

**RESSOURCE PARTITIONING BETWEEN TWO SYMPATRIC LIZARDS  
IN THE CHIRICAHUA MOUNTAINS, ARIZONA**

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## Abstract

Competition for resources between sympatric species can result in decreased fitness. Resource partitioning allows the minimization of competitive pressures, consequently promoting the coexistence of a diversity of organisms. I tested the hypothesis that striped plateau lizards (*Sceloporus virgatus*) and ornate tree lizards (*Urosaurus ornatus*) found in the Chiricahua mountains of Arizona, USA, have distinct ecological niches to minimize interspecific competition. I compared the activity patterns, microhabitat characteristics, and diet of these sympatric insectivorous lizards to test the prediction that they partition resources. Although I found no difference between the two species in the time at which lizards became active in the morning nor in the composition of their diet, indicators of structural microhabitat did differ between species and between males and females. Ornate tree lizards selected higher and narrower perches with a higher percentage of canopy cover than striped plateau lizards, and within both species, males generally occupied higher perches than females. These differences in microhabitat use may reduce interspecific competition and allow these two sympatric species to cohabitate.

## **Acknowledgements**

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## **Introduction**

Why are there so many species on Earth? This is a question that has puzzled evolutionary biologists for over a century. Many hypotheses have been proposed to explain how natural selection has led to such an astonishing level of evolutionary diversification. Amongst the earlier hypotheses is that of ecological opportunity, according to which the environment is made up of various ecological niches (defined by a series of consumable resources such as food and environmental factors such as temperature and humidity), the availability of which may determine the expected number of species (Lack, 1944; Dobzhansky, 1951). Well supported by early research (Crombie, 1946; Elton, 1933; MacArthur, 1964), this idea 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). Therefore, the number of coexisting species can never exceed the number of distinct niches. However, because this concept relied on an idealized relationship between the number of niches and the number of species, the principle of limiting similarity was then described (MacArthur & Levins, 1967; May, 1974; May & Arthur, 1972). This principle postulates that species can be somewhat similar (but only to a certain extent) and still coexist; in other words, they may partition resources along certain axes of a multidimensional niche space while still competing over other axes. Together, the niche dimensionality, competitive exclusion, and limiting similarity hypotheses suggest that if two sympatric species compete for resources, such as good territories, basking spots and prey, 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 any given individual's fitness and, consequently, to population abundance (Schoener, 1983). Many studies have indeed found



interspecific competition to negatively affect different fitness proxies, such as survival, growth rates, or reproduction rates. 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, compared to levels that could be achieved if competitors were absent.

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 organisms (Dufour *et al.*, 2018). In this way, although its relative impact on ecological communities as opposed to that of other factors such as intraspecific competition, predation and parasitism has been debated (Boulangeat *et al.*, 2012; Connell, 1983; Ferson *et al.*, 1986; Jackson *et al.*, 2001), 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). The idea, which has been well supported by recent research (Dufour *et al.*, 2018; Kolbe *et al.*, 2008; Losos, 2009), is that initially ecologically similar species tend to shift resource use in sympatry to minimize competitive pressure (Schluter, 2000; Dufour *et al.*, 2018). Consequently, each species influences the relative abundance of available consumable resources, and so impacts the evolutionary trajectory of competing species (Day and Young, 2004).

Several studies involving Caribbean *Anolis* lizards 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, species within a community often occupy distinct ecological niches, avoiding overlap in resource use (Murray et al., 2016). Thus, although different species share the same collection of resources, each one's individual niche may be properly defined by the extent to which it uses these various resources making up the axes of a multidimensional niche space (Hutchinson, 1957, 1959). These ecological niches tend to differ along three classic 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). These studies describe each *Anolis* species' ecological niche by comparing indicators of structural microhabitat, thermal microhabitat, and prey size (Losos, 2009). For example, Kolbe (2008) evaluated perch height, substrate type, thermal microhabitat, body size, head length, daily activity, and abundance. Murray (2015) used similar indicators to compare the ecological niches of two sympatric insectivorous lizards in the Namib Desert, *Peioplaxis husabensis* and *Rhoptropus bradfieldi*, while also characterizing each species' diet using fecal pellets.

My study focuses on two sympatric insectivorous 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 only in yearling females. Paterson et al. (2018) found no effect of removal of striped plateau lizards on ornate tree lizards' fitness or abundance. In both cases, however, a limited number of niche axes were included, with the main indicator measured being perch height (Paterson et al. 2018), a component of the spatial dimension. I plan to provide a more stringent test of niche differentiation in the face of interspecific competition by estimating the niche axes more completely. I will test the hypothesis that striped

plateau lizards and ornate tree lizards have distinct ecological niches to minimize interspecific competition. Therefore, I seek to characterize and compare their ecological niches to test the prediction that these species partition resources.

## **Methods**

### *Study species and study sites*

Ornate tree lizards and striped plateau lizards are abundant and occur sympatrically along canyon bottoms in the Chiricahua mountains of Arizona, USA. Ten 300 m by 50 m plots located along three creeks within the Middle Fork drainage of Cave Creek were studied from May 1<sup>st</sup> to July 21<sup>st</sup>, 2018 (Figure 1). Each site was centered along a creek bed (wash habitat), where the ground was covered with round 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 cover was mostly composed of leaf litter and scattered boulders (Figure 2). It has been determined that the wash has higher prey density and allows tree lizards to be active at their preferred body temperature for longer proportions of the day than the upland habitat (Paterson and Blouin-Demers, 2018). Therefore, tree lizards prefer and occur at higher densities in the wash habitat (M'Closkey et al., 1990; Paterson and Blouin-Demers, 2018).

