

**Microhabitat use of the Eastern fence lizard (*Sceloporus undulatus*)
on the White Sands ecotone.**

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ABSTRACT

The role of ecology in evolution can be understood by determining how a species adapts to its surrounding environment. Novel environments offer an opportunity to examine how a species adaptively responds to new available resources. One example of a novel environment is White Sands, New Mexico, the largest gypsum dune field in the world. It differs from the surrounding dark soil Chihuahuan desert both biotically and abiotically. I conducted this study the ecotone, which is the ecological transition zone between White Sands and the dark soils. Species that moved to the ecotone are exposed to new ecological pressures and opportunities. I examined relationships between microhabitat use and morphology of the ecotone population of the Eastern fence lizard (*Sceloporus undulatus*). The population is adapting to the novel ecotone environment. I found no significant correlations between morphology (including body size and brightness) and microhabitat use, (distance from cover, percent foliage cover over perch, and perch height and width) which may indicate that lizards are not evolving morphological traits in response to changes in microhabitat use. However, my data did show evidence of a relationship between percent foliage cover over perch and sex over the mating and non-mating season. During the mating season, females were under more cover than during the non-mating season. Conversely, males were under less cover in the mating season than during the non-mating season. These results indicate how multiple factors including sex and time of season may affect behavioral variation in a population.

KEYWORDS

niche ecology, morphology, mate selection, fundamental niche, realized niche

INTRODUCTION

Determining how a species is affected by its surrounding environment is vital for understanding adaptive evolution (Rundle and Nosil 2005). Novel environments that are recently formed offer an opportunity to study the role of ecology in speciation while speciation is still occurring (Rice and Salt 1988, Rundle and Nosil 2005). New abiotic and biotic resources are often available to organisms in novel environments (Losos 2010). Populations that colonize novel environments may evolve unique phenotypes in response to novel selection pressures in new ecosystems (Darwin 1859, Losos 2010). Looking at specific novel environments and investigating how species develop in conjunction with new ecological opportunities can provide specific insights into how evolution is occurring (Losos 2010).

An example of a unique novel environment is White Sands, a gypsum dune field in southern New Mexico that has formed recently within the last 2000-6000 years (Kocurek et al. 2007). The abiotic differences between White Sands and the surrounding dark soil desert are mainly due to the properties of gypsum (Kocurek et al. 2007). Gypsum, composed of calcium sulfate dihydrate, is stark white and forms a less compact substrate than the dark soil in the surrounding Chihuahuan desert (Macdonald 1953, Kocurek et al. 2007). There are also fewer species and less vegetation on White Sands than on the dark soils (Des Roches et al. 2011). These biotic and abiotic differences contribute to making White Sands a distinctive environment that may pose unique selective pressures on its colonists (Rosenblum 2006). The ecotone, an ecological transition zone between White Sands and the Chihuahuan desert, is a mix between the two environments (Rosenblum 2006).

Three lizard species, the Eastern fence lizard (*Sceloporus undulatus*), the Lesser earless lizard (*Holbrookia maculata*), and the Little striped whiptail (*Aspidoscelis inornata*) have colonized the ecotone and White Sands (Rosenblum 2006). Populations on White Sands and the ecotone have evolved a blanched color which may be an adaptation to camouflage with the white substrate (Rosenblum and Harmon 2011). Although blanched coloration is the most visually striking trait of the White Sands lizards, there may also be selection on other phenotypic traits including morphological and behavioral modifications that may be linked to the divergence of populations (Calsbeek and Irschick 2007). The ecotone has fewer predators and competing

species than the surrounding Chihuahuan desert, which may affect *S. undulatus* behavior and morphology (Des Roches et al. 2011, Robertson et al. 2011).

