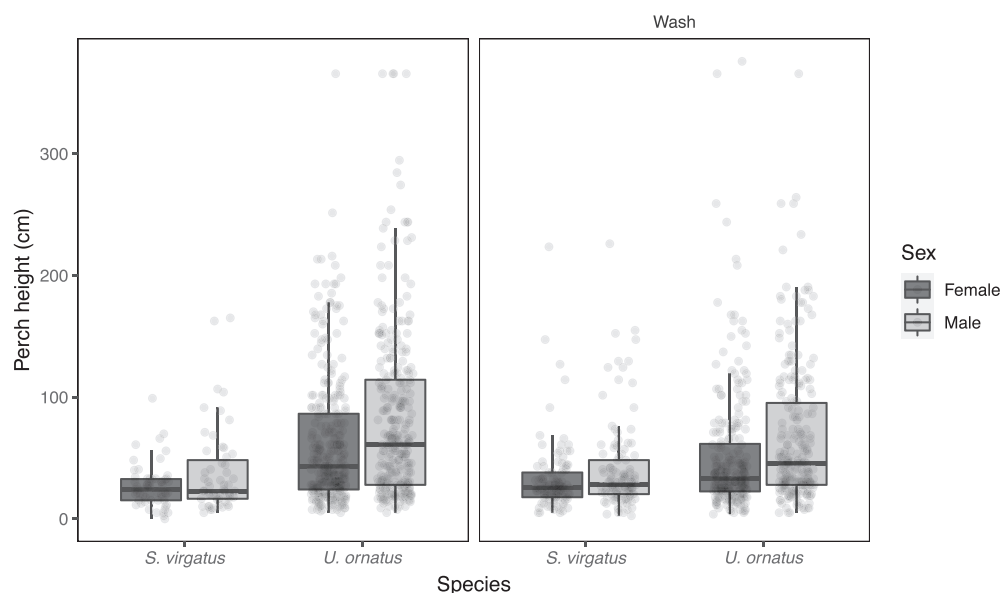
no significant differences in canopy cover between sexes (upland:  $n = 612$ ,  $P = 0.162$ , wash:  $n = 609$ ,  $P = 0.697$ ; Fig. 2).

*Urosaurus ornatus* and *S. virgatus* differed significantly in the mean height and width of the perches on which they were observed. *Urosaurus ornatus* selected perches that were generally higher (upland:  $n = 612$ ,  $P < 0.001$ , wash:  $n = 609$ ,  $P < 0.001$ ; Fig. 3) and narrower (upland:  $n = 612$ ,  $P < 0.001$ , wash:  $n = 609$ ,  $P < 0.001$ ; Fig. 4) than the ones used by *S. virgatus*. Also, males generally occupied higher perches than females (upland:  $n = 612$ ,  $P < 0.001$ , wash:  $n = 609$ ,  $P < 0.001$ ; Fig. 3), although the differences were modest: 17.9 cm in the upland (males:  $74.4 \pm 66.7$  cm, females:  $56.5 \pm 51.5$  cm) and 12.6 cm in the wash (males:  $58.5 \pm 53.4$  cm, females:  $45.9 \pm 47.1$  cm).

Species exhibited correlations about four times stronger than sex with all four indicators of structural microhabitat, both in the upland (species:  $\eta^2 = 0.113$ , sex:  $\eta^2 = 0.033$ ) and in the wash (species:  $\eta^2 = 0.080$ , sex:  $\eta^2 = 0.023$ ), as demonstrated by the eta-squared values. The interaction



**Fig. 2.** Canopy cover at perching sites differed between *Urosaurus ornatus* and *Sceloporus virgatus* in both habitat types (upland and wash), but not between sexes, in the Chiricahua Mountains of Arizona, USA. The boxes span the interquartile range (from the 25<sup>th</sup> percentile to the 75<sup>th</sup> percentile) with the horizontal line within each box representing the median (50<sup>th</sup> percentile), whilst the whiskers extend to the lowest and highest observations excluding outliers.