Each plot was surveyed between 3 and 10 times during the field season. At every visit, each plot was searched throughout the active period of the lizards (from dawn until it became too hot and lizards retreated into refuges). Every encountered tree or plateau lizard was captured by noose and its location recorded with a handheld GPS unit (accuracy  $\pm$  3 m). All captured lizards were released within a few hours at the location where they were first found.

### *Ecological niche characterization*

To properly characterize each species' ecological niche, multiple indicators of each of their three main niche dimensions, spatial, temporal and dietary, were measured. In terms of structural microhabitat (spatial dimension), the type of habitat where lizards were initially located was recorded (wash or upland), substrate type was noted (log, rock, or tree), and perch height and perch width were measured ( $\pm 0.5$  cm). Canopy cover was also measured with a densiometer, as an index of each species' preference in terms of sunlight. The exact time at which every lizard was first observed was recorded, so the first occurrences in the morning for each species could serve as an indicator of activity time. Only the first *U. ornatus* and *S. virgatus* sightings in the morning were used because, although we often arrived on site before or as the first individuals were emerging from their nocturnal refuges, there may still have been a few active lizards when we left at the end of the day (fields days, on average, went from approximately 6:30 to 16:30). Lizards also often took refuge again for a few hours in the afternoon, before reemerging again around 16:00 or 17:00. The beginning of the active period therefore seemed to be a more reliable indicator. The fifth percentiles of capture times for each species were calculated to minimize the effect a few extreme values (generally attributable to idiosyncratic weather conditions or temperatures) may have on results, which were then grouped per week, because when divided by day, species and habitat type, too few observations were left for calculating fifth percentiles.

Within a couple hours of capture, each lizard was given a non-permanent marking on its head with a felt-tip marker. Snout-vent length (SVL) was measured with calipers ( $\pm 0.1$  mm) and mass with a digital scale ( $\pm 0.01$  g), and all captured individuals were sexed according to throat colour and the size of the post-anal scales (Figure 3). Lastly, to describe each species' diet, a total of 200 fecal pellets were collected (100 per species) and preserved in ethanol to be later observed

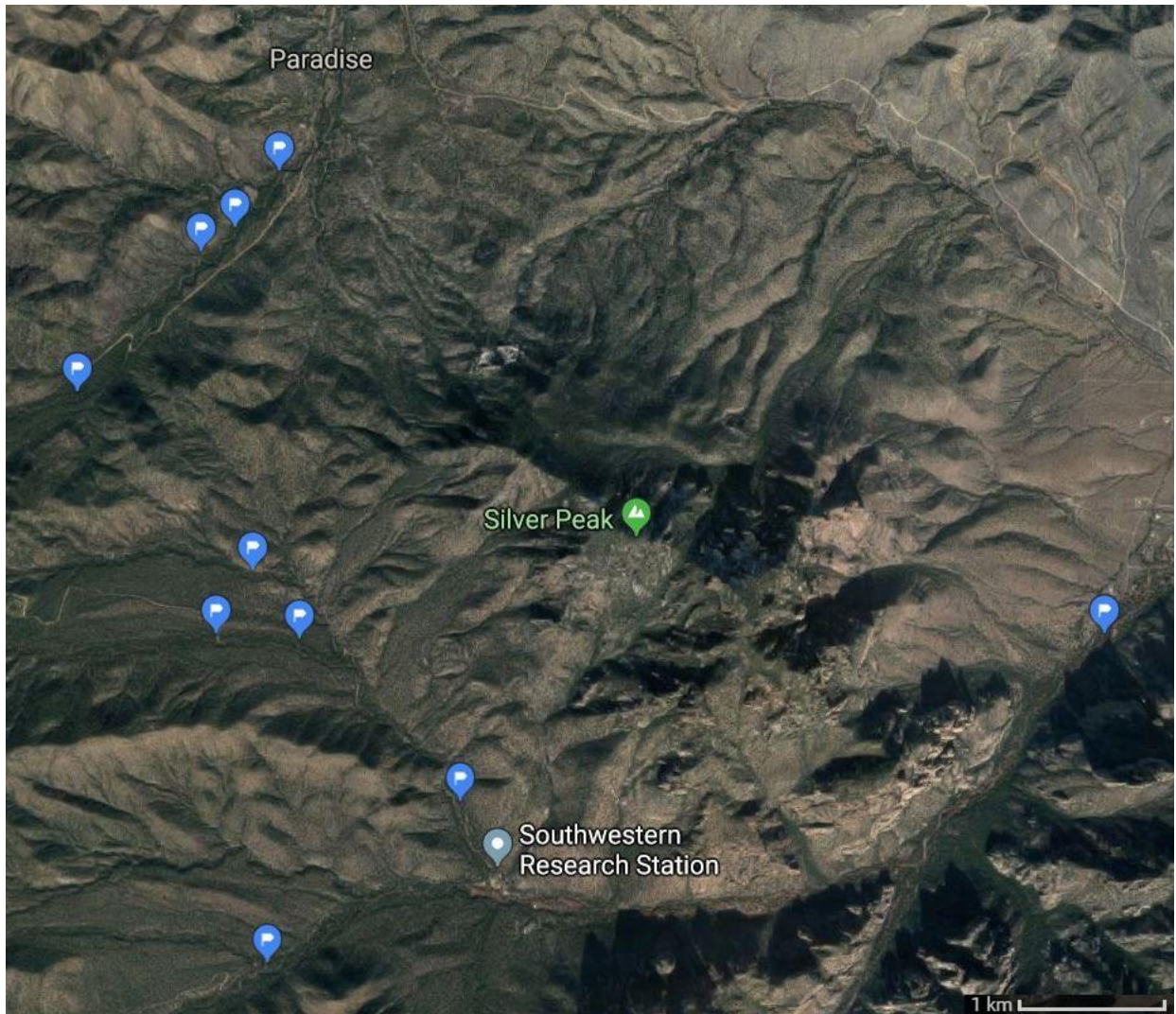
under a dissection microscope. These fecal samples were often found in the cotton bags in which lizards were kept individually. Otherwise, the abdomens of lizards were massaged by hand for approximately 3 minutes in an attempt to induce defecation. Any arthropod parts found in the fecal pellets were identified to order (Murray et al., 2016). Symmetrical dietary niche overlap ( $O_{jk}$ ) between *U. ornatus* and *S. virgatus* 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).