Divergence in microhabitat use behavior between populations may be increased by selection on morphological characteristics that are advantageous in the new environment (Schluter 1993). Morphological traits that are related to microhabitat use include limb length and body size (Melville and Swain 1999, Calsbeek and Irschick 2007). Lizards in White Sands are brighter than lizards in the dark soils, but they do not vary in body size or shape (Rosenblum 2006, Des Roches et al. 2011). Populations of *S. undulatus* on the dark soils use yucca perches significantly more than non-yucca perches, which are shorter and wider, whereas populations on White Sands use non-yucca perches as often as yucca perches (Des Roches et al. 2011). This does not correspond with previous research on other species of lizards, which found that those with longer limbs use shorter and wider perches (Calsbeek and Irschick 2007). Although studies have been conducted on both morphology and microhabitat use for *S. undulatus* on White Sands and on the dark soils, no study has shown if there is a relationship between microhabitat use within the population of *S. undulatus* that occurs on ecotone (Calsbeek and Irschick 2007, Rosenblum and Harmon 2011, Des Roches et al. 2011). Other factors such as age, sex, and breeding patterns may also affect microhabitat use and selection on morphological characteristics (Calder 1973, Jaksic et al. 1980, Leber 1985, McIvor 1988, Baltz et al. 1991, Losos 1993).

I examined the relationship between microhabitat use and morphology of *S. undulatus* on the ecotone of White Sands. Specifically I aimed to answer the questions: 1) Are there any correlations between morphological characteristics and microhabitat use of *S. undulatus* on the ecotone? 2) Is microhabitat use or morphology related to sex during the mating season versus the non-mating season?

I expect that there will be no correlation between morphology and microhabitat use (Des Roches et al. 2011). I also expect that males and females will use their microhabitat differently during the mating season versus the non-mating season due to pressures to find a mate (Haenel et al. 2003).

METHODS

Study site

I conducted my study on the ecotone of White Sands, New Mexico at 32°46'47"N, 106°10'18"W. The ecotone spans the entire perimeter of White Sands separating it from the dark soils of the Chihuahuan desert.

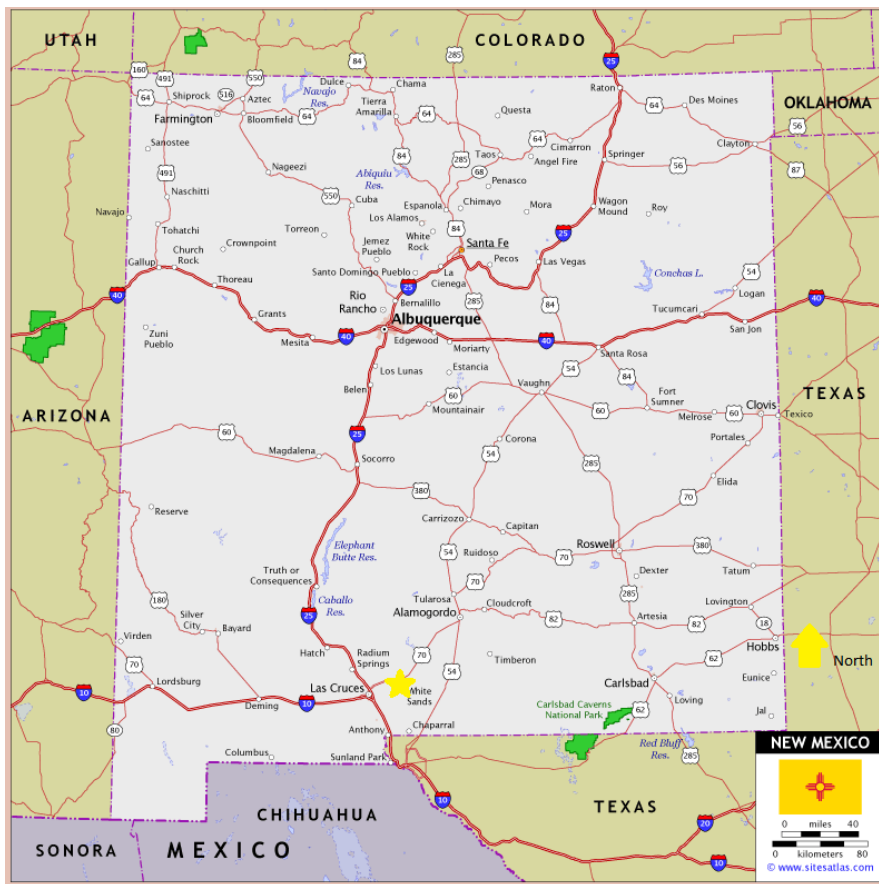


Figure 1. Map of White Sands, NM. Map showing White Sands in New Mexico, USA, denoted by yellow star (www.siteatlas.com, 2012).

