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COMPARATIVE SPATIAL AND BEHAVIORAL ECOLOGY OF THE PRAIRIE
LIZARD *SCELOPORUS CONSOBRINUS* IN THE ARKANSAS RIVER VALLEY

By

E.A. FREE KASHON

Submitted to the Faculty of the Graduate College of
Arkansas Tech University
in partial fulfillment of the requirements
for the degree of
MASTER OF SCIENCE IN FISHERIES AND WILDLIFE SCIENCE
August 2020

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Acknowledgements

I would like to thank my major adviser, Dr. Chris Kellner, for the countless and invaluable conversations about research, reptiles, study design, and everything in between. Without his open-door policy and willingness to answer every question I threw at him this would not have been possible. Thank you to my committee members, Dr. Doug Barron and Dr. Tom Nupp for their assistance in study design, analysis, and reminding that scientific writing is telling a story that people are excited to hear. I would like to extend a heartfelt thank you to the McMahons, who opened their home to me when I had nowhere else to stay. Finally, a very special thank you to Grace, who believed in me when I did not and helped me push through the toughest times.

Abstract

Habitat-driven differences in reptile life-histories have been observed in many species. Prairie lizards, *Sceloporus consobrinus*, in the Arkansas River Valley inhabit rocky, forested, and intermediate habitat types that exhibit different thermal resource availabilities and habitat structures. I studied prairie lizard space usage and antipredator responses to examine whether lizards exhibit habitat-driven differences in ecology, and whether these differences are influenced, in part, by individual personality. I utilized radio telemetry to track lizards in each of these habitat types and established estimates of space usage and daily linear movements. I used behavioral approaches to quantify lizard antipredator responses to a simulated predator. Prairie lizards did not exhibit differences in three estimates of home range size (95% MCPs, 95% KDEs, and 50% KDE core use area estimates) or standardized daily linear movements among the three habitat types. Prairie lizards also did not express an effect of personality on their movements. Lizards did not differ in flight initiation distance or escape distances among the three habitat types. Individual differences in personality explained a significant amount of the variation in escape distances but not flight initiation distances. Overall, lizards exhibited space usage and behavioral responses that were independent of habitat type characteristics and expressed a pattern of generalist life-histories that have not been observed in Sceloporine lizards before. This may be due to population wide response to selection pressures or a late spring freeze that greatly altered the demographics of the local population.

Keywords: habitat differences, home range, substrate usage, flight initiation distance, escape, personality, *Sceloporus consobrinus*

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General Introduction

Study Species

Sceloporus consobrinus is a small Phrynosomatid lizard that ranges from New Mexico to the Mississippi River and from northern Nebraska to central Texas (Leaché 2009). It primarily utilizes forest edges but is known to utilize more open areas (Conant and Collins 1998, Walkup et al. 2017). It is an insectivorous ambush predator and usually observes prey from a tall perch (McElory et al. 2012), and exhibits a polygynous breeding behavior in which males establish home ranges that overlap the home range of as many females as possible (Ruby 1978) Prairie lizards were originally considered a subspecies of *S. undulatus*, listed as *S.u. hyacinthus* (Smith et al. 1992, 1998), but are now considered their own species (Leaché 2009).

Study Sites

All study sites were located within 30 kilometers of Russellville, AR. Russellville is located in southwestern Pope County, east of the Arkansas River. The city is bordered by the Illinois Bayou and Lake Dardanelle along the north and west sides, respectively. The average yearly maximum temperature is 22.9 °C, average annual mean temperature is 16.3 °C, and average yearly minimum temperature is 9.8 °C (NOAA). Temperatures peak during the summer months of July and August where the average temperature usually exceeds 32 °C.

Prairie lizards (*Sceloporus consobrinus*) in Central Arkansas inhabit rocky, forested, and mixed sites, each of which are thermally distinct (Bangs 2016). Rocky habitats exhibit higher average maximum temperatures and heat up more rapidly after daybreak. Rocky habitats are comprised of anthropogenic outcroppings of riprap and concrete proximately located near other man-made structures such as roads, dams, reservoirs, and boat ramps. Forested habitats are generally shady, and lizards actively seek out sun flecks for basking. Forested habitats include

mixed oak (*Quercus* spp.), hickory (*Carya* spp.), and shortleaf pine (*Pinus echinata*) along with an understory of vines and shrubs. Small dirt or paved paths produce breaks in the canopy that provide basking opportunities. Rocky habitats have no forest canopy; the only shade is provided by the rocks which lizards use as refuge from the sun and predators. Mixed sites are either open forest with a rocky understory or forest edges adjacent to large openings (Tomke 2018), and anthropogenic asphalt trails provide physical barriers between patches of forest and natural rock.

General Methods

Lizard Sampling

Data were collected during the spring and summers of 2018 and 2019. I searched for and captured lizards with a noose in 10 sites (Figure 1). After capture, I utilized calipers (Mitutoyo 6 Precision Dial Calipers) and a spring scale (PESOLA10050 Lightline Newton Spring Scale) to measure snout-vent length and mass. Sex was determined by the presence of bright blue ventral scales, which are found on the bellies and chins of male lizards but are absent on females. Juvenile lizards were not utilized due to size limitations and the purpose of this study.

CHAPTER 1:

HOME RANGE, MOVEMENT PATTERNS, AND MICROHABITAT USE OF THE PRAIRIE LIZARD *SCELOPORUS CONSOBRINUS* IN THE ARKANSAS RIVER VALLEY

Introduction

Home range can be defined as the area used by an individual to fulfill its biological requirements (Burt 1943). As such, home ranges can indicate the space an animal needs to fulfill its behavioral and foraging needs (Perry and Garland Jr. 2002). Consequently, factors that influence resource distribution and availability include habitat structure (Davis and Ford 1983, Hult and Germano 2015, Refsnider et al. 2015, Scoular et al. 2011), thermal habitat characteristics (Christian et al. 1983, Grant 1990, Gillis 1991, Huey 1991), and elevation (Ruby and Baird 1994, Ruby and Dunham 1987). Research has also revealed variation in home range as a function of body size (Harestad and Bunnell 1979, Jenkins 1981, Perry and Garland 2002), and sex (Hyslop et al. 2014, Rocha 1999). Animal home ranges are comprised of movements that an animal makes in order to forage, bask, find mates, and avoid predators. These movements are shaped by an individual's physiological and behavioral needs. Competition (Schoener 1977, Schradin et al. 2010) food availability (Jones 1990, Schoepf et al. 2015, Waldschmidt 1983), personality (Cote et al. 2010, Spiegel 2017), reproductive status (Cook 2004, Durbian et al. 2008, Rodewald and Foster 2005), and thermal distributions (George et al. 2017, Tracy and Christian 1986, Waldschmidt and Tracy 1983) combine to shape animal spatial use and cause intraspecific and interspecific variation in home range size.

Ectotherms are especially sensitive to the thermal resource distributions of habitats (Huey 1991, Porter and Gates 1969) because they shuttle between hot and cold microhabitats in order to thermoregulate. Reptiles utilize their environments to fulfill their life-history needs, which

includes shuttling in order to thermoregulate, defending territories, and foraging. Lizard thermoregulatory behaviors are partially dependent on the distribution of thermal resources which can vary spatially (Adolph 1990, Roughgarden et al. 1981). As such, active thermoregulation, which entails changing perch locations and shuttling between relatively hot and cold sites (Dzialowski and O' Connor 2001, Lutterschmidt 2012), requires reptiles to move throughout their environments. These movements differ among different habitat types; different habitat structures exhibit different thermal distributions and require animals to behave differently in order to optimize thermoregulation (Row and Blouin-Demers 2006). Temporal and spatial heterogeneity within a habitat shapes individual space use by requiring animals to shift their spatial usage in response to the distribution of different thermal patches (Tray and Christian 1986). Huey (1974) observed *Anolis cristatellus* travelling further to find sun in landscapes with less sunny patches. Anoles had to move farther in shaded sites to maintain optimal body temperatures than those in open parkland (Huey 1974). Temporal heterogeneity in a landscape also affects ectotherm space usage and may cause seasonal shifts in diel activity and movements. Galapagos land iguanas (*Conolophus subcristatus*) used habitats that differed in thermal availability and shifted their thermal behaviors and habitat usage throughout the seasons. (Christian et al. 1983).

Landscape structure is characterized, among other things, by habitat connectedness (Ross et al. 2012), and the distribution of occurring substrates (Sabo 2003). Animal space usage is influenced by the characteristics of the major habitat; for example, green anoles (*Anolis carolinensis*), exhibit different habitat use across habitat types. Green anoles living on the Tulane University campus which had a different vegetation structure than a nearby field, perched on leaves more than the natural field population.

Habitat structure also influences daily movements of reptiles. Interactions between weather patterns (Packer 1965), forage availability, predation risk, refuge availability, ambient temperature (Martin et al. 2013), and microhabitat structure (Nathan et al. 2008), influence daily movements and space use by reptiles. For example, the black-headed monitor (*Varanus tristis*), and white stripe-tailed goannas (*V. caudolineatus*), exhibit daily movement patterns that are dependent on the distribution of their preferred tree types (Thompson 1993, Thompson et al. 1999). These large lizards make longer movements to find trees when they are sparse. Similarly, snakes exhibit smaller movements when inhabiting their preferred sites; coachwhips (*Masticophis flagellum*) made smaller movements in their preferred Florida scrub habitat over other habitats types (Halsead et al. 2009). Smaller bodied reptiles also exhibit this trend. Texas horned lizards (*Phrynosoma cornutum*) keep distinctive patterns for a few days, and then move to new areas (Fair and Henke 1999). Horned lizards that travelled the greatest distances also had the largest home ranges (Fair and Henke 1999).

Lizards living in different habitats experience different selection pressures and habitat structures. These selection pressures have caused habitat influenced changes in morphology, at both the species (Collar et al. 2010, van Damme 1998, Vanhooydonck and Van Damme 1999, Vervust et al. 2007) and population level (Herrel et al. 2001). Changes in morphology, such as in limb length or head shape (Herrel et al. 2001) will shape lizard locomotive capabilities (Bauwens et al 1995, Losos 1990, Macrini and Irschick 1998), which in turn shapes their ability to move throughout their local habitats (Huey et al. 1989, Losos 1990). Lizards that are larger need to move throughout their habitats more, and in many species the larger the lizard the larger the home range size (Christian and Waldschmidt 1984, Perry and Garland 2002).

Within many species, males and females exhibit differences in home range and territory size (Ferner 1974, Griffiths 1999, Lewis and Saliva 1987, Perry and Garland Jr. 2002, Rocha 1999). This is often a result of reproductive strategies. For example, during the breeding season, males of polygynous species will have larger home ranges in order to encounter as many females as possible (Haenel et al. 2003, Martin 1994, Stamps 1983), while females establish exclusive territories to defend nesting sites and foraging resources (Ruby 1978, Woodley and Moore 1999). For example, male Yarrow's spiny lizards (*Sceloporus jarrovi*), a polygynous species, exhibited larger home range sizes and higher levels of aggression than females, but both males and females exhibited aggressive behavior towards both sexes (Ruby 1978).

The interaction between Sceloporine habitat use and thermal ecology has been well examined (Adolph 1990, Andrews 1999, Angert et al. 2002, Gillis 1991, Grover 1996). That research revealed that spiny lizards are able to maintain a consistent body temperature of 34-35° C (Brattstrom 1965) and are thermally conservative among habitat types and along elevation gradients (Ruby and Baird 1994). For example, a population of *S. occidentalis*, the western fence lizard, in the San Gabriel Mountains maintained consistent body temperatures across their range from 1200 – 2300 m (Adolph 1990).

Sceloporine lizards use different habitats across their range. For example, *Sceloporus undulatus* (now *S. consobrinus* [Leache and Reeder 2002]) in the White Sands Formation in New Mexico utilized two different habitat types within the larger available habitat: darker soils on the edges of white sand gypsum dunes and the dunes themselves (Refsnider et al. 2015). These habitat types differed in vegetation structure and predation pressures, with the dunes having less vegetation and fewer predators. The two populations exhibited differences in perch usage, daily distances travelled, and differences in the variance, but not the mean, of their home range sizes.

Lizards in the central dunes had higher variance in home range sizes than lizards that used edge habitats. Lizards may be able to travel further due to lower predation pressure in the dunes (Refsnider et al. 2015). Williams and McBrayer (2015) compared Florida scrub lizard (*Sceloporus woodi*) microhabitat usage in two different sites that differed in undergrowth, tree diversity, and thermal patchiness. The two populations differed in perch usage, and lizards in sandhill habitats used hardwoods while those in the pine scrub habitat utilized sand pine exclusively (Williams and McBrayer 2015). Similarly, different elevations may also influence habitat usage in *Sceloporus spp.* Ruby and Dunham (1987) and Ruby and Baird (1994) found that *Sceloporus merriami*, the canyon lizard, and *S. jarrovi*, Yarrow's spiny lizard, both had larger home ranges at higher elevations and concluded the difference was due to interactions between food availability, population densities, and differences in female aggression and territoriality.

Although habitat structure has been shown to influence home range in Sceloporine lizards (citations listed above), little research has examined effects of habitat characteristics on daily movements and space usage of Sceloporine lizards. Previous literature has primarily focused on home range sizes or activity patterns; little attention has been given to influence of habitat structure on the movement ecology of *Sceloporus* species. Though previous research has examined their microhabitat usage and temporary occupancy, the literature is dated or based on small sample sizes. For example, an in-depth study of a single northern fence lizard, *Sceloporus undulatus hyacinthinus* (as above, this is now *S. consobrinus*, [Leaché 2009]) indicated that that individual used a small area of habitat composed of a single oak where the lizard spent much of its time (O'Brien et al 1965). Larger sample sizes and in-depth studies of *Sceloporus* species are required to better understand factors that influence the spatial ecology of the genus.

In this study, I examined the spatial ecology of the prairie lizard (*Sceloporus consobrinus*) in the Arkansas River Valley, which inhabit rocky, mixed, and forested habitat types. Because these habitats have different microclimates, substrates, and possibly prey availabilities; they provide an opportunity to study the effects of different habitat characteristics on microhabitats and microclimates on space use of prairie lizards, all of which influence space use in ectotherms (Grant 1990, Huey 1991, Sabo 2003, Simon 1975, Tracy and Christian 1986). I hypothesize that lizards in rocky sites will have smaller home ranges and territories, exhibit more consistent microhabitat selection, and exhibit smaller linear movements than lizards in forested and mixed habitat types because rocky habitats are warmer and exhibit structurally complex microhabitats that provide easy access to basking sites and refugia. I also predict that males will have larger home ranges than females due to the polygynous reproductive strategy of prairie lizards, and that larger lizards will have larger home ranges.

Methods

Initial Capture

Data were collected in the spring and summer of 2018 and 2019. I searched for and captured lizards with a noose in 10 sites (Figure 1). If the lizard was large enough and had an intact tail, I attached a radio transmitter (BioTrack Pip Ag317 transmitters, 21 ms, 52 bpm, and 12 ms, 31 bpm, antenna length 8 cm. .045g) by utilizing super glue (Gorilla Super Glue, Gorilla Glue Inc, Cincinnati, Ohio 2018). I placed transmitters along the pelvic girdle with the antenna along the tail to reduce the inhibition of locomotion. Based on recommended protocol (Knapp and Abarca 2009), I aimed to place transmitters on lizards with a body mass of 6.4 grams or higher in order to keep the transmitter mass less than seven percent of lizard body mass. With

one exception (5.4g) I was able to maintain this rule and limit the range of this ratio (3.13-8.33%).

The effects of transmitters on individual animals has been primarily studied in birds, and though transmitters negatively affect life history traits such as foraging behaviors and survival body condition, the effects were found to be universal and independent of the attributes of the individual animals that bore the transmitters (Barron et al. 2010). As such, the effects of the transmitters were universal. Therefore, lizards bearing transmitters as part of this study likely incurred costs as a result of the transmitters but were equally affected across all individuals and habitat types.

After attaching the transmitter, I obtained a coordinate by utilizing a Trimble Geo 7x GPS unit (Trimble Inc. Sunnyvale, California 2018, +/- .5m). I also recorded the surface temperature of the lizards perch with an infrared thermometer (MiniTemp MT6, Raytek, Wilmington North Carolina, 2018), ambient temperature and relative humidity with a sling psychrometer (Model 1328, Taylor Precision Products, Las Cruces, New Mexico, 2018), wind speed (2018 only) with a handheld weather meter (M-2 Weather Meter, Ambient Weather, Chandler, AZ, 2018) and canopy cover with a canopy densiometer (Forestry Suppliers Spherical Convex Crown Densiometers, 2018).

Relocations

Lizards were relocated at least once or twice a day, five days a week. The first site I visited each morning was randomly chosen, but each subsequent site was visited by proximity, in order to reduce travel time among sites. This reduced potential bias for time of day of lizard relocations. I recorded lizards during their active periods between 0800 -2000 each day. I relocated lizards by utilizing Advanced Telemetry Systems receivers and an Advanced

Telemetry Systems Yagi 3-element antenna to get me sufficiently close to visually locate each lizard. For lizards that I could not visually locate, my field assistants and I identified the location by the strongest signal. At each relocation, I used the Trimble unit to obtain a coordinate with at least 45 averaged points and collected the microhabitat and microclimate data in the manner stated above. I waited at least one hour between sequential relocations to decrease spatial pseudoreplication.

Transects

In 2018 and 2019 I established transects to characterize the substrate type both used and available to lizards. These data were utilized in an analysis of substrate type use. I utilized 30 meter transects and a quadrat to visually estimate ground cover at 0,10,20, and 30 meters. Ground cover types included leaf litter, vegetation, rock, woody debris, gravel, bare ground, or anthropogenic (manmade trails or concrete structures). In 2018, I had not established estimates of the lizards home ranges at the time I established the transects, so I placed a transect through the longest axis of a roughly estimated home range for each lizard to characterize the “used” substrate types. I then established another transect, 20 meters away from the estimated home range, in order to characterize “available” substrates.

In 2019, I had established an estimate of the home ranges for each lizard and was able to more accurately establish these transects. I utilized the longest axis of the home range estimate to establish the transects through the actual home range, and then walked at least 20 meters away from the home range estimate in order to estimate “available” substrates.