### *Statistical analyses*

All statistical analyses were conducted using R version 3.5.1 and Microsoft Excel 365. The times at which the first individuals of each species were sighted in the morning were grouped by week (ranging from 1 to 12, over the duration of the field season), and the 5<sup>th</sup> percentile of these occurrences within each of the two types of habitat (upland and wash) were compared using a mixed ANOVA, with species and habitat as fixed factors, as well as week as a random factor. The preferred substrate type, percentage of canopy cover, perch height and perch width for both species were also compared using separate MANOVAs for each habitat (upland and wash). These were conducted using both species, sex and their interaction as independent variables. Data for perch height, perch width and percentage of canopy cover were not normally distributed. Perch height and width were therefore log-transformed, whilst the percentage of canopy cover was reflected, and then log-transformed. Eta-squared measures were then calculated to obtain an estimate of effect sizes.

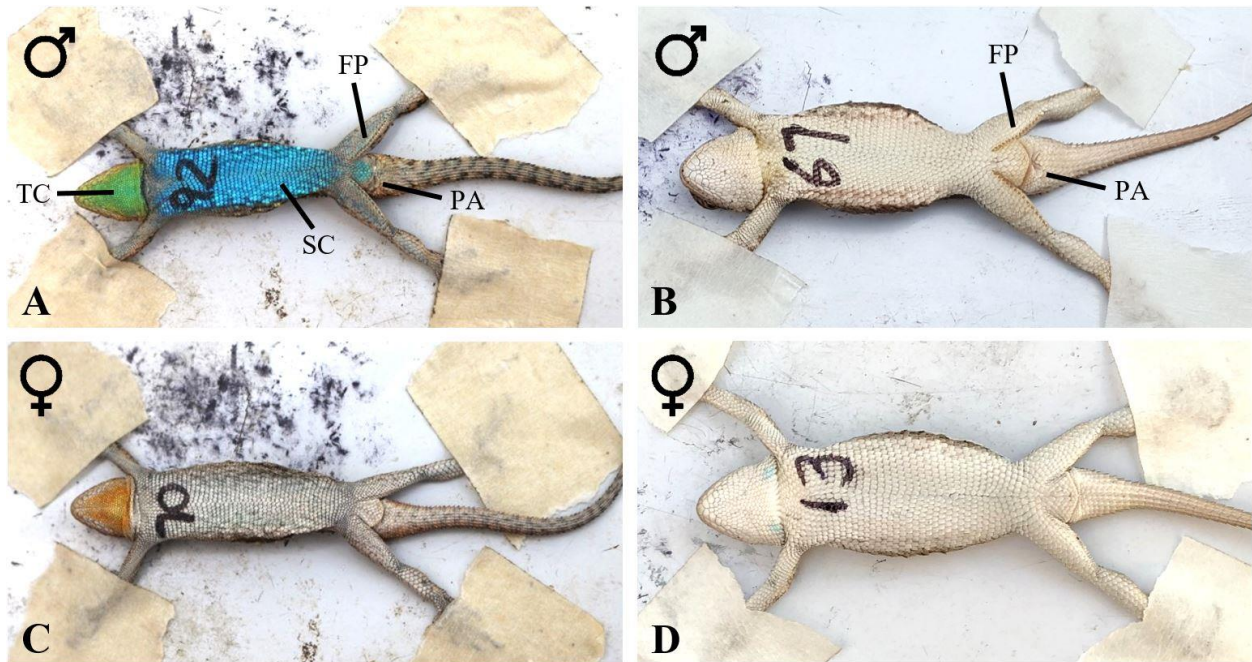


**Figure 1.** Location of the 10 study sites where ornate tree lizards (*Urosaurus ornatus*) and striped plateau lizards (*Sceloporus virgatus*) were studied in the Chiricahua mountains of Arizona, USA.





**Figure 2.** Photographs of the two habitat types used to study resource partitioning between *Urosaurus ornatus* and *Sceloporus virgatus* in the Chiricahua Mountains of Arizona, USA. A) The upland consisted of pine-oak woodlands with some undergrowth vegetation, and B) the wash had little and mainly herbaceous vegetation, a rocky substrate and an open canopy.



**Figure 3.** The ventral side of an adult male ornate tree lizard (*Urosaurus ornatus*) (A) and striped plateau lizard (*Sceloporus virgatus*) (B) and of an adult female ornate tree lizard (C) and striped plateau lizard (D) from the Chiricahua Mountains, Arizona, USA. Male *U. ornatus* are identified by their enlarged post-anal scales (PA) and femoral pores (FP), as well as their stomach (SC) and throat (TC) coloration, whilst male *S. virgatus* are identified by their enlarged post-anal scales (PA) and femoral pores (FP).



## Results

### *Diet*

I identified a total of 3317 individual prey items from 11 arthropod orders, including hexapods (8 of the 11 orders), cheliceriformes (2 of the 11 orders), and crustaceans (1 of the 11 orders). Of those 3317 prey items, 1930 were obtained from 97 fecal samples collected from 45 male and 52 female *Urosaurus ornatus*. Each pellet contained an average of  $20 \pm 17$  (range 1 – 93; median 15) individual prey items. Eight prey items could not be identified and were labelled as “unknown” for analyses of overlap. The remaining 1387 prey items were obtained from 93 fecal samples collected from 38 male and 55 female *Sceloporus virgatus*. Each pellet contained an average of  $15 \pm 14$  (range 1 – 81; median 11) individual prey items. Three prey items could not be identified and were labelled as “unknown” for analyses of overlap (Table 1).