**Fig. 3.** Perch height differed significantly between *Urosaurus ornatus* and *Sceloporus virgatus* as well as between sexes in both habitat types (upland and wash) in the Chiricahua Mountains of Arizona, USA. The boxes span the interquartile range (from the 25<sup>th</sup> percentile to the 75<sup>th</sup> percentile) with the horizontal line within each box representing the median (50<sup>th</sup> percentile), whilst the whiskers extend to the lowest and highest observations excluding outliers.

between species and sex had no significant effect on any of the indicators of structural microhabitat and exhibited weak correlations with microhabitat (upland:  $\eta^2 = 0.003$ , wash:  $\eta^2 = 0.004$ ).

**Activity.**—The time at which lizards were observed throughout the 69 field days varied between 0634 h and 1641 h. The 5<sup>th</sup> percentiles of the time of capture (for each week) were the same for each species ( $n = 48$ ,  $df = 1$ ,  $P = 0.176$ ) and habitat type ( $n = 48$ ,  $df = 1$ ,  $P = 0.521$ ; Fig. 5).

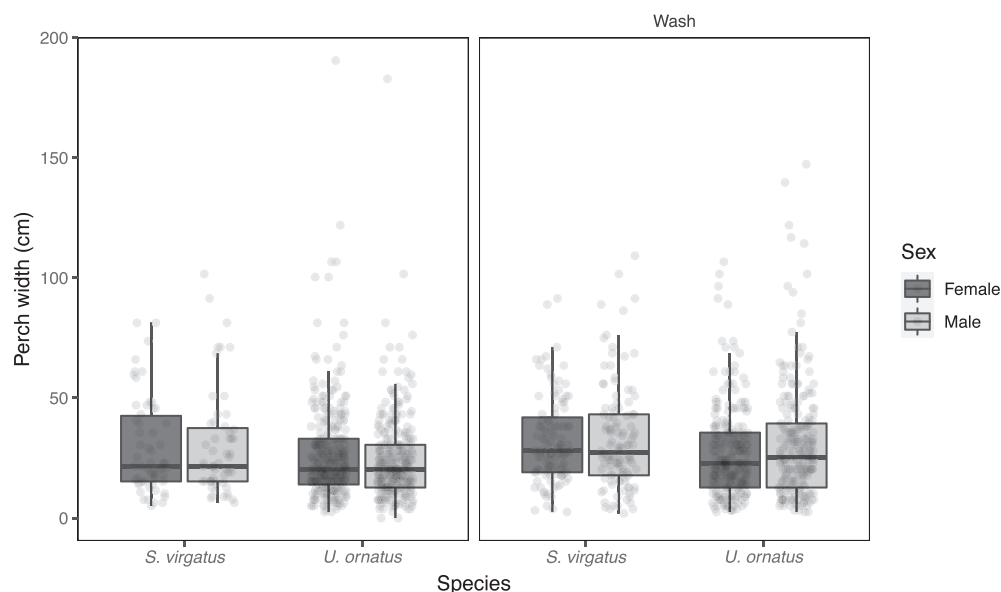
**Diet.**—We identified 3,317 prey items (Table 1) from 11 arthropod orders, including hexapods (8 orders), cheliceriforms (2 orders), and crustaceans (1 order). Of those 3,317 prey items, 1,930 were obtained from 97 fecal samples collected from 45 male and 52 female *U. ornatus*. Each pellet contained an average of  $20 \pm 17$  (range 1–93; median 15) individual prey items. The remaining 1,387 prey items were obtained from 93 fecal samples collected from 38 male and

55 female *S. virgatus*. Each pellet contained an average of  $15 \pm 14$  (range 1–81; median 11) individual prey items.

*Urosaurus ornatus* and *S. virgatus* both fed primarily on ants and other hymenopterans, which made up approximately 75% and 70% of all prey items consumed, respectively. Other important prey categories were coleopterans, which made up 11% of the diet of *U. ornatus* and 8% of the diet of *S. virgatus*, and hemipterans, which made up 7% of the diet of *U. ornatus* and 12% of the diet of *S. virgatus*. All other prey categories represented less than 5% of either species' diet. The dietary niche overlap ( $O_{jk}$ ) between *U. virgatus* and *S. virgatus* was nearly complete (0.996), and dietary overlap was also nearly complete between sexes within each species (0.998 and 0.989, respectively).