Lizard Home Ranges

I used ArcMap 10.3.1 (ESRI, Redlands, California), the Geospatial Modeling Environment (GME, Spatial Ecology LLC), and R 3.6.2 (R Core Team, 2013) in order to

calculate lizard home ranges and daily linear movements. I used minimum convex polygons (MCPs) and Kernel Density Estimators (KDEs) as estimates of individual home range sizes. I utilized a 50% KDE isopleth to estimate the core use area for each lizard.

In order to create each home range estimate, I created point shapefiles of each lizard's relocations, which were downloaded from the Trimble Geo7x GPS unit and postprocessed by utilizing the Trimble GPS Pathfinder software (Trimble 2018). I then used the GME to create 95% minimum convex polygons and kernel density estimators at both the 95% contour (home range) and the 50% contour (core use area). I then used ArcMap to calculate the areas for each of these polygons.

I analyzed potential differences in home range and core use area size by applying a Wilcoxon rank-sum test, and Kruskal-Wallis non-parametric ANOVA to determine whether these measures of use differed between the sexes, and among habitat types.

Daily Linear Movements.

I utilized the Geospatial Modeling Environment and ArcMap 10.3.1 to create measurements of the distance lizards travelled between subsequent relocations. I then standardized these distances as daily linear movements by dividing the distances by the amount of time that had passed between the subsequent relocations. This created standardized movements, which I used in my analyses. I next utilized Kruskal-Wallis non-parametric ANOVAs to determine whether lizard movements differed by habitat type. I also examined whether lizards differed in their daily movements as a function of morphology by using linear models.

During the summer of 2019, I also tracked a subset of lizards (4LFWM4, 4LFWM2, 4NDGF1) in a more intense manner. These lizards were easily observed and located in sites that

facilitated observations with a set time interval between observations. I tracked these lizards every fifteen minutes for a larger number of observations ($n = 17-25$) to characterize the effects of microhabitat structure on lizard movements while maintaining constant intervals between relocations.

Effect of Lizard Identity on Daily Linear Movements

As stated above, I utilized a univariate Kruskal-Wallis ANOVA to analyze potential differences in daily linear movements among the habitat types. Individual animal identity has been implicated as an important factor in movement ecology (Spiegel et al. 2017). In order to account for this, I used a linear mixed model to determine the effects of individual lizard identity on linear movements across the habitat types. My model utilized habitat type as a fixed effect, lizard identity as a random effect, and standardized movements as the response variable. I then utilized the function *repeatable* (Carlson 2018), to parse out the amount of variance attributable to differences in the random effect (lizard identity). This gives the amount of variance explained by the inherent differences due to individual differences in movement behavior. In order to compare the explanatory value of this linear mixed model to the univariate Kruskal-Wallis analysis, I used an ANOVA to compare the explanatory value of each model. This allowed me to determine whether lizard identity is an important factor in lizard daily linear movements.

Habitat Characteristics

I collected ambient and substrate temperatures in the field to characterize the environment of lizards during each relocation. Ambient temperatures experienced by lizards during relocations differed significantly (Kruskal-Wallis $\chi^2 = 8.95$, $df = 2$, $p = 0.011$), and a Dunn's post-hoc test indicated that lizards in mixed and forested habitat types experienced cooler temperatures than those in rocky habitats, but ambient temperatures did not differ between mixed

and forested habitats (Figure 2). Availability of substrate types differed among the habitat types; some substrate types, such as riprap (found in rocky habitats), were exclusive to one habitat type. This resulted in a confounding of habitat type and substrate type. The substrate temperatures experienced by lizards in the three habitat types were also different (Kruskal-Wallis $\chi^2 = 9.23$, $df = 2$, $p = 0.009$; Figure 3), and a Dunn's post-hoc test indicated that rocky habitat substrates were warmer than substrates in mixed and forested habitats. Because substrate temperature and ambient temperature were significantly and positively related ($F_{1,376} = 72.82$, $B = 0.81$, $SE = 0.061$, $p < 0.001$, $R^2 = 0.32$), I did not treat these as separate predictor variables.

Compositional Analysis

I used the data I collected along the transects to perform second-order compositional analysis. I grouped transect data by habitat type. Available habitat was characterized as the average of the ground cover percentages for all lizards inside and outside their home ranges. Used habitat was characterized as the average ground cover percentage calculated from the five measured quadrats for each lizard. I then compared the used habitat to the available habitat to create a metric of lizard habitat preferences. Analysis was performed by utilizing the *compana* command in the *adehabitatHS* package (Calenge 2000) within *R* version 3.6.2. (R Core Team 2020).

Results

Home Ranges

The median MCP home range estimates of lizards in rocky (339.32 m²), forested (185.04 m²), and mixed (240.59 m²) habitat types did not significantly differ (Kruskal-Wallis $\chi^2 = 4.047$, $df = 2$, $p = 0.132$). Male (268.16 m²) and female (212.99 m²) MCP home range estimates did not significantly differ ($W = 43$, $p = 0.470$). Minimum convex polygon size did not increase as a

function of the number of relocations used to estimate them ($F_{1,24} = 0.001$, $B = 0.62$, $p = 0.970$). Neither mass nor snout-vent length had a relationship with home range size. Snout-vent length did not have a significant relationship with MCP size ($F_{1,19} = 0.6101$, $B = -70.78$, $p = 0.444$), and home range was not effected by mass (minimum of 5.8 grams; $F_{1,19} = 0.3845$, $B = -80.25$, $p = 0.543$).

Lizards in rocky (1140.00 m²), forested (1406.59 m²), and mixed (963.02 m²) habitat types exhibited median KDE home range estimates that were not significantly different (Kruskal-Wallis $\chi^2 = 1.80$, $df = 2$, $p = 0.412$). Male (1127.82 m²) and female (1095 m²) KDE estimates did not differ significantly ($W = 43$, $p = 0.450$). KDE size did not increase with snout-vent length ($F_{1,19} = 0.72$, $B = -267.5$, $SE = 316.2$, $p = 0.410$, $R^2 = -0.0144$) nor with mass ($F_{1,18} = 0.51$, $B = -322.3$, $SE = 450.2$, $p = 0.483$, $R^2 = 0.03$).

The core area (50% KDE estimates) of lizards in rocky (166.15 m²), forested (301.43 m²), and mixed habitat types (133.73 m²) were not significantly different (Kruskal-Wallis $\chi^2 = 2.37$, $df = 2$, $p = 0.31$). Male (191.62 m²) and female (83.42 m²) core areas were not significantly different ($W = 33$, $p = 0.153$). Neither SVL ($F_{1,19} = 0.82$, $B = -70.25$, $SE = 77.77$, $p = 0.384$, $R^2 = -0.009$) or mass ($F_{1,18} = 0.49$, $B = -77.92$, $SE = 111.6$, $p = 0.492$, $R^2 = -0.03$) were significantly related with core use area size.

Daily Linear Movements

Lizard daily linear movements in rocky (198 m), forested (192 m), and mixed (164.5m) habitat types were not significantly different (Kruskal-Wallis $\chi^2 = 2.89$, $df = 2$, $p = 0.244$; Figure 4). Males (193.5 m) and females (161.5 m) did not differ in their daily linear movements ($W = 15843$, $p = 0.111$). Neither SVL ($F_{1,11} = 2.00$, $B = -3.74$, $SE = 2.65$, $p = 0.192$, $R^2 = 0.08$) nor mass ($F_{1,11} = 1.84$, $B = -5.30$, $SE = -5.30$, $p = 0.202$, $R^2 = 0.07$)

I accounted for the effects of personality and found that only 3% of the variance in the model was accounted for by lizard identity. When I compared the explanatory value of the linear mixed model with the univariate model, I found that they did not significantly differ ($F_{2,21.725} = 0.85, p = 0.444$).

My detailed analysis of individual lizard indicated that the extent of linear movements performed by lizard 4LFWM4 was primarily determined by substrate type. This lizard utilized riprap, anthropogenic, and vegetation substrates, and exhibited a difference among these substrate types (Kruskal-Wallis $\chi^2 = 8.58, df = 2, p = 0.010$). A Dunn's test indicated that the lizard differed in movements between anthropogenic substrates and riprap but did not exhibit a difference in movements between these substrates and vegetation. Movements by 4LFWM2 and 4NDGF1 did not have a linear relationship with any predictor and did not express differences in movements as a function of substrate type.

Compositional Analysis

I conducted compositional analysis on lizards living in three different habitat types. I found that only lizards in the mixed habitat types exhibited any degree of substrate type use more than what was available ($\Lambda = 0.074, p = 0.110$; Table 1). Comparisons in forested and rocky habitats did not converge, and lizards did not exhibit any form of preference.

Discussion

Space Usage Estimates

Prairie lizards did not exhibit differences in home range size between the sexes for any of the space usage estimates. This refutes my hypothesis, and both supports and contrasts previous findings. For example, Ferner (1974) examined home range size in *S. undulatus erythocheilus*, the red-chinned lizard, and reported that male home ranges were 2-3 times larger than female

home ranges while Jones and Droge (1980) observed no differences in home range size among males and females in *S. undulatus* (this population is now considered *S. consobrinus* [Leache and Reeder 2002, 2009]). *Sceloporus virgatus*, the striped plateau lizard, also exhibited differences between males and females (Smith 1985) and had large degrees of home range overlap in males. Overall, for most species, male *Sceloporus* have larger home ranges than females, and my work contradicts this trend.

Neither prairie lizard home range estimates nor core use estimates were significantly different among the three habitat types, which contradicts my hypothesis and previous research. As mentioned, the home range of *Sceloporus* species and other lizards is influenced by habitat characteristics. For example, European common lizards, *Zootoca vivipara*, (Ortega-Rubio et al. 1972) and the eastern fence lizard, (*Sceloporus undulatus*) both exhibit home ranges that are influenced by the characteristics of their habitat, including ground cover availability and vegetation structure. Other Sceloporine lizards also exhibit differences in home range size among habitat types. *S. merriami*, the canyon lizard, exhibits home range size differences along an elevational gradient (Ruby and Dunham 1987), while *Sceloporus areicolus*, the dunes sagebrush lizard, occupied larger home ranges in unfragmented areas as opposed to fragmented areas.

Prairie lizards exhibited a surprising lack of plasticity among the habitat types. The lack of significant differences in space usage may be due to a rigidity of life-history traits not found in other populations of *Sceloporus consobrinus* or Sceloporine lizards overall. Rocky, forested, and mixed habitats differ in thermal resource distributions and substrate type availability and structure but prairie lizards in my study area did not respond accordingly and instead utilized the available space similarly across all habitat types. Factors of space usage observed in other

Sceloporus species did not affect prairie lizard home range establishment nor the size of their core use areas.

Food availability, which alters home range size and establishment patterns in lizards (Krekorian 1976, van Sluys 1997, Waldschmidt 1983) drives space use but may not have an effect on lizards in the river valley. Even though lizards residing in the three different habitat types probably encountered different availabilities and diversities of prey, it is possible that resource levels in the three habitats were sufficient to reduce the influence of food availability on prairie lizard space use. Prey availability to lizards in rocky habitats may have been subsidized by Lake Dardanelle, which was adjacent to some of the rocky habitats. A similar subsidy has been observed in the western fence lizard (Sabo and Powers 2002). Fence lizards that lived along a riparian zone experienced a subsidy of invertebrate prey that had larger body sizes compared to fence lizards not experiencing this subsidy. The similar subsidy experienced by *Sceloporus consobrinus* may have reduced variance in prairie lizard space usage and reduced the effect of different food availability among the habitat type.

Prairie lizards are thermally conservative, and efficient thermoregulators throughout their daily activity periods (Brattstorm 1965). Though the three habitat types differed in available ambient and substate temperatures, lizards did not differ in their space usage among these different thermal resource distributions. The thermally conservative nature of *Sceloporus consobrinus* may have reduced the effect of thermal resource differences among the habitat types. Though the rocky habitats are hotter than mixed and forested habitats, prairie lizards did not differ in space usage among the habitats.

Overall, prairie lizards exhibited home range estimates independent of habitat structure and thermal availability they were experiencing. Instead of fitting their space usage to their local

habitats, prairie lizards exhibited space usage that was consistent among populations in each of the habitat types. They exhibited space usage that was universal among the habitat types and exhibited a rigidity in life history that reflects previous research on this population. *Sceloporus consobrinus* in the Arkansas River Valley also exhibited similar size and age class distributions (Bangs 2016), and similar mortality rates (Kellner unpublished data 2019).

A possible explanation for this lack of home range differences among habitats was a late season freeze in April of 2018. Sub-freezing temperatures after the start of prairie lizard active season was associated with a large decrease in population size of prairie lizards in the Arkansas River Valley (Kellner pers. Obs.). This great reduction in population may have decreased competition for resources and allowed lizards to expand their home ranges beyond what they normally would have in previous years. Jones and Droge (1980) estimated male and female home range sizes of *Sceloporus undulatus* (now *S. consobrinus*) to be $121.1 (\pm 235.3)$ and $101.1 (\pm 315.7) \text{ m}^2$ for males and females, respectively. This drastic difference in home range estimates between this estimate and prairie lizards in my study, may be due to this late free. Previous studies have reported that the density of competitors influences home range size exclusivity in *Anolis aeneus*, the bronze anole (Stamps and Krishnana 1995,1998); anoles exhibited more exclusive home ranges in less populous areas. The very low densities of prairie lizards in the river valley may have reduced competition and increased home range exclusivity for both sexes.

I cannot say how much of an effect population size had on prairie lizard space usage. I am not aware of any studies that address effects of late season freezes on Scelopoperine lizards, but the number of lizards captured by Tomke (2018;n = 681) were much higher than the number of lizards I observed ($n_{2018} = 49$, $n_{2019} = 91$, $n_{\text{total}} = 140$). This drastic difference in the number of

animals reflects the heavy impact of the late season freeze and may point towards a form of competitive release for the lizards that did survive.

Daily Linear Movements

Prairie lizards did not exhibit differences in daily linear movements among the habitat types. Animals are expected to increase their movements due to different resource distributions (Doherty et al. 2019) but prairie lizards did not follow this trend. This is surprising as rocky, forested, and mixed habitat types differ in structure and thermal availabilities, Rocky habitats are primarily composed of riprap, a complex anthropogenic substrate that heats up quickly, and provides easy access to shelter. Mixed and forested habitats have a larger diversity of biotic substrates, but canopy cover reduces the amount of sun available to prairie lizards and are cooler than rocky habitats. *Sceloporus spp.* exhibit differences in microhabitat usage and movements due to structural habitat differences (Adolph 1990, Williams and McBrayer 2015) but I did not observe this in prairie lizards. Reflecting the lack of differences in home range estimates, lizards exhibited a generalist approach to moving throughout their home ranges. Instead of the thermal and structural differences driving lizard movements, lizard movements were similar throughout the Arkansas River Valley, and independent of external factors.

Lizard home ranges exhibited a significant relationship with the average linear movement of each lizard. This relationship has been observed in horned lizards (Wone and Beauchamp 2003) and indicates that lizards that make larger movements also hold larger home ranges. Thus, lizards who move further are going to traverse more ground and have home ranges that are larger than conspecifics that exhibited smaller movements. Similarly, the more widespread the resources in each home range were, the more the lizards had to move (Doherty et al. 2019), and in turn the larger their home ranges.

Male lizards did not exhibit greater linear distances than females. This is surprising, because Sceloporine lizards employ a polygynous breeding system that drives male behavior. Males typically spend time patrolling their home ranges and defending against other males (Sheldahl and Martins 200) and this territoriality typically drives males to move more than females. Territoriality influences home range size in Sceloporine lizards (Haenel et al. 2003), but prairie lizards that I studied did not exhibit differences in home range size or movements between the sexes, perhaps indicating that territoriality was not an important factor in *S. consobrinus* movements in the Arkansas River Valley.

I found that lizard identity did not account for a significant amount of variation in lizard movements; thus, the explanatory value of the linear mixed model did not significantly differ from the results from a simple Kruskal-Wallis comparison. This indicated that lizard personality was not important in determining how far lizards moved, and that prairie lizards did not move according to innate differences in movement behaviors.

Compositional Analysis

Lizards did not exhibit microhabitat preference within rocky or forested habitats. In mixed habitats, lizards used some substrates more than what was proportionally available. Lizards utilized rocky substrates in rocky habitats and trees and shrubs in forested and mixed habitats. Many studies of *Sceloporus* species have indicated that substrate use varies substantially among populations (Grover 1996). These differences in selection may be a function of availability; lizards in rocky habitats use rocky substrates more than others. Similar microhabitat preference has been observed in western fence lizards. Fence lizards in three habitat types (desert, mountain, valley), exhibited differences in perch height (Asbury and Adolph 2007) but utilized the same perch height when housed in a common area. This plasticity has also been

observed in the eastern fence lizard, which shifted use from primarily rocky outcroppings to woody debris and tree trunks during the active season. This shift in use is primarily driven by changes to available temperatures and possibly predation by collard lizards, *Crotaphytus collaris* (Angert et al. 2002). Differences in microhabitat selection have also been observed in Anolis lizards. The adults of two anole species, *A. gundlachi*, the yellow-chinned anole, and *A. krugi*, the olive brush lizard exhibited different microhabitat use that depended on microhabitat availability. This observed plasticity in lizards was also exhibited by *S. consobrinus* in the Arkansas River Valley. Prairie lizard microhabitat selection may be more dependent on localized availability than an innate preference for habitat types. For example, lizards in rocky habitats utilized rocky substrates, such as riprap, more than biotic substrates which were uncommon, while lizards in mixed habitats used biotic substrates, such as vegetation and leaf litter. This use of the dominate substrate in each habitat type may point towards a population wide plasticity in prairie lizard substrate use.

Refuge distribution, like thermal resource distribution, is an important factor of lizard microhabitat use (Cooper and Wilson 2007). Blunt-nosed leopard lizards (*Gambelia sila*) avoid habitats with thick vegetation, which inhibits their ability to escape predators (Warrick et al. 1998). Similarly, prairie lizards may use microhabitats that provide the best balance of thermal resources and access to refugia (Melville and Schulte II 2001, Warrick et al 1998). In rocky sites lizards utilized the rocky substrate more than). This preference for this microhabitat type may be due to the structure of the substrate, which provides easy access to refugia as well as ready availability of basking sites.