During the season that we surveyed (May through July), *U. ornatus* and *S. virgatus* both fed primarily on ants and other hymenoptera, which made up approximately 75% and 70% of all prey items consumed, respectively. Other important prey categories were coleoptera, which made up 11% of *U. ornatus*' diet and 8% of *S. virgatus*' diet, and hemiptera, which made up 7% of *U. ornatus*' diet and 12% of *S. virgatus*' diet. All other prey categories represented less than 5% of either species' diet. The dietary niche overlap ( $O_{jk}$ ) between *Urosaurus virgatus* and *Sceloporus virgatus* was 0.996, and between sexes within each species, was 0.998 and 0.989 respectively.

### *Activity*

The time at which the very first individual lizard was observed for each of the 69 field days was recorded and varied between 6:34 and 9:31. The earliest occurrences were grouped by week (ranging from 1 to 12, over the duration of the field season), and the 5<sup>th</sup> percentile of these

occurrences for each of the two species within each of the two types of habitat (upland and wash) were compared. Neither the species ( $df = 1$ ,  $P = 0.176$ ) nor the habitat type ( $df = 1$ ,  $P = 0.521$ ) had a significant effect on the 5<sup>th</sup> percentile of the time of first capture obtained for each of the 12 weeks of field work (Figure 4).

### *Microhabitat*

Although both species perched on logs, rocks and trees, the proportion at which they used each of these substrate types was significantly different between the two species within the upland habitat ( $df = 1$ ,  $P < 0.001$ , Figure 2). *U. ornatus* were most often observed on trees and logs, whereas *S. virgatus* tended to perch on rocks (Figure 2). Within the wash habitat, a much higher proportion of *S. virgatus* were found on rocks than on either of the other substrate types, and *U. ornatus* were spread out more or less evenly between the three types of substrates. However, the difference in the proportional use of different substrate types between the two species was not significant in the wash habitat ( $df = 1$ ,  $P = 0.652$ , Figure 2). For both habitats, however, within each species, sex did not have a significant effect on the substrate type on which individuals were most often observed (upland:  $df = 1$ ,  $P = 0.896$ , wash:  $df = 1$ ,  $P = 0.247$ ).

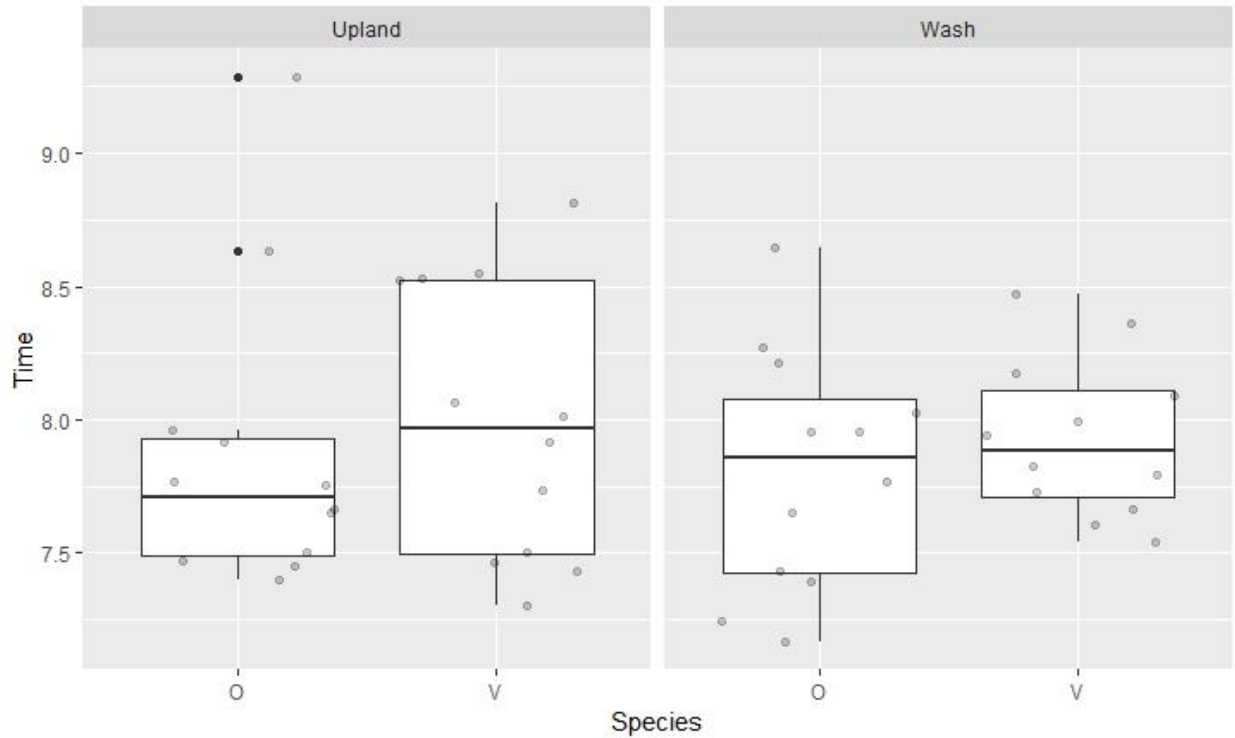
The percentage of canopy cover measured at each surveyed lizard's perch ranged from 11.1% to 100%. *Urosaurus ornatus* were found in habitats characterized by a significantly higher percentage of canopy cover than those where *Sceloporus virgatus* were most often observed, both in the upland ( $df = 1$ ,  $P = 0.009$ , Figure 6) and in the wash ( $df = 1$ ,  $P < 0.001$ , Figure 6). No significant difference in canopy cover was found between sexes within either lizard species (upland:  $df = 1$ ,  $P = 0.162$ , wash:  $df = 1$ ,  $P = 0.697$ , Figure 6).