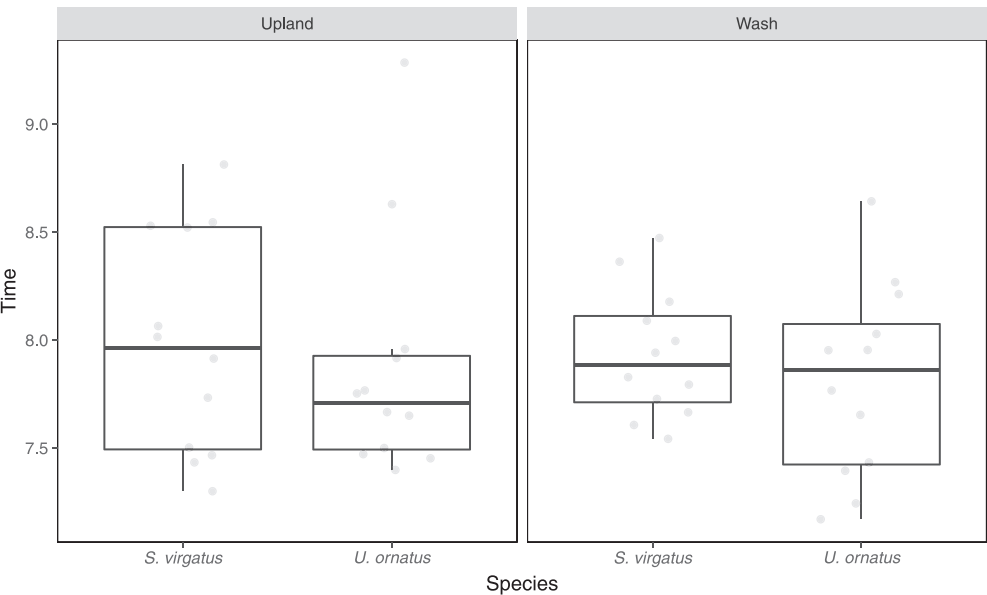
## DISCUSSION

To minimize competitive pressures and the harmful impact they may have on individual fitness (Schoener, 1983), potentially competing species usually partition resource use



**Fig. 4.** Perch width differed significantly between *Urosaurus ornatus* and *Sceloporus virgatus* in both habitat types (upland and wash), but not between sexes, in the Chiricahua Mountains of Arizona, USA. The boxes span the interquartile range (from the 25<sup>th</sup> percentile to the 75<sup>th</sup> percentile) with the horizontal line within each box representing the median (50<sup>th</sup> percentile), whilst the whiskers extend to the lowest and highest observations excluding outliers.





**Fig. 5.** 5<sup>th</sup> percentile of the time at which the first individual was observed daily did not differ between *Urosaurus ornatus* and *Sceloporus virgatus* or habitat types (upland and wash) in the Chiricahua Mountains of Arizona, USA. The boxes span the interquartile range (from the 25<sup>th</sup> percentile to the 75<sup>th</sup> percentile) with the horizontal line within each box representing the median (50<sup>th</sup> percentile), whilst the whiskers extend to the lowest and highest observations excluding outliers.

along at least one of three main ecological niche dimensions: spatial, temporal, and dietary (Kolbe et al., 2008; Losos, 2009). We studied indicators of these three ecological niche dimensions in two species of sympatric lizards commonly found along canyon bottoms in the Chiricahua Mountains of Arizona, USA, to test the hypothesis that these lizards have distinct ecological niches, potentially to minimize interspecific competition. Although the Ornate Tree Lizard and the Striped Plateau Lizard had very similar diets and periods of activity, they differed along the spatial axis of their ecological niches.

**Table 1.** Prey composition of fecal pellets of *Urosaurus ornatus* and *Sceloporus virgatus* in the Chiricahua Mountains of Arizona, USA, characterized by the number of individual prey items (No.), the contribution of that item expressed as a percentage of total number of prey items identified (%N), and the percentage of pellets that contained said prey item (%Freq).