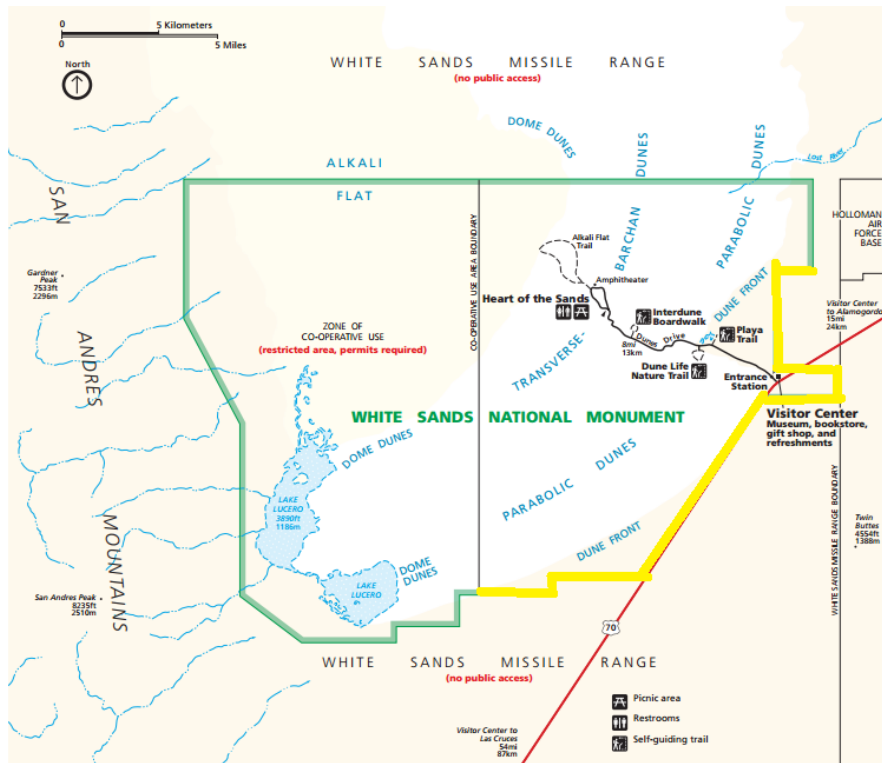


Figure 2. Focused map of White Sands, NM. Map showing White Sands and the surrounding dark soil Chihuahuan desert. The yellow line denotes the area of the ecotone that I sampled (U.S. National Park Service, 2013. White Sands, New Mexico. <http://www.nps.gov/whsa>).

White Sands consists of high sand dunes and surrounding low interdunes that are predominantly vegetated by rabbitbrush (*Chrysothamnus pulchellus*), yucca (*Yucca elata*), Mormon tea (*Ephedra torreyana*), sand verbena (*Phyla incise*), and grasses (*Oryzopsis spp.*, *Sporobolus spp.*). The surrounding Chihuahuan desert has a dark brown adobe substrate and is predominantly vegetated by yucca (*Yucca elata*), mesquite (*Prosopis glandulosa*), cactus (*Opuntia*), and grama grasses (*Bouteloua*) (Rosenblum 2006). The ecotone has similar yet denser vegetation to that found on White Sands. White Sands is windy, hot and dry in the summer and cold and dry in the winter (Hager 2001). The peak temperature on the ecotone is during summer at 39°C and the lowest temperature is at 7°C in the winter (Hager 2001). White Sands experiences 0.59 inches of rain in winter (December, January, February), 0.35 inches in spring (March, April, May), 1.45 inches in summer (June, July, August), and 1.07 inches in the fall (September, October, November).