*Urosaurus ornatus* and *Sceloporus virgatus* differed significantly in the average height and width of the perches on which they were observed. *U. ornatus* selected perches that were generally higher (upland:  $df = 1, P < 0.001$ , wash:  $df = 1, P < 0.001$ , Figure 7) and narrower (upland:  $df = 1, P < 0.001$ , wash:  $df = 1, P < 0.001$ , Figure 8) than the ones where *S. virgatus* were most often found, and these differences were significant in both habitat types. Significant differences in perch height were also observed between sexes within both species. Males generally occupied higher perches than females did (upland:  $df = 1, P < 0.001$ , wash:  $df = 1, P < 0.001$ , Figure 7), and this effect was significant in both habitat types as well.

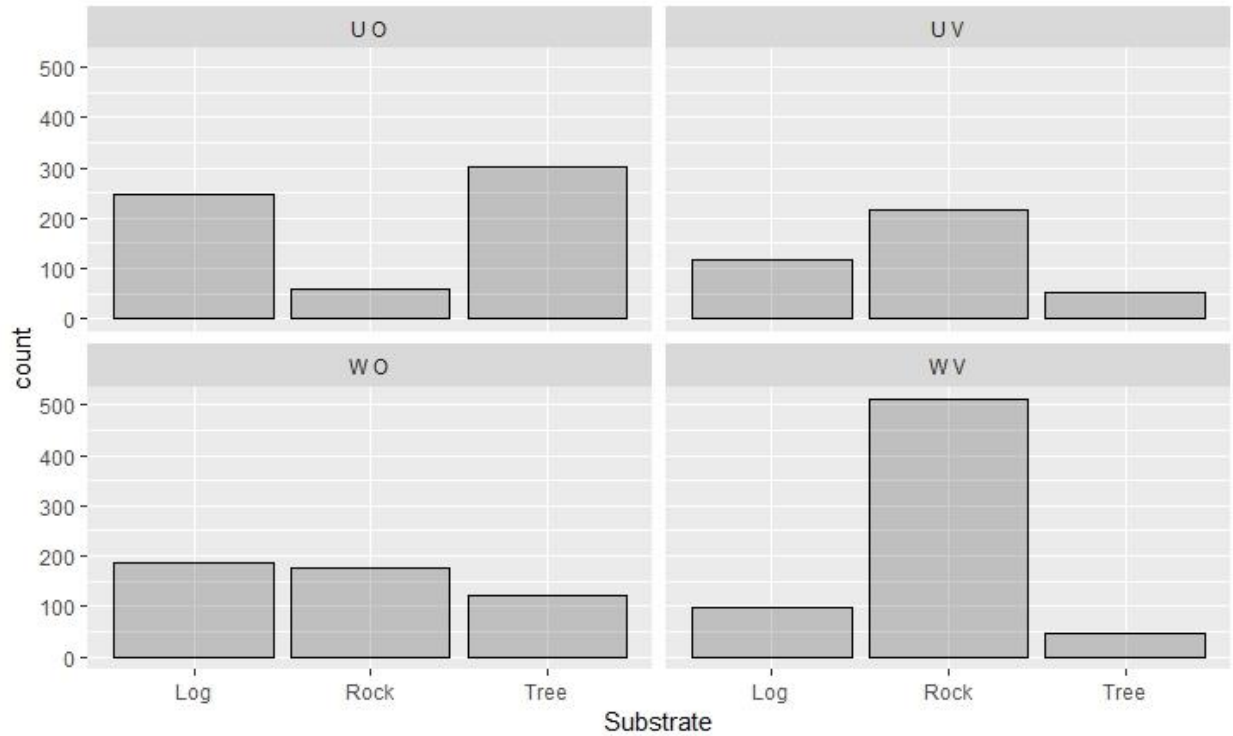
Based on the correlation coefficients obtained for the effect of species on all four indicators of structural microhabitat (substrate type, percentage of canopy cover, perch height and perch width), species explained nearly 4 times more of the variance than sex did, both in the upland (species:  $r = 0.113$ , sex:  $r = 0.033$ ) and in the wash (species:  $r = 0.080$ , sex:  $r = 0.023$ ). The interaction between species and sex had no significant effect on any of the indicators of structural microhabitat and explained a negligible proportion of the variance (upland:  $r = 0.003$ , wash:  $r = 0.004$ ).

**Table 1.** Prey composition of *Urosaurus ornatus* and *Sceloporus virgatus* fecal pellets, 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).