Prey item	<i>U. ornatus</i>			<i>S. virgatus</i>		
	No.	%N	%Freq	No.	%N	%Freq
Hexapoda						
Insecta						
Coleoptera	162	8	58	62	4	42
Diptera	4	<1	4	1	<1	1
Hemiptera	72	4	38	127	9	44
Homoptera	5	<1	4	9	1	9
Hymenoptera	1634	85	98	1142	82	89
Lepidoptera	14	1	14	20	1	22
Mecoptera	2	<1	2	0	0	0
Orthoptera	10	1	7	4	<1	2
Chelicerata						
Arachnida						
Araneae	9	<1	9	18	1	17
Pseudoscorpiones	5	<1	5	0	0	0
Crustacea						
Malacostraca						
Isopoda	5	<1	4	1	<1	1
Unknown	8	<1	7	3	<1	3
<b>Total</b>	<b>1930</b>	<b>100</b>		<b>1387</b>	<b>100</b>	

**Microhabitat.**—The Ornate Tree Lizard and the Striped Plateau Lizard diverged along the microhabitat niche dimension. Although both species perched on logs, rocks, and trees, the proportions at which they used each of these substrates were significantly different, at least within the upland habitat. The Ornate Tree Lizard was most often observed on trees and logs, whereas the Striped Plateau Lizard perched mainly on boulders. Similar patterns were observed in the wash habitat, but they were not statistically significant. This may be attributable to the homogeneity of the wash habitat in terms of available substrates. Indeed, the ground in the wash habitat was almost entirely covered by boulders, and although there were still some logs and trees, they represented a much smaller proportion of the habitat than they did in the upland. This may explain why there was not such a clear divergence between the use of different substrates by the Ornate Tree Lizard and the Striped Plateau Lizard in the wash habitat.

The microhabitat at basking sites used by both species also differed. In both habitats, the Ornate Tree Lizard used higher and narrower perches with more closed canopy than the Striped Plateau Lizard, probably again reflecting their higher tendency to perch on trees and branches instead of boulders. These results are consistent with those of other studies that evaluated resource partitioning in sympatric lizard species (Losos et al., 1993; Losos, 2009; Dufour et al., 2018). For example, after the introduction of *Anolis cristatellus* in Dominica, the native *Anolis oculatus* shifted towards higher perches, whilst the introduced species used low perches (Dufour et al., 2018). Similar patterns were obtained in Grand Cayman where the native *Anolis conspersus* selected higher perches in habitats invaded by *Anolis sagrei* than in habitats where these are still absent (Losos et al., 1993). Furthermore, in Antigua, *Anolis watsi* used lower perches, sunnier microhabitats, and perched more often on the ground in the absence of *Ameiva griswoldi*, whilst it perched higher, more often in the shade, and on trunks in the absence of *Anolis leachii* (Kolbe et al., 2008).

Interestingly, males generally occupied higher perches than females in both habitats. This is commonly observed in lizards, as many field studies have reported that males

perch higher than females (Zucker, 1986; Radder et al., 2006). The Ornate Tree Lizard is no different: males select higher perches than females (Zucker, 1986) year round, although more so during the breeding period, and show greater among-individual variation in perch height (Radder et al., 2006). Two main hypotheses have been proposed to explain these sexual differences in perch height: the food-competition avoidance hypothesis, which suggests that this difference is a means of reducing competition between the sexes for food when food is scarce, and the social-role hypothesis which suggests that sexual differences in social behavior (e.g., male territoriality) are responsible for differences in perch height (Zucker, 1986). Our analyses revealed nearly complete dietary niche overlap between sexes within each species, rendering the first hypothesis unlikely. Also, evidence for size-specific perch selection prior to and during the breeding period supports the latter hypothesis. Indeed, selection of higher perches by males, despite higher predation risk, may help in territory defense, courtship displays, and in advertising their presence to conspecifics (Radder et al., 2006). We are the first to document a difference between the sexes in perch height in the Striped Plateau Lizard, although this difference is fairly small, and further research is necessary to determine whether it is of biological relevance. If the difference between the sexes is biologically relevant, it is plausible that similar mechanisms to those driving this pattern in the Ornate Tree Lizard are responsible.

**Activity.**—Temporal partitioning between species potentially competing for resources such as microhabitat or prey is thought to reduce the effects of this exploitative competition, thereby permitting their coexistence (Pianka, 1973). However, the Ornate Tree Lizard and Striped Plateau Lizard did not exhibit a clear division along the time-of-day dimension of their ecological niches, at least based on the timing of activity initiation. Future work should take measures over the entire daily and seasonal active periods of the lizards to describe better the activity patterns. In the case of the House Gecko (*Hemidactylus frenatus*) and of the Ornate Day Gecko (*Phelsuma ornata*), for example, temporal overlap varied significantly throughout the year: it was high during the dry season, but low during the wet season (Cole and Harris, 2011). It is possible the Ornate Tree Lizard and the Striped Plateau Lizard may display such seasonal variation in their active periods as well. Further research could also include temperature measurements to determine whether these patterns of daily activity are related to thermal constraints in the environment, and if the effect of temperature on the active period is the same for both of these lizards.