Study species

The Eastern fence lizard, *S. undulatus*, is a small diurnal lizard that is distributed across the eastern and southern United States. *S. undulatus* has an average home range of 100m² to 400m² and exhibits territorial behavior (Jones and Droge 1980). *S. undulatus* prefers to be in close proximity to vegetation and can be arboreal, saxicolous, or terrestrial in New Mexico (Dixon 1967, Jones and Droge 1980, Degenhardt et al., 1996 Hager 2001). Populations on White Sands are most active between the hours 0800 and 0900 (Hager 2001). Although no population data on sex has been taken on White Sands, other populations of *S.undulatus* in New Mexico have been found to have a 1:1 sex ratio (Vinegar 1975). Fence lizards breed between May and July (Vinegar 1975). Previous studies conducted on White Sands found that the population had a density of 9.5 individuals/ha in May through October, but no density data exists for the ecotone population (Hager 2001). There are behavioral and morphological variations between White Sands and the dark soil populations of *S. undulatus*. Populations in White Sands use a more diverse selection of perches (Des Roches et al. 2011). White Sands fence lizards also alter their microhabitats use on a seasonal basis across May and August even when monthly temperatures do not vary significantly (Hager 2001).

Capture and sampling

My goal was to collect as large of a percentage of the population of *S. undulatus* on the ecotone as possible. With three other researchers, I looked for lizards in the interdunes of the ecotone on the southeast side of White Sands. I collected lizards from May through June (Season I) while lizards were breeding, and again in August (Season II) when lizards were not actively breeding, during 0800-1300 hours (Vinegar 1975, Hager 2001). I walked along a portion of the ecotone and looked for lizards and attempted to catch every lizard I saw by noose or hand. I resampled each portion for 3 to 4 days in attempts to catch all individuals in the area. To ensure that I did not capture the same lizard twice another field team member marked the tail with permanent ink and injected small plastic elastomer tags under the skin on the ventral side of each lizard. I quantified their microhabitat use, and took measurements of their morphology.

Habitat quantification

I quantified microhabitat use by recording perch characteristics where we first spotted individuals. We recorded perch type (yucca, dead shrub, sage bush, or ground) and whether the perch was exposed to direct sunlight, shade, or filtered sunlight. I estimated the perch height and perch diameter to the nearest 5mm. I estimated percent foliage coverage of the perch by visually approximating foliage cover in a cone created by a 45 degree angle over where the lizard was perched. I also measured the distance the individual was from the cover to the nearest 5mm (Des Roches et al 2011, Losos et al. 1993).

Morphology data collection

I captured lizards by noose or hand and transported them back to the field lab in cages by vehicle. I used a scanner to record an image of the lizard's ventral body. I digitally measured the body length from snout to vent and hind limb length to the nearest millimeter using ImageJ Software (e.g. Melville et al 2006). To measure brightness, I recorded light transmission of the dorsal side of the body in nanometers using a SpectraWiz spectrometer (Stellarnet, Tampa, Florida).

Data analysis

I used linear regression models to determine if there was a correlation between morphology and microhabitat use. Specifically, I examined whether percent foliage cover (PFC), distance from cover (DFC), perch height (PH), and perch diameter (PD) had relationships with morphological characteristics including snout-vent length (SVL), brightness (B), hind limb length (HL), and weight (W). I transformed each of the morphological measurements in order to normalize them. I also used linear models to test the relationships between morphology and microhabitat use across sex and season. I used an analysis of variance (ANOVA) to assess the significance of each linear model. I used Welch's t-test to compare morphology and microhabitat selection within sexes across seasons. I conducted these analyses both for the entire sample and with only individuals that I caught in both seasons to assess trait plasticity. Significant

differences between morphology and microhabitat selection for the same individuals between the two seasons would indicate that these traits are variable for an individual and may change over time. All analyses were conducted in R (R Development Core Team 2011)

RESULTS

Capture

I captured a total of 216 individuals. In season I (May through June), I captured 10 juvenile females, 43 adult females, 6 juvenile males and 29 adult males. In season II (August), I captured 14 juvenile females, 65 adult females, and 13 juvenile males, and 36 adult males

Relationship between microhabitat use, sex, and season

There was a significant difference in percent foliage cover males and females were perched under across season I (May-June) and season II (August). Percent foliage cover was correlated with sex and season (ANOVA, F value= 11.74, p=0.01). In season I, males were perched under less cover than females (Welch's t-test, t=2.09, p=0.04). In season II, males were perched under more cover than females in season I (Welch's t-test, t=-2.37, p=0.02,). In season I, females were perched under more cover than females in season II (Welch's t-test, t=2.64, p=0.01). Conversely in season I males were perched under less cover than males in season II (Welch's t-test, t= -1.86, p=0.01) There was no significant correlation between percent foliage cover and sex and season when considering only individuals that were captured in the season I and recaptured in the season II. I did not find any significant correlations between sex and season with perch diameter, perch height, perch type, and exposure to sunlight.