Overall, prairie lizards utilized microhabitats as a function of availability and thermal resource availability. Plasticity of microhabitat use possibly facilitates thermoregulation and

refuge use in prairie lizards and may have evolutionary consequences. Behavioral shifts in different habitats may buffer or drive natural selection on physiological and morphological traits (Asbury and Adolph 2007, Huey 2003); changes in morphology as a function of habitat structure have been observed extensively in *Anolis* (Elstrott and Irschick 2004, Irschick et al. 2005, Macrini et al. 2003, Moermond 1979). Subpopulations of prairie lizards in rocky sites may develop morphologies more suited to rocky substrates, while lizards in forested sites may adapt better to climbing on and utilizing biotic substrates, however Bangs (2016) did not find morphological differences in prairie lizards among the habitat types.

Conclusion

Sceloporus consobrinus in the Arkansas River Valley exhibit patterns of space usage that are different from previous studies of the spatial ecology of this genus. I did not observe a difference in space usage between males and females, and home range estimates did not differ among the habitat types, which contradicts the expected results based on previous research. The lack of differences between forested, rocky, and mixed habitats may be due to a generalist life history that is exhibited by prairie lizards in this system. Future research into prairie lizard spatial ecology should also include lizard identity in order to further understand the interaction between lizard personality and lizard spatial usage. Factors such as food availability and population size, should also be included in future studies. Food availability has been implicated in previous studies of lizard spatial ecology (Simon 1975) while knowing the current level of competition within a population may shed light on the relationship between habitat structure and space use. Overall, *Sceloporus consobrinus* exhibited spatial usage that is dependent on their personal needs more than microhabitat structure or thermal resource distribution.

CHAPTER 2:
ANTIPREDATOR BEHAVIORS OF THE PRAIRE LIZARD *SCELOPORUS CONSOBRINUS*
IN THE ARKANSAS RIVER VALLEY: DETERMINING THE EFFECTS OF
MORPHOLOGY, HABITAT, AND PERSONALITY ON FLIGHT INITIATION DISTANCES
AND ESCAPE MOVEMENTS

Introduction

Behavioral ecologists used to believe that animals exhibited behaviors that were “appropriate” to their current situation (Coleman and Wilson 1998, Dall et al. 2004, Wolf and Weissing 2012). However, we now know that animal responses to their environment exhibit considerable inter-individual variation (Bell and Sih 2007, Bell and Stamps 2004, Highcock and Carter 2014, Sih et al. 2004*ab*). Those differences in behavior are known as animal personality (Dall et al. 2004). Correlated behaviors such as exploration of novel environments and responses to predators, are known as behavioral syndromes (Sih et al. 2004, Sih and Bell 2008). The variance attributable to differences in behaviors among individuals, is an important component in the analysis of personality. Personality, manifested as repeatable behaviors, has been analyzed as a factor in movement dependent behaviors (Kobler et al. 2001, Pearish et al. 2013), foraging (Kurvers et al. 2020, van Overveld and Matthysen 2010), dispersal (Cote et al. 2010), and even speciation (Ingley and Johnson 2014).

The evolutionary origin and implications of animal personality are poorly understood (Dingemanse and Réale 2005), however, researchers now understand that individual differences in behavior are heritable (Boissy 1995, Koolhaas et al. 1999,) as are behavioral syndromes (van Oers et al. 2004, Bell 2005). Further, personalities can be influenced by intrinsic factors such as morphology (Le Galliard et al. 2013), and physiology (Biro et al. 2014, Careau et al. 2008, Goulet et al. 2016), and external factors such as habitat structure (Serrano-Davies et al. 2017), food availability (van Overveld and Matthysen 2009), and predation pressure (Brydges et al

2008). Within species, selection pressures arising from those factors may shape behavioral responses at the population and individual level. Similarly, animals exhibiting differences in morphology and physiology may exhibit differences in their abilities to forage (Johnson et al. 2008, McBrayer and Wylie 2009), locomote (Braña 2003, Husak and Rouse 2006), mate (Sinervo et al. 2000) and escape from predators (Jaksić and Núñez 1979).

Behavior and morphology are linked, and differences in one cause differences in the other. For example, capuchin monkeys exhibit variation in facial features, which has been linked to differences in neuroticism, attentiveness, and assertiveness (Wilson et al. 2010), while larger hatchling keelback snakes (*Tropidonophis mairii*) expressed higher levels of boldness and emerged from shelter faster than their smaller, shyer siblings (Mayer et al. 2016). Selection for behavioral phenotypes shapes morphology as well (Dingemanse et al. 2009, Kern et al. 2019, Santos 2015). For example, zebrafish (*Danio rerio*) artificially selected for boldness also had more elongate bodies and larger caudal regions (Kern et al. 2016). This bidirectional relationship may result from behaviors that are best facilitated by certain body types. Bolder zebrafish may allow predators to get closer, which requires a more hydrodynamic body for faster escapes, while having a larger body from hatching provides better defensive capabilities. As selection pressures shape behaviors, the morphological phenotypes that best facilitate these behaviors are also selected for, coupling morphology and behavior.

Internal factors, such as physiology, also influence animal personalities. Links between physiology and behavior have been examined previously in vertebrates, and differences in behavior are linked to energy expenditure (Careau et al. 2008, Biro and Stamps 2010, Careau and Garland 2012, Cote, J., J. Clobert, T. Brodin, S. Fogarty, A. Sih. 2010). For example, common wall lizards (*Podarcis muralis*) exhibit a negative relationship between their metabolic rates and

variation in sociability and activity (Mell et al. 2016). Metabolic rates differ among individuals, and these inherent differences may be the result of selection pressures for different “paces-of-life” that are connected to individual physiological processes (Biro and Stamps 2010).

Body temperature has also been linked to behavior in ectotherms (Rand 1964, Goulet et al. 2017). Some ectotherms are known to exhibit hot and cold thermotypes (Goulet et al. 2017). Hot individuals maintain body temperatures at the higher end of a species’ range, while cold individuals maintain the opposite. These different thermal types sometimes exhibit differences in habitat selection, locomotion, endocrine function, and energy budgets (Brodie and Russell 1999, Goulet et al. 2016, Goulet et al. 2017, Kashon and Carlson 2018, Langkilde and Boronow 2012, Stapley 2006). These thermal types may have implications for survival. “Hot” individuals may explore, forage, and mate more, while “colder” individuals will exhibit less risky behaviors. For example, eastern box turtles (*Terrapene carolina*) that maintained warmer body temperatures expressed higher levels of boldness (Kashon and Carlson 2018). This higher level of boldness may have resulted in more chances to mate but bolder turtles also experienced higher levels of predation (measured as a function of injury score on the carapace and plastron). “Hot” ectotherms also bask more in order to maintain higher body temperatures which also puts them at risk of predation (Goulet et al. 2016, Goulet et al. 2017, Kashon and Carlson 2018).

Thermal preferences have been strongly linked to behavior in wild populations. For example, Nile Tilapia (*Oreochromis niloticus*) exhibit a gradient of thermal preferences and individuals that favored warmer waters were characterized as proactive whereas animals that preferred colder waters were reactive (Cerquiera et al 2016). Zebrafish also exhibit these trends; warmer individuals express higher levels of boldness, aggressiveness, and are more risk prone than shy, colder fish (Rey et al. 2015). These trends have also been observed in lizards;

mountain log skinks (*Pseudemoia entrecasteaui*) exhibit differences in preferred body temperatures. Males with orange ventral colors had higher preferred body temperatures and were bolder and more aggressive than males with white venters (Stapley 2006). Males with orange venters required higher body temperatures to maintain their high levels of aggression as they fought off males with white venters and dominated mating opportunities (Stapley 2006).

Thermal preferences, metabolism, and behavior are closely linked in ectotherms and together regulate behavior (Goulet et al 2017, Michelangeli et al. 2018). Individuals with high metabolic rates, are often more active, aggressive, and bold, as these behaviors are linked with high foraging rates (Michelangeli et al. 2017), and thus high metabolic needs (Biro and Stamps 2010). Individuals with high metabolic rates spend more time basking in order to maintain body temperatures to sustain their “metabolic machinery” (Goulet et al 2017, Hixon 1980), and thus exhibit behavioral patterns that maximize energy assimilation (Brodie and Russell 1999, Careau and Garland 2012), which may include riskier behaviors (such as continuing to bask in the presence of a predator).

Behavior and habitat use have been linked in many animals (Holtmann et al. 2017, Wolf and Weissing 2012). For example, bolder bank voles (*Myodes glareolus*) occupied larger home ranges, and preferred areas with more vegetation. Similarly, house sparrows (*Passer domesticus*) exhibited different behavioral syndromes in habitats with different levels of urbanization. Birds in urban areas exhibited behavioral syndromes that included object neophobia and risk taking, while birds from rural areas also exhibited food neophobia in this syndrome (Bókony et al. 2012). Habitat structure has also been implicated in behavioral differences in Townsend’s ground squirrels (*Spermophilus townsendii*). The amount of time squirrels were vigilant in winterfat (*Krascheninikovia lanata*) dominated and winterfat-sagebrush (*Artemisia tridentata*)

dominated habitats was more than twice that of ground squirrels in sagebrush-dominated habitat (Sharpe and Van Horne 1998). Selection may cause animals to develop behaviors that are appropriate to their local environments and facilitate habitat related differences in behavior. For example, populations of Corsican blue tits (*Cyanistes caeruleus*) exhibit lower levels of aggression in deciduous downy oak forests (*Quercus pubescens*) than in evergreen holm oak forests (*Quercus ilex*; Dubuc-Messier et al. 2017). Habitat quality also affects animal behaviors; Mud crabs (*Panopeus herbstii*) were bolder in rich habitats than in poorer, adjacent habitats (Belgrad and Griffin 2018).

Different habitats may also be associated with differences in predation pressure, which can shape personality at the population and individual level (Smith and Blumstein 2008). For example, guppies (*Poecilia reticulata*) exhibit differences in emergence latencies after a predation event. Fish from high predation regimes emerged sooner after encountering a perceived threat than fish from low predation regimes (Harris et al. 2010). Heavy predation on three-spined sticklebacks (*Gasterosteus aculeatus*) increased boldness and aggression (Bell and Sih 2007) and boldness in perch (*Perca fluviatilis*) was associated with predation risk; fish that experienced increased predation pressures expressed more risk-taking behaviors (Magnhagen and Borchertding 2008). Behavioral changes within individual animals has been observed after exposure to predators. Delicate skinks (*Lampropholis delicata*) that had complete tail loss after a predator encounter exhibited lower activity and exploration levels and exhibited a decrease in within-individual behavioral variance (Michelangeli et al. 2019). The loss of their tail decreased their locomotive performance and mediated behaviors that were more consistent and were also less active within a behavioral syndrome. Brown anoles (*Anolis sagrei*) exhibited differences in their latencies to initiate exploration after exposure to a predator and exhibited differences in

exploration when raised in the presence or absence of predators. (Lapiedra et al. 2018). Overall, differences in predation pressure can shape behavioral syndromes, and animals will develop personality traits in accordance to their natal predation pressures (Harris et al. 2010).

Animal responses to predation have been used to quantify effects of personality in many animals (e.g. Sih et al. 2003, Lopez et al. 2005, Cooper 2009). Animals often exhibit either “shy” or “bold” personalities when responding to predators. Shy animals escape earlier and hide longer, while bold individuals will allow predators to approach closer and emerge from hiding sooner. Boldness has been evaluated in many lizards, and models of behavior have been developed that evaluate lizard escape behavior (*i.e.* optimal escape theory, Ydenberg and Dill 1986, Cooper and Frederickson 2007, Wilson and Cooper 2007) and this taxon exhibits links between boldness and body temperature, and habitat use (Wolf and Weissing 2012). For example, viviparous lizards (*Zootoca vivipara*) exhibit a relationship between morphology, thermal physiology, and behavior, and research has revealed repeatable levels of activity, aggressiveness (a form of boldness), and risk taking (Mell et al. 2016). Furthermore, lizards are known to exhibit behavioral syndromes which include boldness. Bolder goanna (*Varanus panoptes*) had larger home ranges and higher mating success than shy individuals (Ward-Fear et al. 2018), while bolder Namibian rock agamas (*Agama planiceps*) exhibited higher trapability (Carter et al. 2012).

Effects of personality on life histories has been studied in Spiny lizards (*Sceloporus spp.*) which are often common and are easily observed. These lizards exhibit habitat and personality driven differences in flight initiation distances which is a common measure of boldness (Cooper 2009) and escape distances (Cooper 2009). Research on spiny lizard behavior has revealed the effects of predation risk, (Avalos and Cooper 2010, Cooper 2005, Cooper 2009, Cooper 2011b),

age (Cooper 2011a), sex (Cooper and Wilson 2007), angle and starting distances of predator approach (Cooper 2005, Cooper and Avalos 2010) and cost of refuge use (Wilson and Cooper 2007, Cooper and Wilson 2008).

Prairie lizards are small spiny lizards that are ideal for studying boldness because they are abundant and easily observed. Their range extends from New Mexico to the Mississippi River and from northern Nebraska to central Texas (Leaché 2009). In the Arkansas River Valley, these lizards inhabit different habitats types (rocky, forested, and mixed; described in the previous chapter) that differ in microhabitat and thermal resource availability (Bangs 2016). Rocky sites are the hottest, least shaded, and most homogenous of the habitats, while mixed and forested sites are cooler and provide lizards access to biotic substrates and shade.

The primary objectives of this study are to (1) determine whether lizards exhibited habitat-dependent differences in anti-predator behaviors and (2) determine whether lizards exhibit intra-individual differences in flight initiation distances and escape distances. Lizards in rocky habitats should exhibit the shortest flight initiation distances due to abundant refuges (Wilson and Cooper 2007) and ease of thermoregulation (Bangs 2016). Prairie lizards living in rocky habitats are capable of easily shuttling between refugia and basking sites which are both readily available throughout the habitat

Methods

Initial Capture

Data were collected during the spring and summer of 2018 and 2019 (sample statistics in Table 2). I searched for and captured lizards by noosing them in 10 sites. My field assistant and I attempted to capture and mark all lizards in each site to facilitate multiple observations on many lizards. However, some lizards were able to consistently avoid capture. Upon a successful capture,

lizards were given a unique code composed of different colored spots of acrylic paint that were placed on the dorsal pelvic region of each lizard. These codes allowed me to make repeated approaches on known lizards (Table 2). For lizards that were given a radio transmitter (see previous chapter), the codes were placed along the tail instead of the pelvis.

Behavioral approaches

To conduct behavioral trials, I located marked lizards, and initiated a stereotypic sequence on each individual. If a lizard was not marked, we attempted to capture it instead of evaluating its behavior. If the attempt failed, I walked away from the lizard and observed it until it resumed foraging or basking before approaching for a behavioral trial. These behavioral trials were utilized in analyses comparing lizard antipredator responses among habitat types.

Upon locating a lizard, I marked both my location and the lizard's location then approached the lizard directly *sensu* Cooper (2012), acting as a simulated predator, until the lizard moved at least one body length. The distance between me and the lizard when it initiated its movement was recorded as the flight initiation distance (FID). I also measured how far it fled (escape distance) as a measure of its antipredator response. I also measured the distance between me and the lizard at the time it was first spotted, in order to account for the affect initial predator distance had on antipredator behaviors. A 40-meter tape was used to measure distances to the nearest centimeter. I measured the temperature of the substrate on which the lizard was initially located by using an infrared laser thermometer (MiniTemp MT6, Raytek, Wilmington North Carolina, 2018). An ambient temperature was taken as the dry bulb reading on a sling psychrometer (Model 1328, Taylor Precision Products, Las Cruces, New Mexico, 2018). The substrate type on which the lizard was first located was visually determined. Substrate type

categories included riprap (anthropogenic rocky structures), vegetation, woody debris, asphalt trails and natural rocks.

Statistical Analyses

Because my data were not normally distributed, I evaluated differences in FIDs and escape movements (298 observations, 27 lizards) by habitat type and substrate type with a Kruskal-Wallis nonparametric ANOVA. I then examined relationships between FIDs and escape distances as dependent variables and individual morphology and microhabitat factors as independent variables. Independent variables included snout-vent length, ambient temperatures, substrate temperatures, substrate type, and habitat type. Substrate type was substantially confounded with habitat type. For example, rocky habitats were dominated by riprap, while other habitat types did not have this substrate. In my analysis, I maintained habitat type and substrate type as separate variables.

I used linear models to examine the relationships between FIDs, escape distances and the linear predictors (snout-vent length, ambient temperature, substrate temperature, and number of observations). Kruskal-Wallis tests were used to compare relationships between antipredator behaviors and categorical predictors (habitat type, substrate type, and site).

Any of the above relationships that had a p -value of 0.1 or lower was included in a linear mixed model that utilized morphological and microhabitat factors as fixed effects and lizard identity as a random effect. This approach reduced the number of variables that the variance is partitioned among and increased statistical power.

I also utilized a linear mixed model to determine whether the number of trials ($n = 1-16$) that were performed on each lizard affected its behavior. This allowed me to account for potential habituation or sensitization to the observers.

I created models for both the FIDs ($n = 100$, lizards = 15) and escape movements ($n = 68$, lizards = 15). After running the models, I utilized the function *repeatable* (Carlson 2019) that determines the ratio of within individual variance to the total variance (among individual variance/[among individual variance + residual variance]). This creates an estimate of behavioral repeatability, which is the amount of variance in the model that can be ascribed to differences among individuals in FIDs and escape distances. I then estimated confidence intervals around the estimates of repeatability by using the *confint* function (*lme4*) which bootstraps the confidence limits. This creates confidence intervals around how much of the variance attribute to the model is due to consistent differences among lizards. I also used the *rpt* function (*rptR*) which creates confidence intervals around fixed effects.