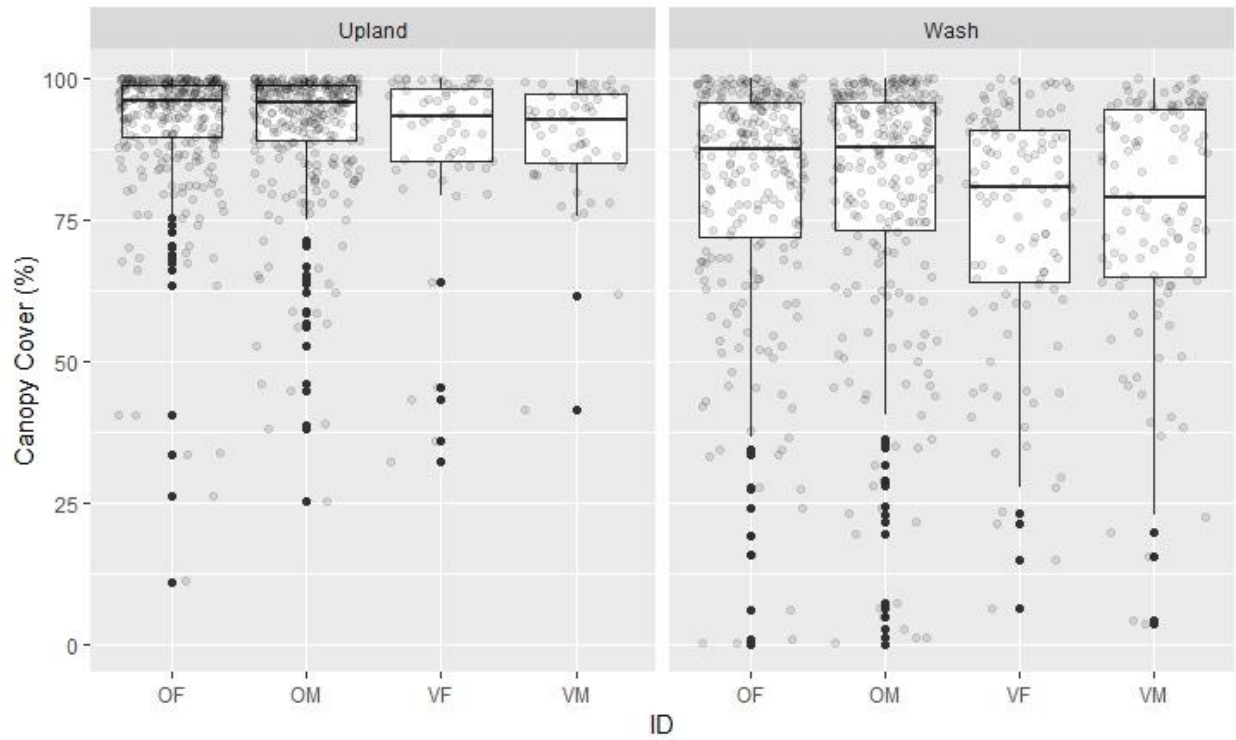
Prey item	<i>U. ornatus</i>			<i>S. virgatus</i>		
	No.	%N	%Freq	No.	%N	%Freq
Hexapoda						
Insecta						
Coleoptera	162	8	58	62	4	42
Diptera	4	<1	4	1	<1	1
Hemiptera	72	4	38	127	9	44
Homoptera	5	<1	4	9	1	9
Hymenoptera	1634	85	98	1142	82	89
Lepidoptera	14	1	14	20	1	22
Mecoptera	2	<1	2	0	0	0
Orthoptera	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>	



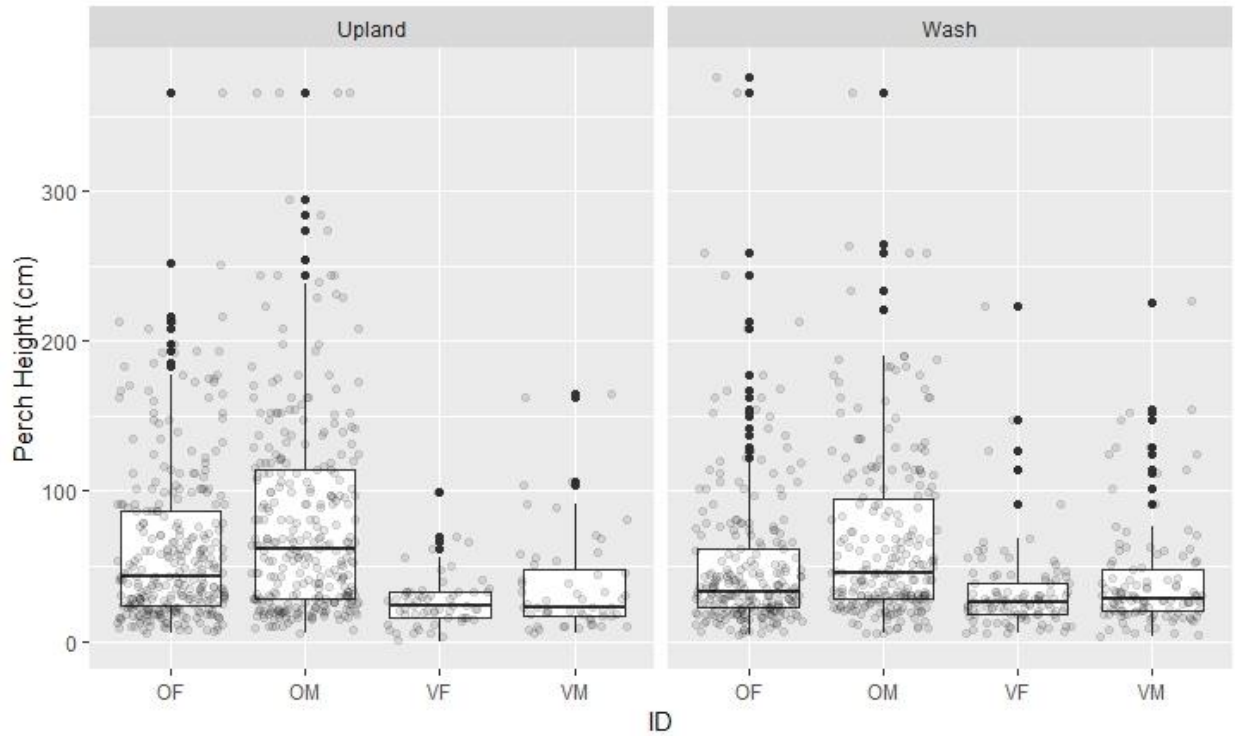
**Figure 4.** 5<sup>th</sup> percentile of the time at which the first individual was observed daily did not differ between species (*Urosaurus ornatus* and *Sceloporus virgatus*) or habitat types (upland and wash) at ten sites in the Chiricahua Mountains of Arizona, USA. *Urosaurus ornatus* lizards are represented by the letter “O”, whilst *Sceloporus virgatus* lizards are represented by the letter “V”.