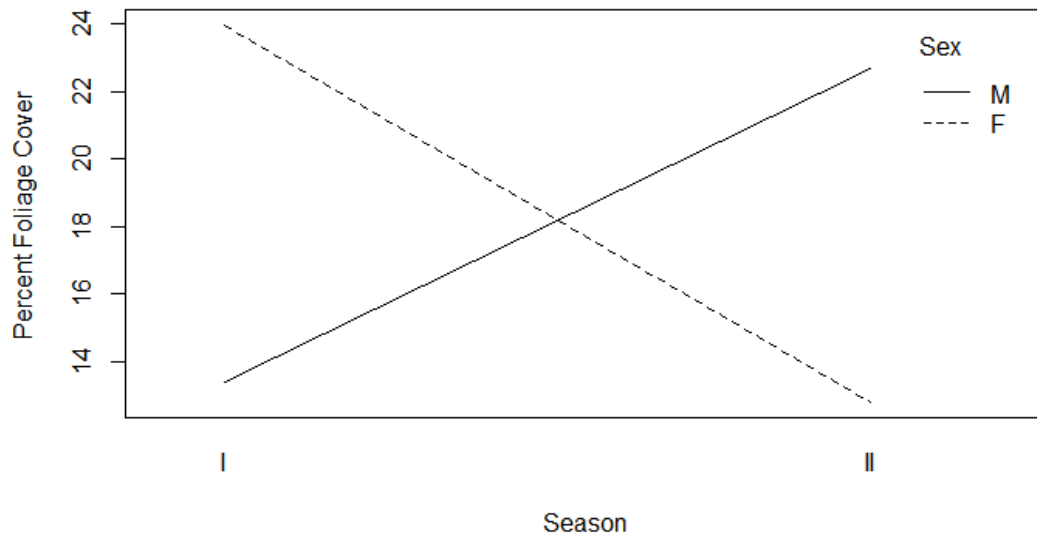


Figure 3. Percent foliage cover over season I and season II between sexes. Interaction plot shows that percent foliage cover over perch increased for males from season I (when lizards are actively breeding) to season II (when they are not actively breeding) (Welch's T-test, $t=-2.37$, $p=0.01$), while for females percent foliage cover over perch decreases from season I to season II (Welch's T-test, $t=2.64$, $p=0.01$).

Relationship between morphology, sex, and season

I found evidence of significant correlations between morphology and sex and season. Females were brighter than males in both seasons (ANOVA, F value= 5.69, $p=0.02$). Brightness was not correlated with sex across seasons in the sample including only recaptured lizards (ANOVA, F value= 0.20 $p=0.65$). Snout-vent length was correlated with season but not sex both in the whole sample (ANOVA, F value= 15.88, $p=0.000009$) and in the sample including only recaptured lizards (ANOVA, F value= 9.01, $p=0.004$). Males and females had larger snout-vent lengths in season II. Hind limb length increased significantly with season in entire sample (ANOVA, F value= 13.41, $p=0.003$) and in the recaptured sample (ANOVA, F value=9.28 $p=0.0004$).