Results

The calculated confidence intervals for several fixed effects in the flight initiation linear mixed model, and all of the fixed effects in the escape distance model included zero (Table 3). Thus, none of the fixed effects within the linear mixed models had explanatory value. However, the amount of variability attributed to the random effect (lizard identity) still allowed me to identify how much of the variance was attributed personality. I used two approaches to evaluate independent variables, a simple univariate analysis and also directly from the linear mixed models.

Lizards did not exhibit different flight initiation distances among habitats (Figure 5a). Lizards exhibited median FIDs of 1.32, 1.36, and 1.62 m in forested, rocky, and mixed habitats that were not significantly different (Kruskal-Wallis $\chi^2 = 0.67$, $df = 2$, $p = 0.72$) (Figure 5a). In contrast, lizards on asphalt trails (2.82 m), riprap (1.38 m), rocky (1.17 m), and woody debris (1.09 m) exhibited significantly different FIDs ($\chi^2 = 22.494$, $df = 3$, $p < .0001$) (Fig. 5b). A Dunn's test indicated that lizard FIDs on asphalt trails were significantly longer than on other

substrates, but the other substrates did not differ significantly from each other. Ambient temperature was significantly and positively related to FIDs ($F_{1,294} = 9.17$, $B = 0.10$, $p = 0.003$) though the relationship was very weak ($r^2 = 0.03$, $B = 0.10$; Figure 6a). Lizards also exhibited a significant positive relationship between initial approach distance and FIDs ($F_{1,294} = 146.8$, $B = 0.42$, $p < .001$) which was relatively robust ($r^2 = 0.333$; $B = 0.42$; Figure 6b). Prairie lizards did not exhibit a relationship between FIDs and snout-vent length ($F_{1,87} = 1.541$, $B = 0.033$, $p = 0.218$, $r^2 = .006$; Figure 7a) or mass ($F_{1,87} = 0.0001$, $B = -0.0005$, $p = 0.99$, $r^2 = -.0012$; Figure 7b). The estimated repeatability (variance attributed to differences in personality(r) from the model of FIDs was not significant ($r = .09$, 95% CI [0, 0.299]) which suggests that personality did not influence FIDs. After accounting for environmental conditions and morphology, repeatability of flight initiation distances remained non-significant ($r = 0.12$, 95% CI [0, 0.49]).

Lizards did not exhibit escape distances that were significantly different among forested (0.60 m), rocky (0.50 m), and mixed (0.48 m) habitats (Kruskal-Wallis $\chi^2 = 4.412$, $df = 2$, $p = 0.110$) (Figure 8a). In contrast, lizards on different substrates exhibited different escape movements; lizards exhibited median escape movements on asphalt trails (1.02 m), riprap (0.49 m), rocky (0.42 m) and woody debris (1.57m), (Kruskal-Wallis $\chi^2 = 26.971$, $df = 3$, $p < 0.001$; Figure 8b). A Dunn's test indicated that the asphalt trails were significantly different from the other substrates and lizards exhibited longer escape distances on asphalt than the other substrates. Ambient temperature did not have a significant correlation with escape distances ($F_{1,74} = 1.27$, $B = 0.045$, $p = 0.26$, $r^2 = 0.004$; Figure 9a). The initial distance of approach did not have a significant effect on escape distances (Figure 9b) but was enough to add to the model ($F_{1,74} = 1.86$, $p = 0.182$, $r^2 = 0.01$). Lizards exhibited a nearly significant positive relationship between snout-vent length and escape distances ($F_{1,66} = 3.79$, $B = .060$, $p = 0.056$, $R^2 = 0.040$) (Figure

10a) , and exhibited a positive relationship between mass and escape distances ($F_{1,66} = 6.37$, $B = 0.14$, $p = 0.014$, $R^2 = 0.074$; Figure 10b)

Lizard escape distances were repeatable. In the simplest model, the amount of variation in the model attributed to personality was large ($r = 0.723$) and had confidence intervals that indicated a large amount of variance attributed to lizard identity (95% CI [0.451, 0.848]). After accounting for environmental conditions and morphology, the amount of variance attributable to lizard identity remained large ($r = .628$) and maintained a confidence interval that indicated that lizard identity was an important factor that influenced escape movements (95% CI [0.418, 0.842]).

Discussion

Effects of Habitat Type on Behavior

Lizards living among different habitat types and levels of urbanization often behave differently (Bókony et al. 2012, Corti et al. 2009, Lapiedra et al. 2017, Michelangeli et al. 2018, Moule et al. 2016, Sol et al. 2011). In contrast, I found that lizards in the Arkansas River Valley did not exhibit differences in antipredator behaviors among three structurally, and thermally different habitat types. My findings suggest that populations of lizards in the Arkansas River Valley may have adapted generally predation as opposed to developing different behaviors in each habitat. This may be due to a generalist approach to life histories in *Sceloporus spp.* This example still goes against your findings because *S. occidentalis* only behaved similarly when they were all put in the same habitat. Mesquite lizards, *S. grammicus*, from high and low altitude sites exhibited the same growth rates, survival and active body temperatures (Lemos-Espinal 1992) while Bangs (2016) observed similar survival and morphology among prairie lizards in the Arkansas River Valley. Similarly, prairie lizards that I studied exhibited the same behavioral

responses among the three habitat types, reflecting observed consistency in life-history traits among geographically separated Sceloporine lizard populations.

Substrate Effects on Behavior

Habitats that offer ready and close access to refuge promote short FIDs and escape distances. Lizards on more conspicuous microhabitats flee earlier, while those on more complex microhabitats may allow predators a closer approach (Cooper and Blumstein 2015, Martin and López 1995). For example, *Sceloporus virgatus*, the striped plateau lizard, exhibited increased FIDs as distance to refuge increased and *S. virgatus* found on rocky habitats fled to close crevices while those on the ground fled to different, but close microhabitats to access refuge (Cooper and Wilson 2007). Similarly, I found that prairie lizards on asphalt trails exhibited the largest FIDs and escape distances compared to lizards on other substrates; those differences may have been due to the absence of close refuges. Asphalt trails had brush and forest on each side of the trail but the trails proper were flat and devoid of cover. So, to access safety they had to move longer distances. Riprap and boulders had more accessible refugia and lizards could quickly gain safety without having to move very far. Thus, lizards on riprap and rocks could wait until predators were relatively close before initiating escape, as they did not have to travel far to find safety. In addition, lizards on asphalt trails were able to observe predators from a longer distance. Prairie lizards had longer FIDs and escape movements on trails, perhaps because lizards are able to alter their escape behavior based on how far they are from perceived safety. For example, *S. virgatus* increased their FIDs as distance to refuge increased (Cooper and Wilson 2007), which is similar to what I observed in *S. consobrinus* on asphalt trails. In addition, prairie lizards on asphalt paths were often in the middle of the path, which put them at a greater distance from cover in comparison to lizards on other substrates, such as riprap, where lizards were able to

move into crevices beneath their basking spots. Asphalt paths often had much higher surface temperatures than the ambient temperature and were able to provide efficient basking spots. Lizards that bask on warm substrates may also be “giving up” on their basking sites sooner because they are already at an optimal body temperature and do not need to utilize the basking site any longer. Lizards exhibited similar escape behaviors on the other substrate types (riprap, rocky/boulder, and woody debris). Each of these substrates grants the lizards immediate access to refuge and would decrease their FIDs and escape movements, as was found in *Sceloporus virgatus* (Cooper and Wilson 2007).

In summary, lizards on asphalt paths can see predators earlier and may be at a preferred body temperature, thus they flee earlier because the thermal costs of refuge use are not as high as they may be on other substrates (Cooper 2000). Habitat types varied in their resource availability and a relationship between habitat type and temperature may exist. Future research should attempt to disentangle their relative effects and ensure that differences in lizard escape behaviors on different substrates are due to substrate structure and refuge availability and not solely due to differences in available thermal resources.

Thermal resources

Forested, rocky, and mixed habitats had different average temperatures. Bangs (2016) found that rocky habitats exhibited the hottest average temperatures, and forested habitats the lowest. Despite these differences, prairie lizards among my study sites maintained a small range of body temperatures (Bangs 2016), which may reduce the effect of different temperature regimes at the habitat level on lizard antipredator behaviors. *Sceloporus* lizards in general have efficient thermal regulatory capabilities (Andrews 1998, Angilleta et al. 2001, Gillis 1991), and maintain a narrow range of body temperatures throughout their daily activities (Huey 1982,

Angilleta et al. 2001). Different habitats may cause differences in thermoregulatory behaviors (Huey 1976), which in turn result in different predation risks associated with these behaviors. (Hertz et al. 1982, Losos 1988).

Sceloporus physical performance is correlated to body temperature (Angilleta et al. 2002), as is escape behavior (Rang 1964, Bennet 1980). I found that ambient temperatures were a significant predictor of lizard FIDs and lizard escape distances. Lizards exhibited slightly longer escape distances with an increase in temperature, though the effect size was very small. Air temperature has been found to influence the behaviors of other small bodied lizards which exhibit riskier behaviors in higher ambient temperatures. For example, the keeled earless lizard (*Holbrookia propinqua*) traveled further from their burrows when ambient temperatures were warmer, which in turn caused the lizards to have further escape movements to the nearest burrow (Cooper 2000). Lizards exhibit different response to their thermal environments (Rand 1964), which in turn, affects their behavior. Future studies of *Sceloporus consobrinus* behavioral ecology should include internal body temperatures which could be incorporated into models of prairie lizards' antipredator behaviors. This would help determine whether lizards exhibit correlations between ambient temperatures, internal body temperatures, and boldness.

Morphology

Lizard morphologies are influenced by their habitat types (Goodman et al. 2008, Moermond 1979) and lizards exhibit differences in antipredator behavior as a function of their morphology. For example, bolder adult male Iberian rock lizards (*Lacerta monticola*) had larger absolute body sizes and relatively larger heads (López et al. 2005), while collard lizards that exhibited longer hind limbs also had longer FIDs (Husak and Rouse 2006). I found that prairie lizards exhibited marginally positive relationships between escape distances and morphology,

(though the fixed effects ultimately had little explanatory value in the linear mixed models). This slight increase in escape distances mirrors the increase in FIDs found in *Sceloporus woodi*, the Florida scrub lizard (Stiller and McBrayer 2013). Larger individual scrub lizards had larger FIDs, suggesting that smaller lizards may rely on crypsis more than escape behaviors or may not move as far away from refugia as larger, older individuals (Stiller and McBrayer 2013).

Repeatability of Antipredator Behaviors

I found that prairie lizard flight initiation distances were not influenced by personality, but escape behaviors were, indicating that lizards were not exhibiting a behavioral syndrome incorporating FIDs and escape distances, but were responding in a generalist manner to predators and according to their innate personalities when deciding how far to escape. Lizard escape distances were not related to FIDs, i.e., the two behaviors are decoupled. Prairie lizards in the Arkansas River Valley may be responding to predators in a universal manner when deciding how close they allow a predator to approach, but are reliant on their personalities and how far away they are from perceived safety to inform how far they escape.

Lizards exhibit a variety of repeated behaviors. For example, *Sceloporus virgatus* exhibited repeated measures of FIDs in several tests (Cooper 2009) and Namibian rock agamas (*Agama planiceps*) also exhibit highly consistent FIDs within individuals even across measurements spanning 50 days (Carter 2010). In contrast, I did not find repeatable FIDs in prairie lizards. This lack of repeatability in prairie lizards may be due to population-wide selection for plasticity in FIDs among individual animals. Flight initiation distance is the end result of factors that include the initial distance of a predator (Cooper 2005, Cooper and Blumstein 2015, Cooper and Frederickson 2007), the angle of approach (Cooper 2009), each lizard's body temperature (Hertz et al. 1982, Michelangeli et al. 2017), and the microhabitat

(Martin and López 1995, Wilson and Cooper 2007). Prairie lizards in the river valley exhibited FIDs that were influenced by the initial approach distance of predators and the substrate. These factors were more important in explaining FID than lizard personality.

In contrast, escape movements among prairie lizards were influenced by personality. At least 34% of the variation among lizard escape movements was accounted for by individual identity. As noted previously, the distribution of refugia was habitat dependent, and lizard behaviors were shaped by their distance to a refuge. I propose that the distance a lizard chooses to move away from a refuge is also an important factor in escape movements. Asphalt trails and riprap sites differ in refuge availability, but lizards are capable of repeatedly choosing how much risk they wish to take as a function of how far away they move from refuge. Lizards that are bolder may travel further distances from perceived distances than shyer animals.

Intrinsic factors

Behavior is affected by intrinsic factors I was not able to measure. These include hormones (Mason and Adkins 1976, Mell 2016, Sinervo et al. 2000, Sinervo and Miles 2011), genetics (Dingemanse et al. 2012), habituation to a simulated predator (Rodríguez-Prieto et al. 2010), age (Cooper 2011) and parasite load. *Sceloporus* exhibit elevated levels of cortisol as a result of stress (Dunlap and Wingfield 1995), and different lizards may have different levels of cortisol production as a function of previous experience, resulting in different behavioral responses to predation. These physiological differences in cortisol production may also be a function of genetic differences. Lizards in the river valley exhibit genetic differences across sites (Tomke 2016), and individual lizards within subpopulations that I studied may also have genetic differences in stress hormone production as well as other genetically driven differences in behavior. These genetic differences may influence lizard ability to handle predation, and higher

levels of boldness have been associated with a better ability to habituate to predation pressures (Rodríguez-Prieto et al. 2010). Age may affect lizard FIDs through learning and because neonates may assess risk differently due to their energetic needs and cryptic coloring (Cooper 2015). Finally, an individual animal's behavior may be influenced by its parasite load (Schall and Sarni 1987), which can alter ectotherm thermoregulation and antipredator behaviors by increasing time spent basking and decreasing locomotive capabilities (Main and Bull 2000)

Conclusions

Prairie lizards in the Arkansas River Valley exhibit behaviors that differ among substrate types, but not habitat types. Unfortunately, I did not record the substrate that the lizards fled to, and I believe that lizards may have varied greatly in the substrates they used as refuge from a perceived predator. For example, lizards in forested habitats can move up trees for safety, while lizards in rocky habitats will move within the crevices between the rocks. Lizards exhibited differences in antipredator behaviors among the substrate types. These substrates provide different access to refugia and predator visibility, which likely altered lizard escape behaviors. Prairie lizards exhibit repeatable escape movements to refuge, but not flight initiation distances. The intensity of lizard antipredator responses appears to be determined by their personalities, but the distance at which they begin their escape behaviors arise from factors not identified in this study.

Literature Cited

- Adolph, S.C. 1990. Influence of behavioral thermoregulation on microhabitat use by two *Sceloporus* lizards. *Ecology* 71: 315-327
- Adolph, S.C. 1990. Height selection by juvenile *Sceloporus* lizards: interspecific differences to habitat use. *Journal of Herpetology* 24: 69-75
- Aerts, P., R. Van Damme, B. Vanhooydonck, A. Zaaf, A. Herrel. 2000. Lizard locomotion: How morphology meets ecology. *Netherlands Journal of Zoology* 50: 261-277
- Andrews, R., F. la Cruz, F. Cruz, M. Rodriguez-Romero, F. 1999. Field and selected body temperatures of the lizards *Sceloporus aeneus* and *Sceloporus bicanthalis*. *Journal of Herpetology* 33: 93-100
- Angert, A.L., D. Hutchison, D. Glossip, J.B. Losos. 2002. Microhabitat use and thermal biology of the collar lizard (*Crotaphytus collaris collaris*) and the fence lizard (*Sceloporus consobrinus hyacinthinus*) in Missouri glades. *Journal of Herpetology* 36: 23-29
- Angilleta, M.J. Jr. 2001. Thermal and physiological constraints on energy assimilation in a widespread lizard (*Sceloporus undulatus*). *Ecology* 82: 3044-3056
- Angilleta, M.J. Jr., T. Hill, M. A. Robson. 2002. Is physiological performance optimized by thermoregulatory behavior?: a case study of the eastern fence lizard, *Sceloporus undulatus*. *Journal of Thermal Biology* 27: 199-204
- Asbury, D.A., S.C. Adolph. 2007. Behavioural plasticity in an ecological generalist: microhabitat use by western fence lizards. *Evolutionary Ecology Research* 9: 801-815
- Avalos, A., W.E. Cooper. 2010. Predation risk, escape and refuge use by mountain spiny lizards (*Sceloporus jarrovii*)

- Bangs, A. 2016. Ecology of *Sceloporus consobrinus*: Populations in two thermally different habitats. Thesis. Arkansas Tech University.
- Barron, D.G., J.D. Brawn, P.J. Weatherhead. 2010. Meta-analysis of transmitter effects on avian behaviour and ecology. *Methods in Ecology and Evolution* 1: 180-187
- Bauwens, D., T. Garland Jr., A. M. Castilia, R. Van Damme. Evolution of sprint speed in Lacertid lizards: Morphological, physiological, and behavioral covariation. *Evolution*: 49: 848-863
- Bell, A.M., A. Sih. 2007. Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*). *Ecology Letters* 10: 828-834
- Bell, A.M., J.A. Stamps. 2004. Development of behavioural differences between individuals and populations of sticklebacks, *Gasterosteus aculeatus*. *Animal Behaviour* 68: 1339-1348
- Belgrad, B. A., Griffen, B. D. 2017. Habitat quality mediates personality through differences in social context. *Oecologia* 184: 431–440.
- Belgrad, B.A., B.D. Griffen. 2018. Personality interacts with habitat quality to govern individual mortality and dispersal patterns. *Ecology and Evolution* 8: 7216-7227
- Bennet. A. 1980. The thermal dependence of lizard behaviour. *Animal Behaviour* 28: 752-763
- Biro, P.A., J.A. Stamps. 2010. Do consistent individual differences in metabolic rate promote consistent individual differences in behavior? *Trends in Ecology and Evolution* 25: 653-659
- Bókony, V., A. Kulcsár, Z. Tóth, A. Liker. 2012. Personality traits and behavioral syndromes in differently urbanized populations of house sparrows (*Passer domesticus*). *PLoS One* 7: e36639
- Boyle, S.A., W. C. Lourenço, L.R. da Silva, A.T. Smith. 2009. Home range estimates vary with sample size and methods. *Folia Primatology* 80: 33-42