**Figure 5.** Proportional usage of each substrate type (log, rock and tree) differed between species in the upland habitat but did not differ in the wash habitat nor between sexes within each species (*Urosaurus ornatus* and *Sceloporus virgatus*). “U O” represents *U. ornatus* individuals found in the upland habitat, “U V” represents *S. virgatus* individuals found in the upland habitat, “W O” represents *U. ornatus* individuals found in the wash habitat, and “W V” represents *S. virgatus* individuals found in the wash habitat.

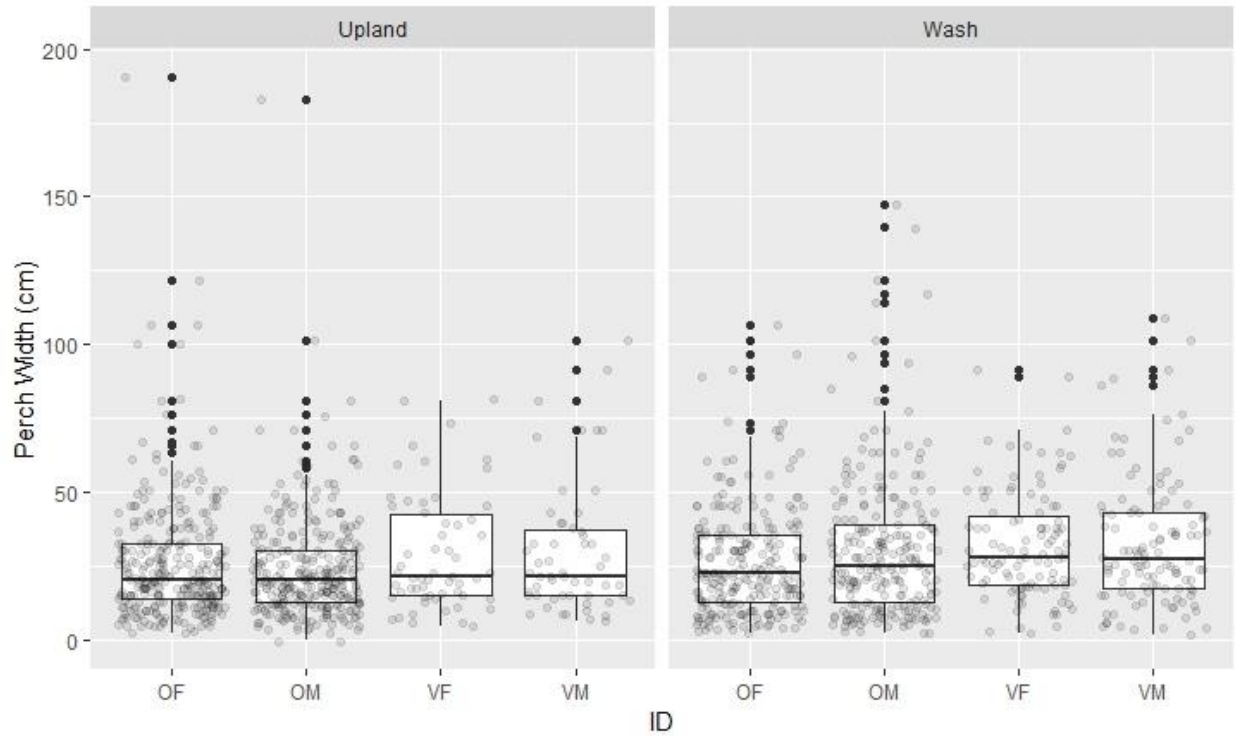


**Figure 6.** Percentage of canopy cover measured at each lizard’s individual perch differed between species in bot habitat type (upland and wash), but not between sexes. “OF” represent *U. ornatus* females, “OM” represents *U. ornatus* males, “VF” represents *S. virgatus* females, and “VM” represents *S. virgatus* males.



**Figure 7.** Height of the perch at which each lizard was observed differed significantly between species as well as between sexes in both habitat types (upland and wash). “OF” represents *U. ornatus* females, “OM” represents *U. ornatus* males, “VF” represents *S. virgatus* females, and “VM” represents *S. virgatus* males.





**Figure 8.** Width of the perch at which each lizard was observed differed significantly between species in both habitat types (upland and wash), but between sexes in neither. “OF” represents *U. ornatus* females, “OM” represents *U. ornatus* males, “VF” represents *S. virgatus* females, and “VM” represents *S. virgatus* males.

## Discussion

To minimize competitive pressures and the harmful impact they may have on individual fitness (Schoener, 1983), potentially competing sympatric species often partition resource use along at least one of three main ecological niche dimensions: spatial, temporal, and dietary (Kolbe et al., 2008; Losos, 2009). I studied indicators of these three ecological niche dimensions in two species of sympatric, insectivorous lizards commonly found along canyon bottoms in the Chiricahua Mountains of Arizona, USA, to test the hypothesis that these lizards have distinct ecological niches to minimize interspecific competition. Although the ornate tree lizard (*Urosaurus ornatus*) and the striped plateau lizard (*Sceloporus virgatus*) had very similar diets and periods of activity, they differed along the spatial axis of their ecological niches.