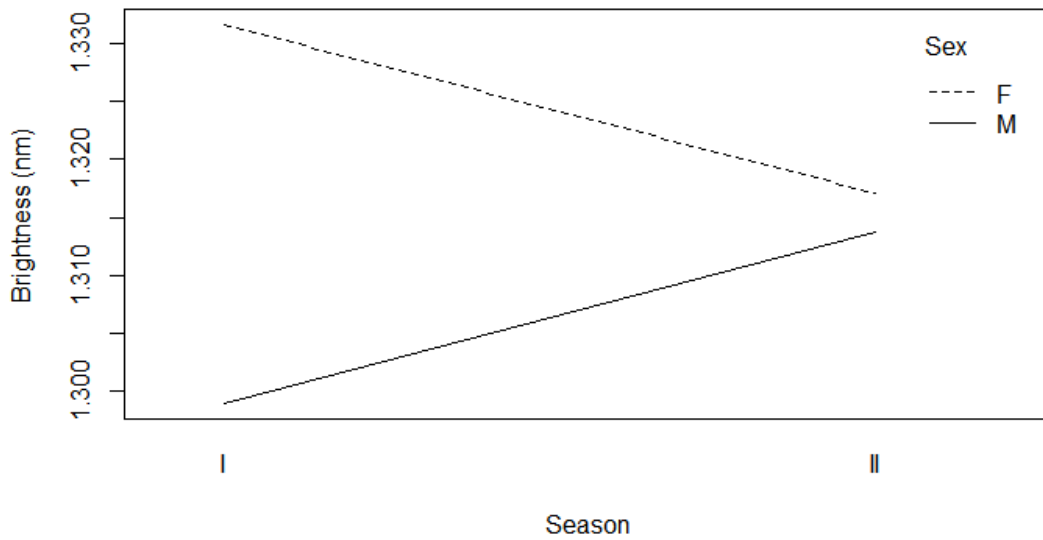


Figure 4. Brightness (nm) of dorsal sides over season I (mating season, May-June) and season II (non-mating season, August) between sexes. Females are brighter than males in both seasons (ANOVA, F value= 5.69, $p=0.03$).

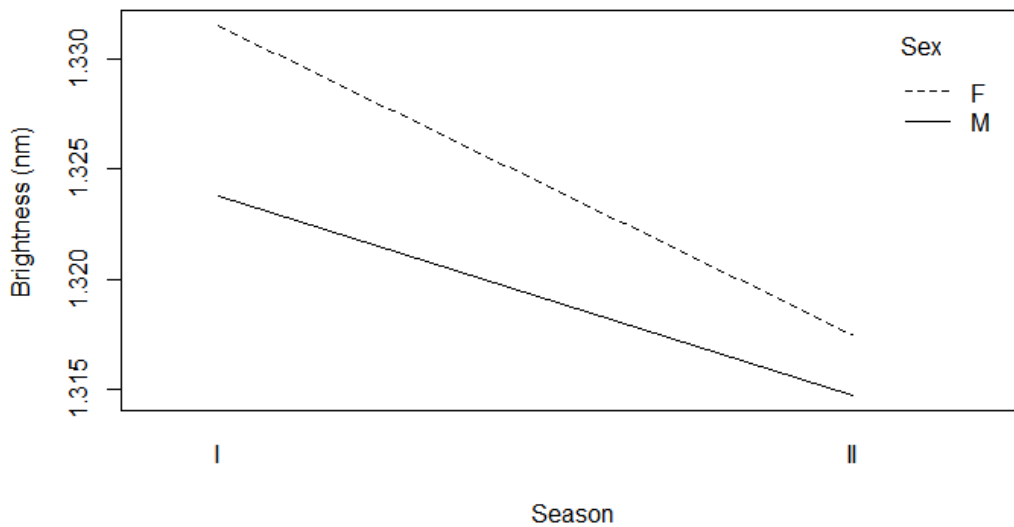


Figure 5. Brightness (nm) of dorsal sides over season I (mating season, May-June) and season II (non-mating season, August) between the sexes for recaptures. There is a trend that both males and females are both brighter in season I than season II but the relationship is not significant (ANOVA, F value= 0.20, $p=0.65$).