- Braña, F. 2003. Morphological correlates of burst speed and field movement patterns: the behavioural adjustment of locomotion in wall lizards (*Podarcis muralis*). *Biological Journal of the Linnean Society* 80: 135-146
- Brattstrom, B.H. 1965. Body temperatures of reptiles. *The American Midland Naturalist* 73: 376-422
- Brodie III, E.D., N. H. Russell. 1999. The consistency of individual differences in behaviour: temperature effects on antipredator behaviour in garter snakes. *Animal Behaviour* 57: 445-451
- Brydges, N.M., N. Colegrave, R.J.P. Heathcote. V.A. Braithwaite. 2008. Habitat stability and predation pressure affect temperament behaviours in population of three-spined sticklebacks. *Journal of Animal Ecology* 77: 229-235
- Burt, W.H. 1943. Territoriality and home range concepts as applied to mammals. *Journal of Mammology* 24: 346-352
- Careau, V., T. Garland Jr., 2012. Performance, Personality, and Energetics: Correlation, Causation, and Mechanism. *Physiological and Biochemical Zoology* 85: 543-571
- Careau, V., D. Thomas, M.M. Humphries, D. Réale. 2008. Energy Metabolism and Animal Personality. *Oikos* 117: 641-653
- Carter, A.J., R. Heinsohn, A. W. Goldizen, P.A. Biro. 2012. Boldness, trappability and sampling bias in wild lizards. *Animal Behaviour* 83: 1051-1058
- Carter. A.J., A.W. Goldizen, S.A. Tromp. 2011. Agamas exhibit behavioral syndromes: bolder males bask and feed more but may suffer higher predation. *Behavioral Ecology* 21: 655-661

- Cerquiera, M., S. Rey, T. Silva, Z. Featherstone, M. Crumlish, S. MacKenzie. 2016. Thermal preference predicts animal personality in Nile tilapia *Oreochromis niloticus*. *Journal of Animal Ecology* 85: 1389-1400
- Christian, K., C.R. Tracy, W.P Porter. 1983. Seasonal shifts in body temperatures and use of microhabitat by Galapagos land iguanas (*Conolophus pallidus*). *Ecology* 64: 463-468
- Christian, K.A., S. Waldschmidt. 1986. The relationship between lizard home range and body size: A reanalysis of the data. *Herpetologica* 40: 68-75
- Collar, D.C., J.A. Schulte, B.C. O'Meara, J.B. Losos. 2010. Habitat use affects morphological diversification in dragon lizards. *Journal of Evolutionary Biology* 23: 1033-1049
- Coleman, K., D.S. Wilson. 1998. Shyness and boldness in pumpkinseed sunfish; individual differences are context-specific. *Animal Behaviour* 56: 927-936
- Cook, R. 2004. Dispersal, home range establishment, survival, and reproduction of translocated eastern box turtles, *Terrapene c. carolina*. *Applied Herpetology* 1: 197-228
- Cooper, W.E. Jr. 1997. Escape by a refuging prey, the broad-headed skink (*Eumeces laticeps*). *Canadian Journal of Zoology* 75: 943-947
- Cooper, W.E. Jr. 2000. Effect of temperature on escape behaviour by an ectothermic vertebrate, the keeled earless lizard (*Holbrookia propinqua*). *Behaviour* 137: 1299-1315
- Cooper, W.E. Jr. 2005. When and how do predator starting distances affect flight initiation distances? *Canadian Journal of Zoology* 83: 1045-1050

- Cooper, W.E. Jr. 2009. Optimal escape theory predicts escape behaviors beyond flight initiation distance: risk assessment and escape by striped plateau lizards *Sceloporus virgatus*. *Current Zoology* 55: 123-131
- Cooper, W.E. Jr. 2009. Variation in escape behaviors among individuals of the striped plateau lizard *Sceloporus virgatus* may reflect differences in boldness. *Journal of Herpetology* 43: 495-502
- Cooper, W.E. Jr. 2011. Age, sex, and escape behaviour in the striped plateau lizard (*Sceloporus virgatus*) and the mountain spiny lizard (*S. jarrovi*), with a review of age and sex effects on escape by lizards. *Behaviour* 148: 1215-1238
- Cooper, W.E. Jr. 2011. Influence of some potential predation risk factors and interaction between predation risk and cost of fleeing on escape by the lizard *Sceloporus virgatus*. *Ethology* 117: 620-629
- Cooper, W.E. Jr. 2012. Risk, escape from ambush, and hiding time in the lizard *Sceloporus virgatus*. *Herpetologica* 68: 505-513
- Cooper, W.E. Jr., A. Avalos. 2010. Predation risk, escape and refuge use by mountain spiny lizards (*Sceloporus jarrovi*). *Amphibia-Reptilia* 31: 363-373
- Cooper, W.E. Jr., W. G. Frederick. 2007. Optimal flight initiation distance. *Journal of Theoretical Biology* 244: 59-67
- Cooper, W.E., M.J. Whiting. 2007. Universal optimization of flight initiation distances and habitat-driven variation in escape tactics in a Namibian lizard assemblage. *Ethology* 113: 661-672

- Cooper, W.E. Jr., D.S. Wilson. 2007. Beyond optimal escape theory: microhabitats as well as predation risk affect escape and refuge use by the phrynosomatid lizard *Sceloporus virgatus*. *Behaviour* 144: 1235-1254
- Cooper, W.E. Jr., D.S. Wilson. 2007. Sex and social costs of escaping in the striped plateau lizard *Sceloporus virgatus*. *Behavioral Ecology* 18: 764-768
- Cooper, W.E., Jr., D.S. Wilson. 2008. Thermal cost of refuge use affects refuge entry and hiding time by striped plateau lizards *Sceloporus virgatus*. *Herpetologica* 64: 406-412
- Corti, C., M. Biaggini, R. Berti. 2009. Different habitats, different pressures? Analysis of escape behaviour and ectoparasite load in *Podarcis sicula* (Lacertidae) populations in different agricultural habitats. *Amphibia-Reptilia* 30: 453-461
- Cote, J., J. Clobert. 2007. Social personalities influence natal dispersal in a lizard. *Proceedings of the Royal Society B*. 274: 383-390
- Cote, J., J. Clobert, T. Brodin, S. Fogarty, A. Sih. 2010. Personality-dependent dispersal: characterization, ontogeny, and consequences for spatially structured populations. *Philosophical Transactions of the Royal Society B* 365: 4065-4076
- Dall, S.R.X., A. I. Houston, J.M. McNamara. 2004. The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecology Letters* 7: 734-739
- Davis, J., R. Ford. 1983. Home range in the Western Fence Lizard (*Sceloporus occidentalis* *occidentalis*). *Copeia* 4: 933-940

- Dingemanse, N.J., I. Barber, J. Wright, J.E. Brommer. 2012. Quantitative genetics of behavioural reaction norms: genetic correlations between personality and behavioural plasticity vary across stickleback populations. *Journal of Evolutionary Biology* 25: 485-496
- Dingemanse, N.J., C. Both, A.J. van Noordwijk, A.L. Rutten, P.J. Drent. 2003. Natal dispersal and personalities and personalities in great tits (*Parus major*). *Proceedings of the Royal Society B* 270: 741-747
- Dingemanse, N.J., D Réale. 2005. Natural selection and animal personality. *Behaviour* 142: 1159-1184
- Dingemanse, N.J., F. Van der Plas, J. Wright, D. Reale, M. Scharma, D. A. Roff, E. Van der Zee, Iain Barer. 2009. Individual experience and evolutionary history of predation affect expression of heritable variation in fish personality and morphology. *Proceedings of the Royal Society B* 276: 1285-1293
- Doherty, T.S., C.N. Fitt, D.A. Driscoll. 2019. Animal movement varies with resource availability, landscape configuration and body size: a conceptual model and empirical example. *Landscape Ecology* 34: 603-614
- Downs, J.A., M.W. Horner. 2008. Effects of point pattern shape on home-range estimates. *Journal of Wildlife Management* 72: 1813-1818
- Dubuc-Messier, G., D. Réale, P. Perret, A. Charmantier. 2017. Environmental heterogeneity and population differences in blue tits personality traits. *Behavioral Ecology* 28: 448-459
- Dunham, A.E. 1987. Variation in home range size along an elevational gradient in the iguanid lizard *Sceloporus merriami*. *Oecologia* 71: 473-480

- Dzialowski, E.M., M.P. O'Connor. 2001. Physiological control of warming and cooling during simulated shuttling and basking in lizards. *Physiological and Biochemical Zoology: Ecological and Evolutionary Approaches* Vol 74: 679-693
- Elstrott, J., D.J. Irschick. 2004. Evolutionary correlations among morphology, habitat use and clinging performance in Caribbean *Anolis* lizards. *Biological Journal of the Linnean Society* 83: 389-398
- Fair, W. S., S.E. Henke. 1999. Movements, home ranges, and survival of Texas horned lizards (*Phrynosoma cornutum*). *Journal of Herpetology* 33: 517-525
- Ferner, J.W. 1974. Home-Range size and overlap in *Sceloporus undulatus erythrocheilus* (Reptilia: Iguanidae). *Copeia* 2: 332-337
- George, A.D. 2017. Resource selection by an ectothermic predator in a dynamic thermal landscape. *Ecology and Evolution* 7: 9557-9566
- Gillis, R. 1991. Thermal biology of two populations of red-chinned lizards (*Sceloporus undulatus erythrocheilus*) living in different habitats in Southcentral Colorado. *Journal of Herpetology* 25: 18-23
- Goulet, C.T., J. Ingle, I. Scharf, J.N. Pruitt. 2016. Thermal effects on survival and reproductive performance vary according to personality type. *Behavioral Ecology* 27: 1635-1641
- Goulet, C.T., M.B. Thompson., D.G. Chapple. 2016. Repeatability and correlation of physiological traits: Do ectotherms have a “thermal type”? *Ecology and Evolution* 7: 710-7190
- Goulet, C.T., M.B. Thompson, M. Michelangeli, B.B.M. Wong, D.G. Chapple. 2017. Thermal physiology: A new dimension of the pace-of-life syndrome. *Journal of Animal Ecology* 86: 1269-1280

- Grant, B.W. 1990. Trade-offs in activity time and physiological performance for thermoregulating desert lizards, *Sceloporus merriami*. *Ecology* 71: 2323-2333
- Griffits, A.D. 1999. Demography and home range of the frillneck lizard, *Chlamydosaurus kingii* (Agamidae), in Northern Australia. *Copeia* 1089-1096.
- Grover, M.C. 1996. Microhabitat use and thermal ecology of two narrowly sympatric *Sceloporus* (Phrynosomatidae) lizards. *Journal of Herpetology* 30: 152–160
- Haenel, G.J. L.C. Smith, H. B. John-Alder. 2003. Home-Range analysis in *Sceloporus undulatus*. II. A test of spatial relationships and reproductive success. *Copeia* 1: 113-123
- Halsead, B.J. H.R. Mushinsky, E.D. McCoy. *Masticophis flagellum* selects Florida scrub habitat at multiple spatial scales. *Herpetologica* 65: 268-279
- Harestad, A.S., F.L. Bunnell. 1979. Home range and body weight – a reevaluation. *Ecology* 60:389-402
- Harris, S., I. W. Ramnarine, H.G Smith, L B. Pettersson. 2010. Picking personalities apart: estimating the influence of predation, sex and body size on boldness in the guppy *Poecilia reticulata*. *Oikos* 119: 1711-1718
- Herrel, A., J.J. Meyeres, B. Vanhooydonck. 2001. Correlations between habitat use and body shape in a phrynosomatid lizard (*Urosaurus ornatus*): a population-level analysis. *Biological Journal of the Linnean Society* 74: 305-314
- Hertz, P.E., R.B. Huey, E. Nevo. 1982. Fight versus flight: Body temperature influences defensive responses of lizards. *Animal Behavior* 30: 676-679
- Highcock, L., A.J. Carter. 2014. Intraindividual variability of boldness is repeatable across contexts in a wild lizard. *PloS One*: 9: e95179

- Hixon, M.A. 1980. Energy maximizers and time minimizers: theory and reality. *The American Naturalist* 119: 596-599
- Holtmann, B., E.S.A. Santos, C.E. Lara, S. Nakagawa. 2017. Personality-matching habitat choice, rather than behavioural plasticity, is a likely driver of a phenotype – environment covariance. *Proceedings of the Royal Society B* 284: 20170943
- Huey, R. 1974. Behavioral thermoregulation in lizards: Importance of regulation costs. *Science* 184: 1001-1003
- Huey, R. 1991. Physiological consequences of habitat selection. *The American Naturalist* 137: S91-S115
- Huey, R.B., A.E. Dunham, K. L. Overall, R.A. Newman. 1989. Variation in locomotor performance in demographically known populations of the lizard *Sceloporus merriami*. *Physiological Zoology* 63: 845-872
- Hult, S.M, and D. J. Germano. 2015. Habitat use and home range of *Phrynosoma blainvilli* in the San Joaquin Desert of California. *Herpetological Conservation and Biology* 10: 850-863
- Husak, J.F., M. N. Rouse. 2003. Population variation in escape behavior and limb morphology of collard lizards (*Crotaphytus collaris*) in Oklahoma. *Herpetologica* 62: 156-163
- Hyslop, N.L., J.M. Meyers, R.J. Cooper, D.J. Stevenson. 2014. Effects of body size and sex of *Drymarchon couperi* (eastern indigo snake) on habitat use, movements, and home range size in Georgia. *The Journal of Wildlife Management* 78:101-111
- Ingley, S.J., J.B. Johnson. 2014. Animal personality as a driver of reproductive isolation. *Trends in Ecology & Evolution* 29: 369-371

- Irschick, D., E. Carlisle, E. Elstrott, J. Ramos, M. Buckley, C. Vanhooydonck, B. Meyers, J. Herrel, A. 2005. A comparison of habitat use, morphology, clinging performance and escape behaviour among two divergent green anole lizard (*Anolis carolinensis*) populations. *Biological Journal of the Linnean Society* 85: 223-234
- Jaksić, F.M., H. Núñez. 1979. Escaping behavioral and morphological correlates in two *Liolaemus* species of central Chile (Lacertilia: Iguanidae). *Oecologica* 42: 119-122s
- Jenkins, S.H. 1981. Common patterns in home range – body size relationships of birds and mammals. *The American Naturalist* 118: 126-128
- Johnson, M.A., R. Kirby, S. Wang, J.B. Losos. 2006. What drives variation in habitat use by *Anolis* lizards: habitat availability or selectivity. *Canadian Journal of Zoology* 84: 877-886
- Jones, S.M., D.L. Droge. 1980. Home range size and spatial distributions of two sympatric lizard species (*Sceloporus undulatus*, *holbrookii maculata*) in the Sand Hills of Nebraska. *Herpetologica* 36: 127-132
- Kashon, E.A.F., B.E. Carlson. 2018. Consistently bolder turtles maintain higher body temperatures in the field by may experience greater predation risk. *Behavioral Ecology and Sociobiology* 72: 1-13
- Knapp, C.R., J.G. Abarca. 2009. Effects of radio transmitter burdening on locomotor ability and survival of iguana hatchlings. *Herpetologica* 65: 362-272
- Kobler, A., G. Maes, Y. Humblet, F. Volckaert, M. Eens. 2011. Temperament traits and microhabitat use in bullhead, *Cottus perifretum*: fish associated with complex habitats are less aggressive. *Behaviour* 148: 603-625

- Kohldorf, T., T. Garland Jr., C.A. Navas. 2001. Limb and tail length in relation to substrate usage in *Tropidurus* lizards. *Journal of Morphology* 248: 151-164
- Krekorian, C. O., 1976. Home range size and overall and their relationship to food abundance in the desert iguana, *Dipsosaurus dorsalis*. *Herpetologica* 32: 405-412
- Kurvers, R.H.J.M., H.H.T Prins, S.E. van Wieren, K, van Oers, B.a. Nolet, R.C. Ydenberg. 2010. The effect of personality on social foraging; shy barnacle geese scrounge more. *Proceedings of the Royal Society B* 277: 601-608
- Langkilde, T., K. Boronow. 2012. Hot boys are blue: Temperature-dependent color change in male eastern fence lizards. *Journal of Herpetology* 46: 461-465
- Lapiedra, O., Z. Chejanovski, J.J. Kolbe. 2017. Urbanization and biological invasion shape animal personalities. *Global Change Biology* 23: 592-603
- Le Galliard, J., M. Paquet, M. Cisel, L. Montes-Poloni. 2013. Personality and the ace of life syndrome: variation and selection on exploration, metabolism and locomotor performances. *Functional Ecology* 27: 136-144
- Leache, A. D., T.W. Reeder. 2002. Molecular systematics of the eastern fence lizard (*Sceloporus undulatus*): A Comparison of Parsimony, Likelihood, and Bayesian Approaches. *Systematic Biology* 51: 44-68
- Leaché, A.D. 2009. Species tree discordance traces to phylogeographic clade boundaries in North American fence lizards (*Sceloporus*). *Systematic Biology* 58: 547-559

- Lemos-Espinal, J.A. 1992. Ecology and comparative demography of the lizard *Sceloporus grammicus*: Life history of an altitudinal generalists on the eastern slope of the Iztaccihuatl Volcano, Puebla, Mexico. Thesis. University of Nebraska Press.
- Lewis, A.R., J.E. Saliva. 1987. Effects of sex and size on home range, dominance, and activity budgets in *Ameiva exsul* (Lacertillia: Teiidae). *Herpetologica* 43: 373-383
- López, P., D. Hawlena, V. Polo, L. Amo, J. Martín. 2005. Sources of individual shy-bold variations in antipredator behaviour of male Iberian rock lizards. *Animal Behaviour* 69: 1-9
- Losos, J.B. 1988. Thermoregulatory correlates of escape behavior by a desert lizard, *Ctenophorus isolepis*. *Journal of Herpetology* 22: 353-356
- Losos, J.B. 1990. The evolution of form and function: Morphology and locomotor performance in West Indian *Anolis* lizards. *Evolution* 44: 1189-1203
- Macrini, T.E., D.J. Irschick. 1998. An intraspecific analysis of trade-offs in sprinting performance in a West Indian lizard species (*Anolis lineatopus*). *Biological Journal of the Linnean Society* 63: 579-591
- Macrini, T.E., D. J. Irschick, J.B. Losos. 2003. Ecomorphological differences in toepad characteristics between mainland and island Anoles. *Journal of Herpetology* 37: 52-58
- Magnhagen, C., J. Borchering. 2007. Risk-taking behaviour in foraging perch: does predation pressure influence age-specific boldness? *Animal Behaviour* 75: 509-517
- Main, A.R., C.M. Bull. 2000. The impact of tick parasites on the behaviour of the lizard *Tilqua rugosa*. *Oecologia* 122: 574-581.