**Diet.**—The Ornate Tree Lizard and the Striped Plateau Lizard are diurnal, insectivorous, sit-and-wait foragers, and there was no evidence that they feed on different prey. In fact, dietary overlap was nearly complete. Arthropods were the main food resource used by both species, hymenopterans in particular (mainly ants), a trend commonly observed in other diurnal sit-and-wait foraging lizards such as the geckos *Lygodactylus capensis* (Pianka and Huey, 1978) and *Pristurus* sp. (Arnold, 2009). Indeed, in both the Ornate Tree Lizard and the Striped Plateau Lizard, hymenopterans made up approximately 75% of all prey items consumed, whilst no other prey item represented more than 12% of the diet. To

the best of our knowledge, our study is the first to quantify diet for the Ornate Tree Lizard and the Striped Plateau Lizard and indicates that these two species do not partition resources along the dietary component of their ecological niches.

Perhaps these species partition dietary resources at other times of year. We only had data for May through July, so we cannot exclude the possibility that partitioning occurs at other times of year, maybe during times when resources are more scarce and interspecific competition becomes more intense. For example, as the Striped Plateau Lizard and the Ornate Tree Lizard share similar life cycles and all hatchlings emerge approximately at the same time (Smith, 1981), competition may then be considerable and lead to divergence in resource use. This seems unlikely, however, as hatching occurs at the end of the wet season for both species, when plant biomass and seed production are greatly increased and insects are plentiful (Beatley, 1969; Holmgren et al., 2006). Cole and Harris (2011) found, rather, that although overlap in diet between the House Gecko and the Ornate Day Gecko was extremely high in the warm wet season when invertebrates were abundant and the degree of temporal partitioning between the two species was greater, it was reduced in the warm dry season when food resources became limited and House Geckos altered their activity period to compensate for the prey reduction, increasing temporal overlap in activity.

Maybe the Ornate Tree Lizard and the Striped Plateau Lizard partition dietary resources at a finer taxonomic level. We identified prey items down to order, and although both species fed primarily on ants (and other hymenopterans), they may have been selecting different genera and species of ants. Such a pattern could arise in part by a slightly different use of available microhabitats by the lizards, as different microhabitats could harbor different ant species. It is also possible that although both species preyed upon insects of the same orders, they may have been preferentially selecting prey items of different sizes, within the same order (or even species). Lizards with larger heads typically benefit from an increased gape, and potentially from greater bite force (Herrel et al., 1999, 2001a; Huyghe et al., 2009), both of which have been associated with the consumption of larger and harder prey items (Herrel et al., 2001b; Verwaijen et al., 2002). As such, because the Striped Plateau Lizard is slightly larger than the Ornate Tree Lizard (Smith, 1981), it likely benefits from a larger and/or stronger bite, and so it is conceivable that it targets larger prey items within the same order.

A potential concern in examining lizard diet via fecal pellet analyses is that soft-bodied arthropod prey could be under-represented. However, past work has shown that this is not the case (Pérez-Mellado et al., 2011) and soft-bodied prey could often be identified by characteristic hard parts, such as mandibles or butterfly (Lepidoptera) scales.

**Conclusion.**—Interspecific competition for resources is potentially harmful to individual fitness (Schoener, 1983). Thus, rather than being randomly distributed across available habitats, species within a community often occupy distinct ecological niches, avoiding overlap in resource use (Murray et al., 2016). These ecological niches tend to differ along three main dimensions: spatial, temporal, and dietary, though niche complementarity dictates that species can be similar along some niche axes while differing along others (Kolbe et

al., 2008). We showed that the Ornate Tree Lizard and the Striped Plateau Lizard, two sympatric lizards found in the Chiricahua mountains of Arizona, USA, diverge along the spatial dimension of their ecological niches by using perches of different heights, widths, and canopy openness, as well as different types of substrate, plausibly to minimize interspecific competition.

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