### *Diet*

*U. ornatus* and *S. virgatus* are diurnal, insectivorous, sit-and-wait foragers, and there was no evidence that they were selectively feeding on different types of prey items, as dissections of lizard fecal pellets showed. In fact, dietary overlap was 0.996 (on a scale of 0-1, with 0 indicating no overlap), indicating nearly perfectly identical resource use between the two species. Arthropods were the main food resource used by both species, hymenopteran insects 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 ornate tree lizards and striped plateau lizards, hymenoptera made up approximately three quarters of all prey items consumed, whilst no other prey item identified represented more than 12% of the diet. Therefore, it seems *U. ornatus* and *S. virgatus* do not partition resources along the dietary component of their ecological niches.

Perhaps *U. ornatus* and *S. virgatus* 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 throughout the year, maybe during times when resources are more scarce and interspecific competition becomes more intense. Cole and Harris (2011) found that, although overlap in diet between the house gecko (*Hemidactylus frenatus*) and the ornate day gecko (*Phelsuma ornate*) 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 *U. ornatus* and *S. virgatus* partition dietary resources at a finer taxonomic level. We identified prey items down to order, and so although both species fed primarily on ants (and other hymenopterans), they might 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.

A potential concern in examining lizard diet via fecal pellet analyses is that soft-bodied arthropod prey may 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. The data presented here also represents the first quantitative diet study that we know of for *U. ornatus* and *S. virgatus*.

### *Activity*

Temporal partitioning between sympatric 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, ornate tree lizards (*Urosaurus ornatus*) and striped plateau lizards (*Sceloporus virgatus*) 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 active period of the lizards, and study seasonal variation as well, to better describe the activity patterns of these lizards. In the case of the house gecko (*Hemidactylus frenatus*) and the ornate day gecko (*Phelsuma ornate*), for example, temporal overlap varied significantly throughout the year: it was quite high during the dry season, but very low during the wet season (Cole and Harris, 2011). It is possible that *U. ornatus* and *S. virgatus* may display such seasonal variations in their active periods as well. Further research could also include continuous temperature measurements to determine whether these patterns of daily activity are related mainly to thermal constraints in the environment, and if the effect of temperature on the active period is the same for both the ornate tree lizard and the striped plateau lizard.

### *Microhabitat*

The ornate tree lizard (*Urosaurus ornatus*) and the striped plateau lizard (*Sceloporus virgatus*) diverged along the spatial microhabitat niche dimension. Although both species perched on logs, rocks and tree, the proportion at which they used each of these substrates was significantly different, at least within the upland habitat. Ornate tree lizards were most often observed on trees and logs, whereas striped plateau lizards perched mainly on the boulders scattered on the ground in these pine-oak woodlands. 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 made up of 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 *U. ornatus* and *S. virgatus* in the wash habitat.

The perches both species used the most also differed in their canopy openness, height and width. In both habitat types, the ornate tree lizard used higher and narrower perches with a greater percentage of canopy cover than the striped plateau lizards. These results are in line with those obtained by other studies that evaluated resource partitioning and ecological niche separation in sympatric lizard species (Losos et al., 1993; Losos, 2009; Dufour et al., 2018). For example, after the introduction and invasion of *Anolis cristatellus* in Dominica, the native *Anolis oculatus* shifted towards higher perches, whilst the introduced species moved downwards (Dufour et al., 2018). Similar patterns were obtained in Grand Cayman, where the native *Anolis conspersus* was found to select 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* was found to use lower perches, sunnier microhabitats and perch 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, within both lizard species, there were also significant differences in perch height between sexes: males generally occupied higher perches than females, and this effect was significant in both habitat types. This is a commonly observed trend in lizards, as many field studies have reported that males perch higher than females (Zucker, 1986; Radder et al., 2006). Ornate tree lizards are no different: males have been found to select higher perches than females (Zucker, 1986) year round, although even more so during the breeding period, and showed 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 items when food is scarce, and the social-role hypothesis which suggests that sexual differences in social behavior (e.g. male territoriality) are responsible (Zucker, 1986). However, our analyses revealed near perfect dietary niche overlap ( $O_{jk}$  values of 0.998 for *U. ornatus* and 0.989 for *S. virgatus*) between sexes within each species, rendering the first hypothesis unlikely in this case. 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). Although my study is the first to show a difference between sexes in perch height in *Sceloporus virgatus*, it is plausible that similar mechanisms to those driving this pattern in *Urosaurus ornatus* are responsible.

Despite these significant effects species and sex were found to have on multiple indicators of structural microhabitat, correlation coefficients showed that effect sizes were fairly small. Overall, species explained approximately 11% of the variance in microhabitat in the upland and 8% of the variance in microhabitat in the wash, whilst 3% of the variance could be attributed to sex in the upland, and 2% could be attributed to sex in the wash. Therefore, although differences in microhabitat use may help explain why very little evidence of interspecific competition between these two sympatric insectivorous lizard species has been found, other factors that could not be measured or accounted for in this case likely play a significant role.

It is also important to note that, although the order of visits to each site was arranged to minimize this issue, because lizards were not marked permanently, recaptures could not all be accounted for. Therefore, some degree of pseudoreplication may have been at play. However, total

populations of *U. ornatus* were estimated at 9 out of our 10 study sites in 2016, and were found to range from approximately 80 to 370 individuals (Paterson and Blouin-Demers, 2018). Therefore, as populations were fairly large, this degree of pseudoreplication was likely reasonably small.

### *Conclusion*

Interspecific competition for resources is potentially harmful to any given individual's 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). I showed that the ornate tree lizard (*Urosaurus ornatus*) and the striped plateau lizard (*Sceloporus virgatus*), two sympatric insectivorous 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. In the upland habitat, the ornate tree lizard was most often sighted on trees, whilst the striped plateau lizard was generally found on rocks, and in both types of habitat (upland and wash), the ornate tree lizard used higher and narrower perches with a greater percentage of canopy cover than the striped plateau lizard did. I characterized and compared these two lizard species' ecological niches, and found that they partition resources, plausibly to minimize interspecific competition.

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