- Martin, J., P. López. 1995. Influence of habitat structure on the escape tactics of the lizard *Psammmodromus algirus*. *Canadian Journal of Zoology* 73: 129-132
- Martins, E.P. 1993. A comparative study of the evolution of *Sceloporus* push-up displays. *American Naturalist* 142:994-1018
- Mason, P., E. K. Adkins. 1976. Hormones and social behavior in the lizard, *Anolis carolinensis*. *Hormones and Behavior* 7: 75-86
- Mayer, M., R. Shine, G.P. Brown. 2016. Bigger babies are bolder: effects of body size on personality of hatchling snakes. *Behaviour* 153: 313-323
- McBrayer, L.D., J.E. Wylie. 2009. Concordance between locomotor morphology and foraging mode in lacertid lizards. *Zoology* 112: 370-378
- Mell, H., R. Josserand, B. Decenière, P. Artacho, S. Meylan, J. Le Galliard. 2016. Do personalities co-vary with metabolic expenditure and glucocorticoid stress response in adult lizards? *Behavioral Ecology and Sociobiology* 70: 951-961
- Melville, J., J.A. Schulte II. 2001. Correlates of active body temperatures and microhabitat occupation in nine species of central Australian agamid lizards. *Australian Ecology* 26: 660-669
- Michelangeli, M. D.G. Chapple, C.T. Goulet, M.G. Bertram, B.B.M. Wong. 2018. Behavioral syndromes vary among geographically distinct populations in a reptile. *Behavioral Ecology* 30: 393-401
- Michelangeli, M., C. T. Goulet, H.S. Kang, B.B.M. Wong, D.G. Chapple. 2017. Integrating thermal physiology within a syndrome: Locomotion, personality and habitat selection in an ectotherm. *Functional Ecology* 32: 970-981

- Michelangeli, M., B. Melki-Wegner, K. Laskowski, B.B.M. Wong, D.G. Chapple. 2019. Impacts of caudal autonomy on personality. *Animal Behaviour* 162: 67-78
- Moermond, T.C., 1979. Habitat constraints on the behavior, morphology, and community structure of *Anolis* lizards. *Ecology* 60: 152-164
- Moule, H., M. Michelangeli, M. Thompson, D.G. Chapple. 2016. The influence of urbanization on the behaviour of an Australian lizard and the presence of an activity-exploratory behavioural syndrome. *Journal of Zoology* 298: 103-111
- Nathan, R., W.M., Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, P.E. Smouse. 2008. A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences of the United States of America* 105: 19052-19059
- Nilsson, J.A. C. Bronmark, L.A. Hansson, B.B. Chapman. 2014. Individuality in movement: the role of personality. *in* *Animal Movement Across Scales* (eds. Hansson, L.A., S. Akesson). Oxford University Press. Oxford, U.K. p 1-39.
- O'Brien, G.P. H.K. Smith, J.R. Meyer. 1965. An activity study of a radioisotope-tagged lizard, *Sceloporus undulatus hyacinthus* (Sauria: Iguanidae). *The Southwestern Naturalist* 10: 179-187.
- Ortega-Rubio, A., T. Pilorge, M. Khodadoost, L. Arriagal. 1972. Interpopulation home range comparison of a temperate lizard. *Herpetology* 3: 71-80
- Packer, W.C. 1965. Environmental influences on daily and seasonal activity in *Setonix brachyurus* (Quoy and Gaimard) (Marsupialia). *Animal Behaviour* 13: 270-283
- Pianka, E.R., L.J. Vitt. 2003. *Lizards: Windows to the evolution of diversity*. University of California Press, Los Angeles, California.

- Pearish, S., L. Hostert, A.M. Bell. 2015 Behavioral type-environment correlations in the field: a study of three-spined stickleback. *Behavioral Ecology and Sociobiology* 67: 765-774
- Perry, G., T. Gardland Jr. 2002. Lizard home ranges revisited: effects of sex, body size, diet, habitat, and phylogeny. *Ecology* 83: 1870-1885
- Porter, W.P., and D.M. Gates. 1969. Thermodynamic equilibria of animals with environment. *Ecological Monographs* 39:227-244
- Rand, A.S. 1964. Inverse relationship between temperature and shyness in the lizard *Anolis lineatopus*. *Ecology* 45: 863-864
- Réale, D., S. M. Reader, D. Sol, P.T. McDougall, N.J. Dingemanse. 2007. Integrating animal temperament within ecology and evolution. *Biological Review* 82: 291-318
- Refsnider, J., S. Des Roches, E. Rosenblum. 2015. Evidence for ecological release for a fine spatial scale in a lizard from the White Sands formation. *Oikos* 124: 1624-1631
- Rey, S., N. Digka, S. MacKenzie. 2015. Animal personality relates to thermal preference in wild-type zebrafish, *Danio rerio*. *Zebrafish* 00: 1-7.
- Rocha, C.F.D. 1999. Home range of the tropidurid lizard *Liolaemus lutzae*: Sexual and body size differences. *Revista Brasileira de Biologia* 59: 1-4
- Rodewald, A.D., S.A. Foster. 2005. Effects of gravidity on habitat use and antipredator behavior in three-spined sticklebacks. *Journal of Fish Biology* 52: 973-984
- Rodríguez-Prieto, I. J. Martin, E. F Fernández-Juricic. 2010. Individual variation in behavioural plasticity: direct and indirect effects of boldness, exploration and sociability on habituation to predators in lizards. *Proceedings of the Royal Society B*. 278: 266-273

- Ross, S., B. Munkhtsog, S. Harris. 2012. Determinants of mesocarnivore home range: Relative effects of prey and habitat properties on Pallas's cat home-range size. *Journal of Mammology* 93: 1292-1300.
- Roughgarden, J., W. Porter, D. Heckel. Resource portioning of space and its relationship to body temperature in *Anolis* lizard populations. *Oecologia* 50: 256-264
- Row, J.R., G. Blouin-Demer. 2006. Thermal quality influences effectiveness of thermoregulation, habitat use, and behaviour in milk snake. *Oecologia* 148: 1-11
- Ruby, D. E., D. I. Baird. 1994. Intraspecific variation in behavior: Comparisons between populations at different altitudes of the lizard *Sceloporus jarrovi*. *Journal of Herpetology* 28: 70-78
- Ruby, D.E., A.E. Dunham. 1987. Variation in home range size along an elevational gradient in the iguanid lizard *Sceloporus merriami*. *Oecologia* 71: 473-480
- Sabo, J. 2003. Hot rocks or no hot rocks: Overnight retreat availability and selection by a diurnal lizard. *Oecologia* 136: 329-335
- Santos, C.D., J.F. Cramer, L. G. Pârâu, A. C. Miranda, M. Wikelski, D.K.N. Dechmann. 2015. Personality and morphological traits affect pigeon survival from raptor attacks. *Scientific Reports* 5: 15490
- Schall, J.J., G.A. Sarni. 1987. Malarial parasitism and the behavior of the lizard, *Sceloporus occidentalis*. *Copeia* 1: 84-93
- Schoener, T.W. 1977. Competition and the niche. In C. Gans and D.W. Tinkle (eds.) *Biology of the Reptilia*. Vol 7. Pp 35-136. Academic Press, New York.

- Schoepf, I. G. Schmohl, B. Konig, N. Pillay, C. Schradin. 2015. Manipulation of population density and food availability affects home range sizes of African striped mouse females. *Animal Behaviour* 99: 53-60
- Schradin, C., G. Schmohl, H. Rodel, I. Schoepf, S.M. Treffler, J. Brenner, M. Bleeker, M. Schubert, B. Konig, N. Pillay. 2010. Female home range is regulated by resource distribution and intraspecific competition: a long-term field study. *Animal Behaviour* 79: 195-203
- Scoular, K.M., W.C. Caffry, J.L. Tillman, E.S. Finan, S.K. Schwartz, B. Sinervo, P.A. Zani. 2011. Multiyear home-range ecology of common side-blotched lizards in eastern Oregon with additional analysis of geographic variation in home-range size. *Herpetological Monographs* 25: 52-75
- Serrano-Davies, E., Y.G. Araya-Ajoy, N.J. Dingemanse, J.J. Sanz. 2017. Personality-related differences in response to habitat in Mediterranean blue tits. *Ethology* 123: 861-869
- Sharpe, P.B., B. Van Horne. 1998. Influence of habitat on behavior of Townsends' ground squirrels (*Spermophilus townsendii*). *Journal of Mammology* 79: 906-919
- Sheldahl, L.A., E. P. Martins. 2000. The territorial behavior of the western fence lizard, *Sceloporus occidentalis*. *Herpetologica* 56: 469-479
- Sih, A., A. Bell, J.C. Johnson. 2004. Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology and Evolution* 19: 372-378
- Sih, A., A. Bell, J.C. Johnson, R.E. Ziemba. 2004. Behavior syndromes: An integrative overview. *The Quarterly Review of Biology* 79: 241-277

- Simon, C. 1975. The influence of food abundance on territory size in the iguanid lizard *Sceloporus jarrovi*. *Ecology* 56: 993-998.
- Sinervo, B., D.B. Miles. 2011. Hormones and Behavior of Reptiles. Hormones and Reproduction of Vertebrates. Academic Press 215 -246.
- Sinervo, B., D.B. Miles, A. Frankino, M. Klukowski, D.F. DeNardo. 2000. Testosterone, endurance, and Darwinian fitness: Natural and sexual selection on the physiological bases of alternative male behaviors in side-blotched lizards. *Hormones and Behavior* 38: 222-233
- Smith, D.C. 1985. Home range and territory in the striped plateau lizard (*Sceloporus virgatus*). *Animal Behaviour* 33: 417-427
- Smith, H.M., D. Chiszar. J.A. Lemos-Espinal. 1992 Adaptive convergence in the lizard superspecies *Sceloporus undulatus*. *Bulletin of the Maryland Herpetological Society* 28: 123–149.
- Smith, H.M., D. Chiszar. J.A. Lemos-Espinal. 1995. A new subspecies of the polytypic lizard species *Sceloporus undulatus* (Sauria: Iguanidae) from northern Mexico. *Texas Journal of Science* 47 117–143.
- Sol, D., A.S. Griffin, I. Bartomeus, H. Boyce. 2011. Exploring or avoiding novel food resources? The novelty conflict in an invasive bird. *PLoS One* 6: e19545
- Stamps, J.A., T.G.G. Groothuis. 2010. Developmental perspectives on personality: implications for ecological and evolutionary studies of individual differences.
- Stamps, J.A., V.V. Krishnan. 1995. Territory acquisition in lizards: III. Competing for space. *Animal Behavior* 49: 679-693

- Stamps, J.A., V.V. Krishnan. 1998. Territory acquisition in lizards IV. Obtaining high status and exclusive home ranges. *Animal Behavior* 55: 461-472
- Stark, S.C., S.F. Fox, D.M. Leslie Jr. 2005. Male Texas horned lizards increase daily movements and area covered in spring: A mate searching strategy? *Journal of Herpetology* 39: 169-173
- Stenger, J. 1958. Food habits and available food of ovenbirds in relation to territory size. *The Auk* 75: 335-346
- Stiller, R.B., L.D. McBrayer. 2013. The ontogeny of escape behavior, locomotor performance, and the hind limb in *Sceloporus woodi*. *Zoology* 13: 1-7
- Stone, P.A., T. A. Baird. 2002. Estimating lizard home range: The Rose model revisited. *Journal of Herpetology* e36: 427-436
- Thompson, G., 1993. Daily movement patterns and habitat preferences of *Varanus caudolineatus* (Reptilia: Varanidae). *Wildlife Research* 20: 227-231
- Thompson, G.G., M. De Boer, E.R. Pianka. 1999. Activity areas and daily movements of an arboreal monitor lizard, *Varanus tristis* (Squamata: Varanidae) during the breeding season. *Australian Journal of Ecology* 23: 117-122
- Tracy, C.R., and K. A. Christian. 1986, Ecological relations among space, time, and thermal niche axes. *Ecology* 67: 609-613
- Tomke, S. 2018. Regional population genetic structure of the prairie lizard *Sceloporus consobrinus* in a fragmented landscape. Thesis. Arkansas Tech University, Russellville, USA.

- Van Damme, R., P. Aerts, B. Vanhooydonck. 1998. Variation in morphology, gait characteristics and speed of locomotion in two populations of lizards. *Biology Journal of the Linnean Society* 63: 409-427
- Vanhooydonck, B., R. Van Damme. 1999. Evolutionary relationships between body shape and habitat use in lacertid lizards. *Evolutionary Ecology Research* 1: 785-805
- van Oers, K. S., D.L. Sinn. 2013. Quantitative and molecular genetics of animal personality. *Animal Personalities: Behavior, Physiology, and Evolution*. 149-200. University of Chicago Press.
- van Overveld, T., E. Matthysen. 2009. Personality predicts spatial responses to food manipulations in free-ranging great tits (*Parus major*). *Biology Letters* 6: 187-190
- van Overveld, T., E. Matthysen. 2010. Personality depicts spatial responses to food manipulations in free-ranging great tis (*Parus major*). *Biological Letters* 6: 187-190
- van Sluys, M., 1997. Home range of the saxicolous lizard *Tropidurus itambere* (Tropiduridae) in southeastern Brazil. *Copeia* 3: 623-628
- Waldschmidt, S. 1983. The effect of supplemental feeding on home range size and activity patterns in the lizard *Uta stansburiana*. *Oecologia* 57: 1-5.
- Waldschmidt, S., Tracy C.R. 1983. Interactions between a lizard and its thermal environment: Implications for sprint performance and space utilization in the lizard *Uta stansburiana*. *Ecology* 64: 476-484

- Ward-Fear, G., G. P. Brown, D.J. Pearson, A. West, L.A. Rollins, R. Shine. 2018. The ecological and life history correlates of boldness in free-ranging lizards. *Ecosphere* 9: 1-13
- Warrick, G.D., T.T. Kato, B. R. Rose. 1998. Microhabitat use and home range characteristics of blunt-nosed leopard lizards *Journal of Herpetology* 32: 183-191
- Williams, S., McBrayer. Behavioral and ecological differences of the Florida scrub lizard (*Sceloporus woodi*) in scrub and sandhill habitat. *Florida Scientist* 78: 95-110
- Wone, B., B. Beauchamp. 2003. Movement, home range, and activity patterns of the horned lizard, *Phrynosoma mcallii*. *Journal of Herpetology* 37: 679-686
- Woodley, S.K., M.C. Moore. 1999. Female territorial aggression and steroid hormones in mountain spiny lizards. *Animal Behaviour* 57: 1083-1089

Table 1. Tables of habitat preferences for lizards in mixed habitat. Leaf = Leaf Litter, Woody = Woody debris and tree trunks, Bare = bare ground, Anthro = Anthropogenic. + and - indicate non-significant differences in usage. +++ and --- indicate lizards utilized this substrate significantly more than the other.

$\Lambda = 0.074, p = .11$

Substrate	Leaf	Vegetation	Rock	Woody	Gravel	Bare	Anthro
Leaf Litter	0	+++	+++	---	---	+++	---
Vegetation	---	0	+++	---	---	+	---
Rock	---	---	0	---	---	-	---
Woody	+++	+++	+++	0	-	+++	-
Gravel	+++	+++	+++	+	0	+++	+
Bare	---	---	+++	---	---	0	----
Anthro	+++	+++	+	+	-	+++	0

Substrate	Leaf	Vegetation	Rock	Woody	Gravel	Bare	Anthro
Leaf Litter	0	1.28	7.77	-3.48	-4.85	4.04	-4.79
Vegetation	-1.28	0	6.34	-4.76	-6.13	2.76	-6.08
Rock	-7.77	-6.34	0	-11.88	-12.16	-4.29	-12.72
Woody	3.47	4.76	11.88	0	-1.37	7.520	-1.32
Gravel	34.84	6.12	12.16	1.37	0	8.88	-0.05
Bare	-4.04	-2.76	4.29	-7.52	-8.89	0	-8.84
Anthro	4.80	6.08	12.72	1.320	-0.05	8.84	0

Table 2 Sample Statistics

Variable	Category	Sample Size (<i>n</i>) or mean (and range)
Lizards with code		15
Total Lizards Approached		28
Assays/Site	Rocky	83
	Mixed	83
	Forested	128
Mean Assays/Lizard		2.733 (1-8)
Mean Population FID		2.07 (0-22.62)
Mean Population Escape Movement		0.794 (.02-7.48)

Table 3. Coefficients and confidence intervals of fixed effects in the linear mixed models of flight initiation distances and escape distances. Fixed effects in bold remained significant when placed in the full model.

Model	<i>B</i>	95% CI
a) FIDs		
Ambient Temperature	0.74	(-0.10, 0.14)
Initial Distance of Approach	0.23	(0.11, 0.37)
Asphalt Trails	0.74	(-2.864, 4.21)
Riprap	-0.748	(-2.07, 0.711)
Rocky/Boulder	-1.55	(-2.83, -0.10)
Woody Debris	-1.211	(-0.012, 0.10)
Snout-Vent Length	0.044	(-0.011, 0.106)
b) Escape Movements		
Asphalt Trails	0.004	(-2.89, 3.25)
Riprap	0.052	(-1.09, 1.19)
Rocky/Boulder	-0.53	(-1.48, 0.46)
Woody Debris	-0.47	(-1.73, 0.70)
Ambient Temperature	0.051	(-0.05, 0.15)
Snout-Vent Length	0.133	(0, 0.28)
Initial Distance of Approach	0.0260	(-0.066, 0.11)
Snout-Vent Length	0.11	(-0.016, 0.10)
Mass	0.19	(-0.009, 0.74)

Map of Sites Utilized in the Arkansas River Valley

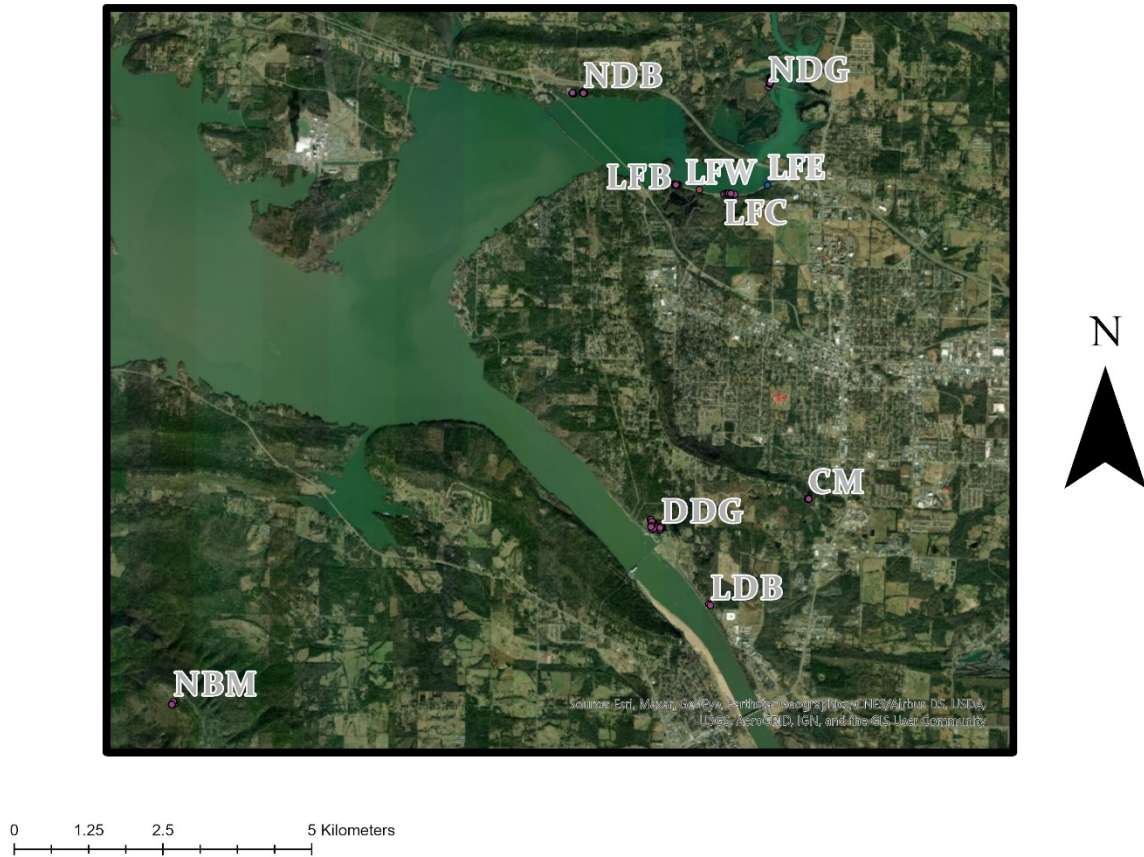


Figure 1. Map of study sites utilized in the Arkansas River Valley. Sites were named and coded to ease lizard identification and to provide variable names for analyses. NDB = North Dardanelle Boat, NDG = North Disc Golf, LFB – Lake Front Boat, LFW = Lake Front West, LFC = Lake Front Central, LFE = Lake Front West, LFB = Lake Front Boat, CM = Confederate Mothers, LDB = Lock and Dam Boat, DDG = Dardanelle Disc Golf, NBM = Nebo Big Machine.

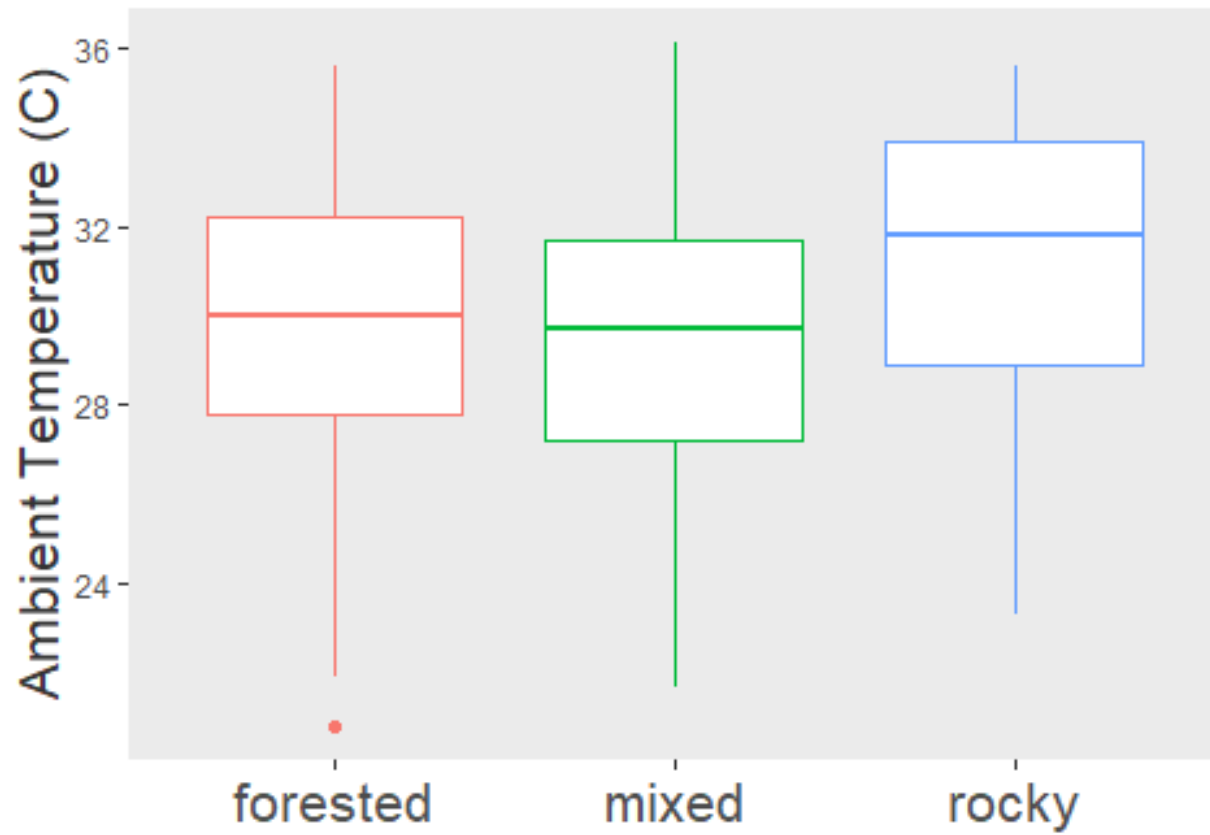


Figure 2. Ambient temperatures in Forested, Mixed, and Rocky habitat types. These were not significantly different.

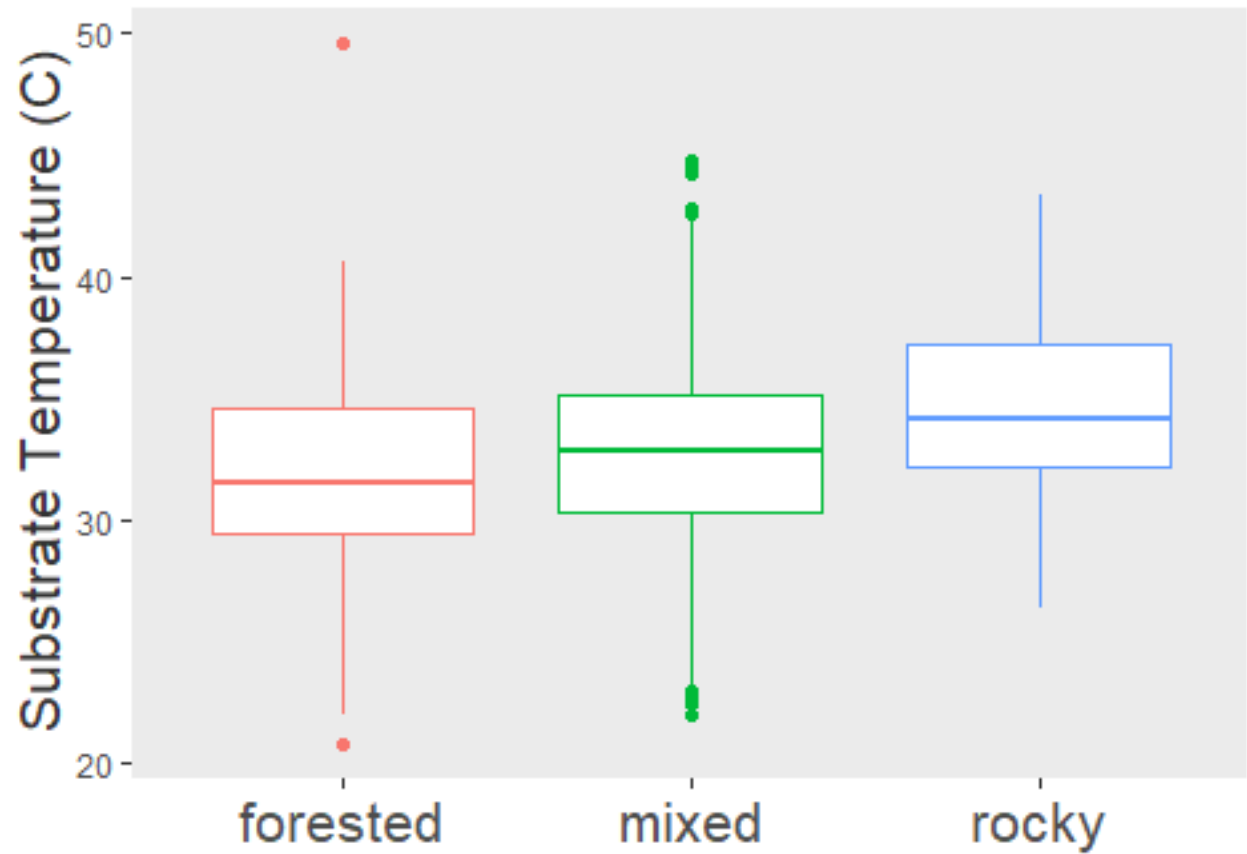


Figure 3. Substrate temperatures in Forested, Mixed, and Rocky habitat types. Rocky habitat types exhibit higher substrate temperatures than forested and mixed habitat types.

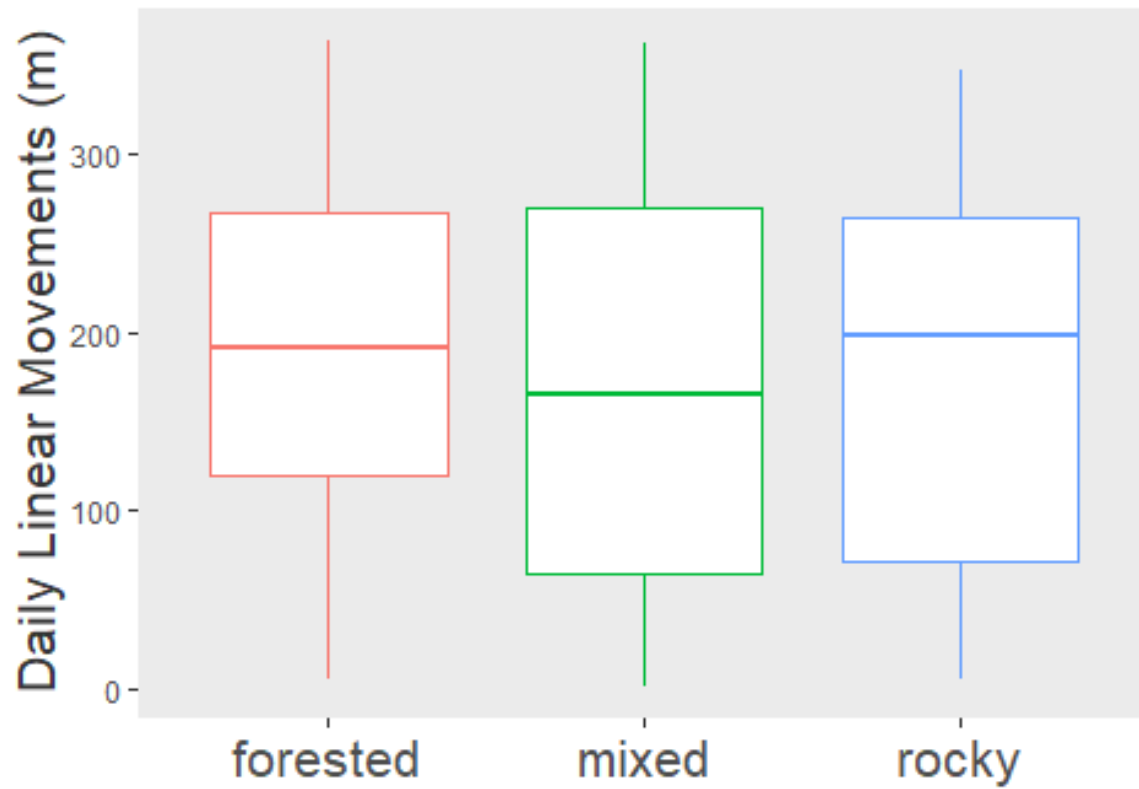
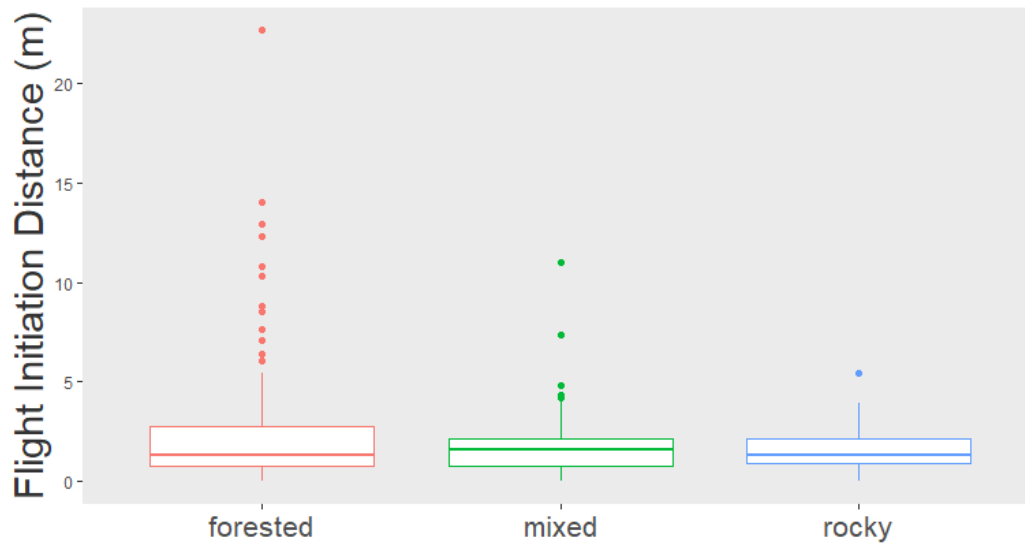


Figure 4. Standardized daily linear movements among Forested, Mixed, and Rocky habitat types. Lizards did not exhibit significant differences in linear movements among the habitat types.

a.



b.

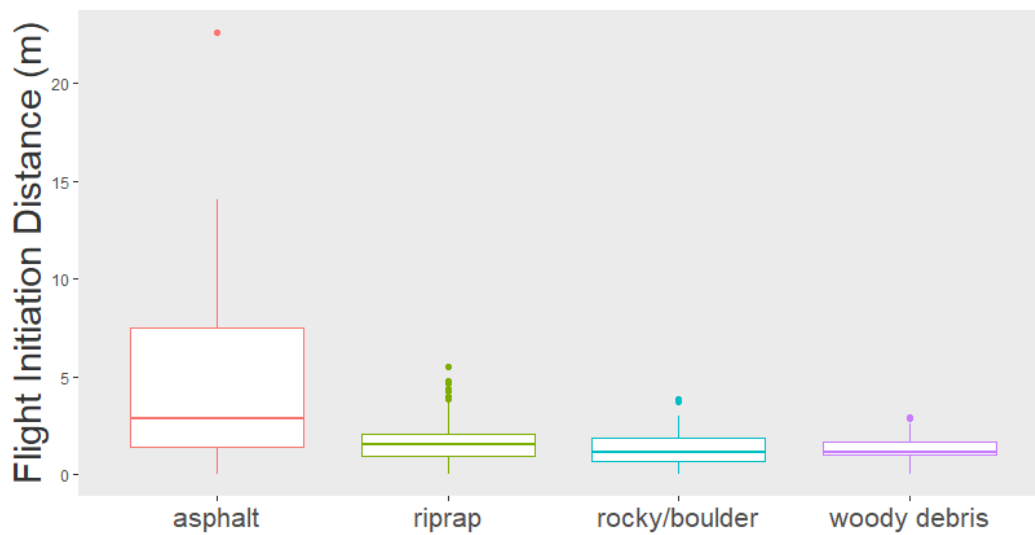
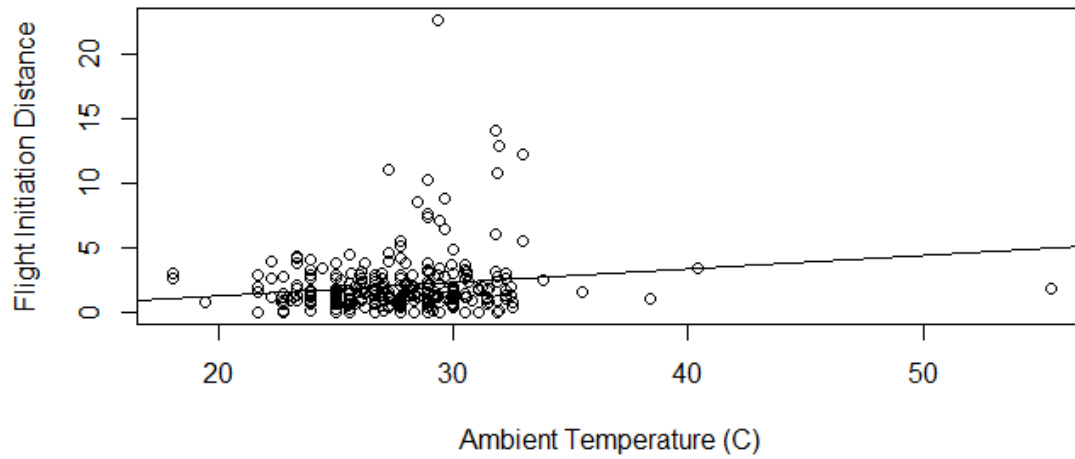


Figure 5. Flight initiation distances in different habitats (*a*) and substrate types (*b*). Lizards did not differ in FIDs among the habitat types, but did exhibit longer FIDs on the asphalt substrate type than all other substrates. Make sure the y-axis font is the same for a and b.

a.



b.

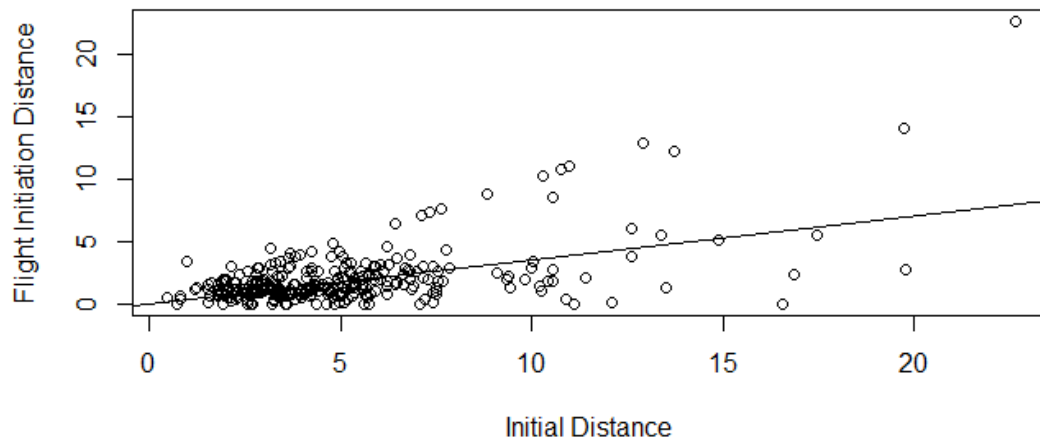
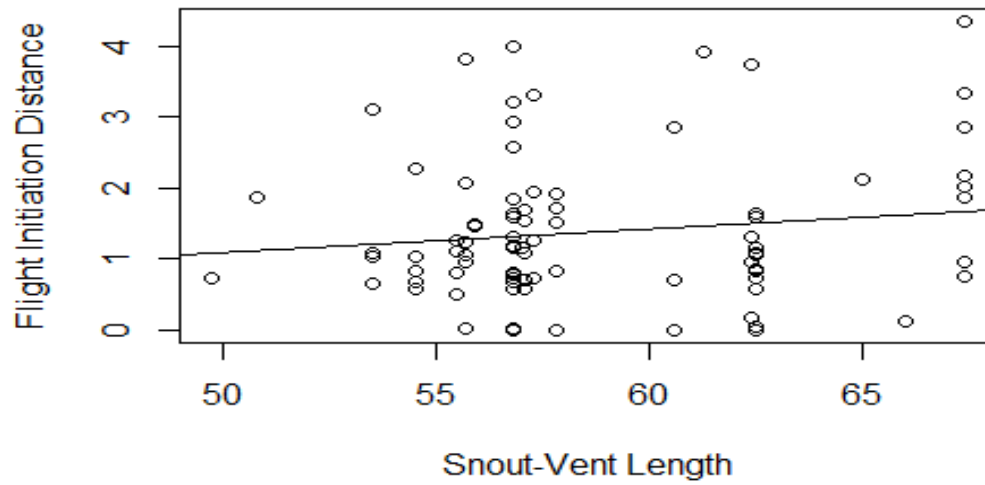


Figure 6. Flight initiation distances as a function of ambient temperature (*a*) and initial distance of predator approach (*b*) with lines representing the model for each variable. Lizard FIDs exhibited a significant relationship with ambient temperature, but it was weak. Lizards also exhibited a significant, and strong relationship between their FIDs and the initial distance of simulated predator approach.

a.



b.

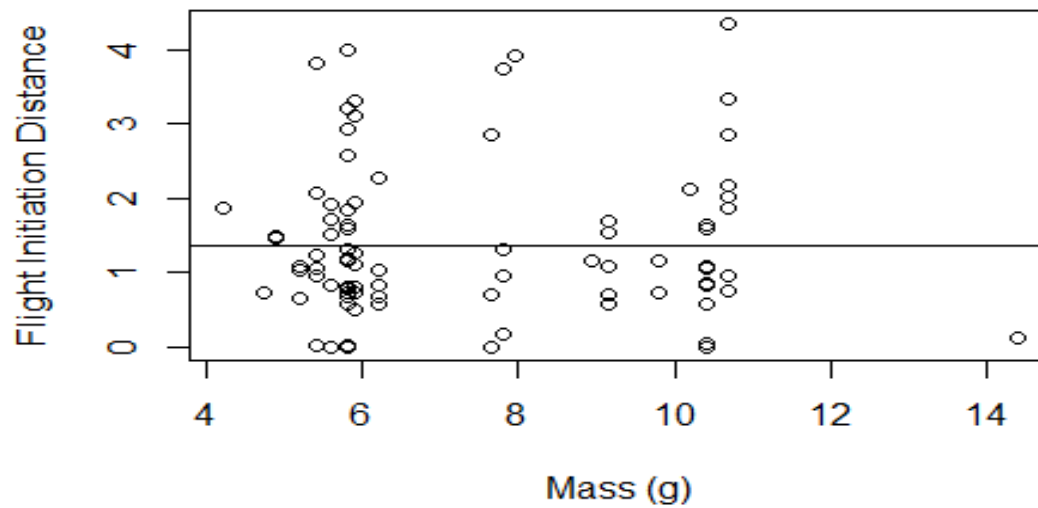
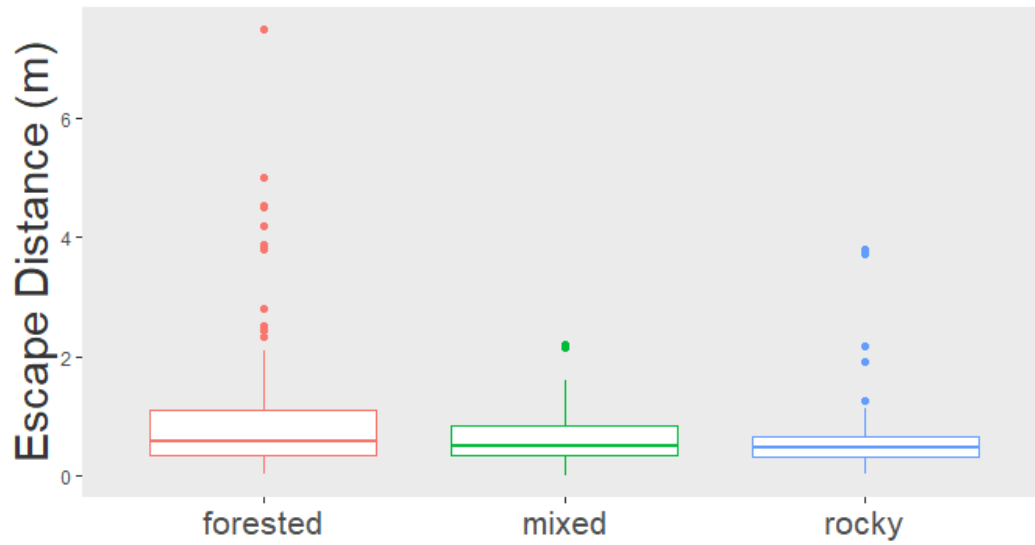


Figure 7. Flight initiation distances as a function of snout-vent length (*a*) and mass (*b*) with lines representing the model of each variable. Lizards did not exhibit a significant relationship between morphology and their FIDs.

a



b.

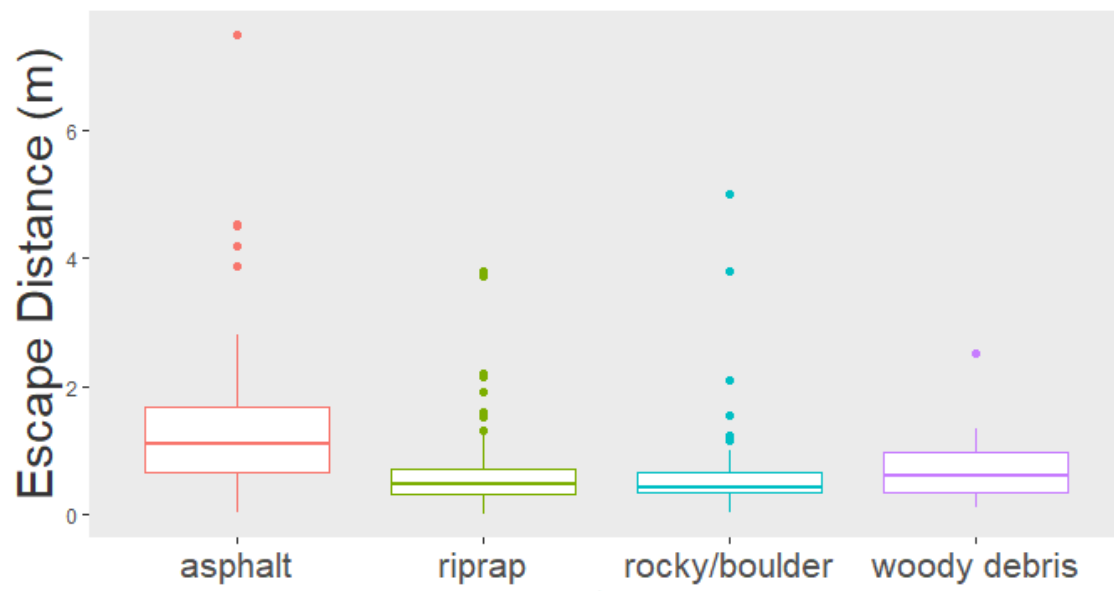
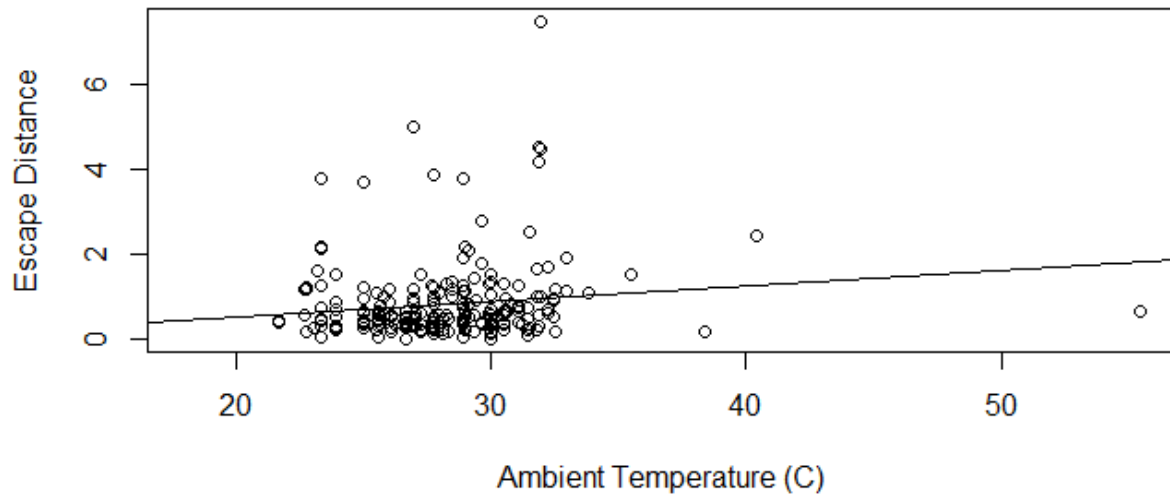


Figure 8. Escape distance in different habitats (*a*) and substrate types (*b*). Lizards exhibited longer escape distances on asphalt substrate types than all other substrate types. Riprap, rocky/boulder, and woody debris did not differ from each other.

a.



b.

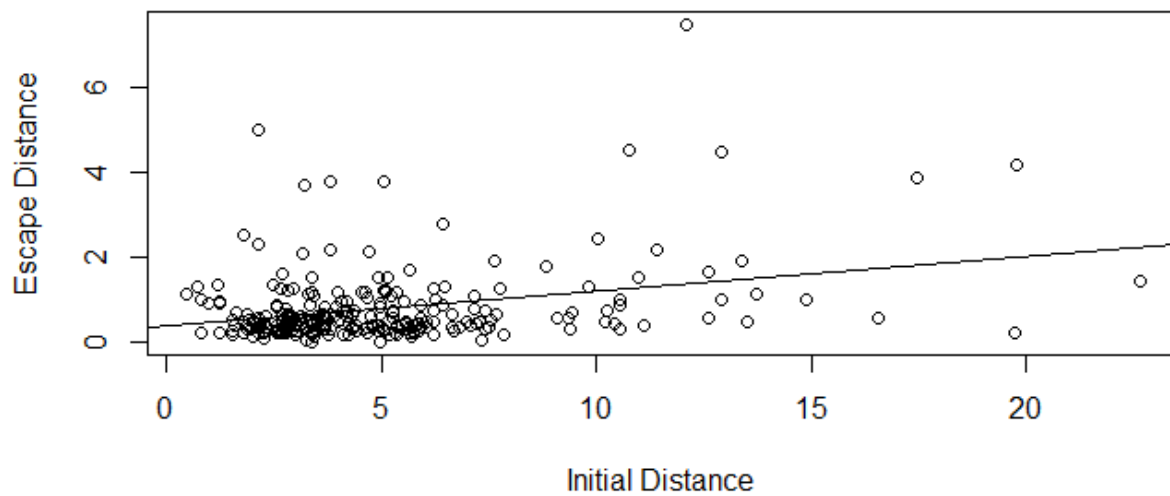
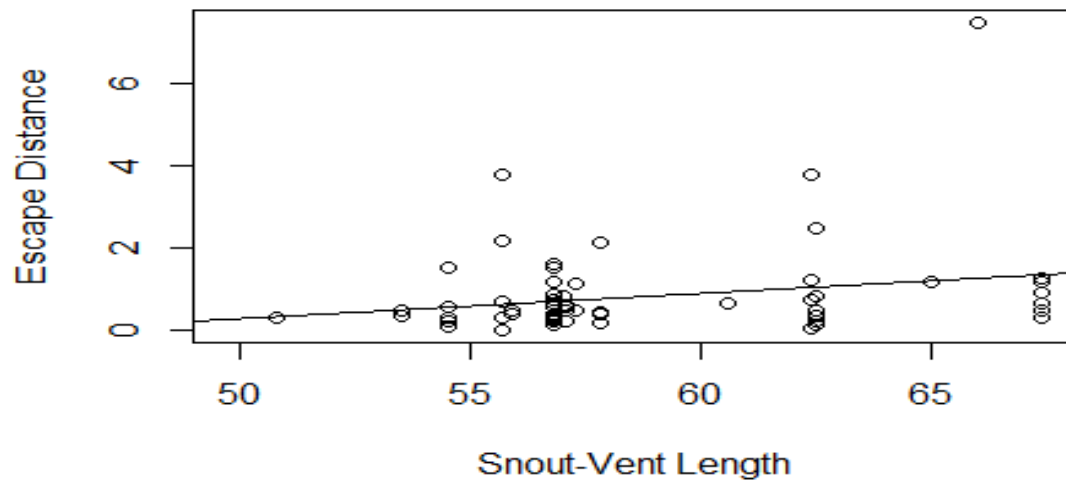


Figure 9. Escape distances as a function of ambient temperature (*a*) and initial distance (*b*) with models representing the model for each variable. Lizards exhibited longer escape distances the higher the temperature, and the longer the initial distance of approach, the further lizards escaped.

a.



b.

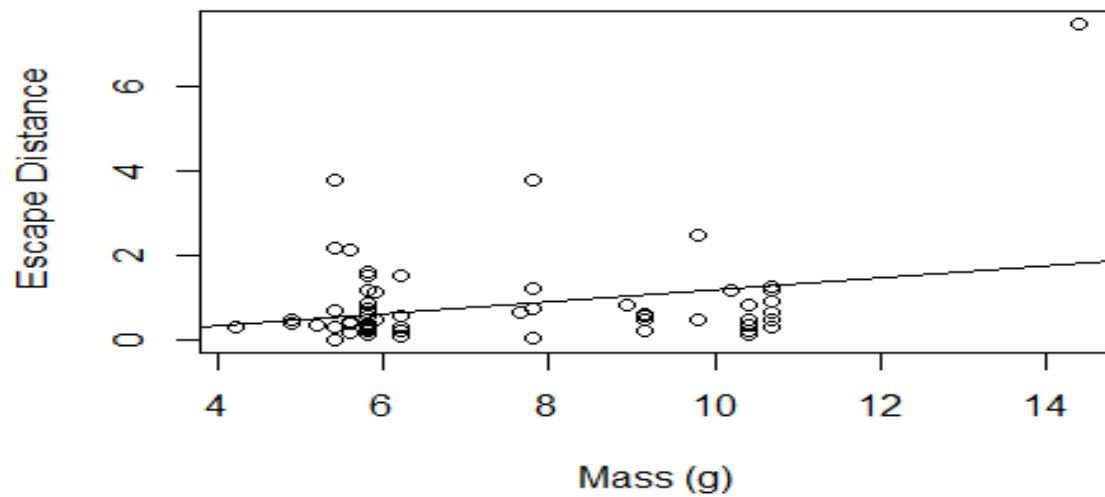


Figure 10. Escape Distances as a function of snout-vent length (*a*) and mass (*b*) with a line representing the model for each variable. Lizards exhibited longer escape distances the longer and larger they are.