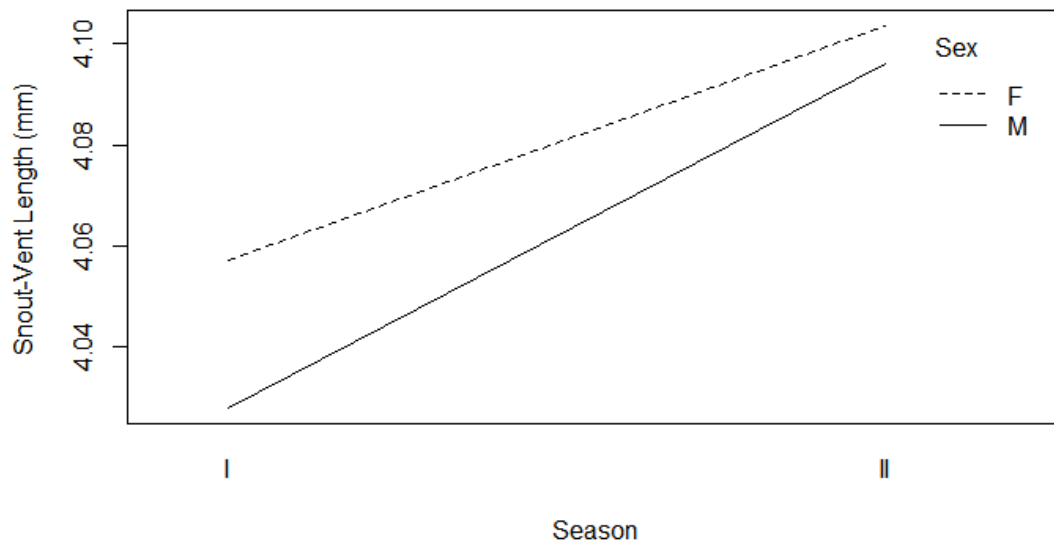


Figure 6. Snout-vent length over season I (mating season, May-June) and season II (non-mating season, August) between sexes. Recaptures increase in snout-vent length from season I to season II (ANOVA, F value= 15.88, $p=0.000009$).

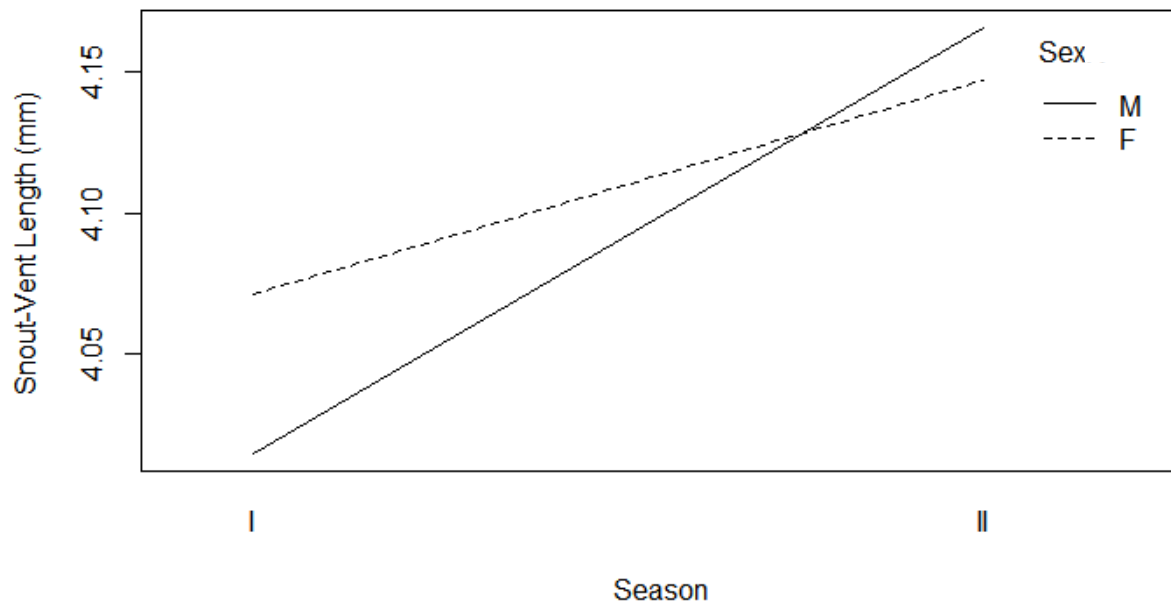


Figure 7. Snout-vent length over season I and season II between sexes for recaptures. Recaptures have an increased snout-vent length from season I to season II (ANOVA, F value= 9.01, $p=0.004$).

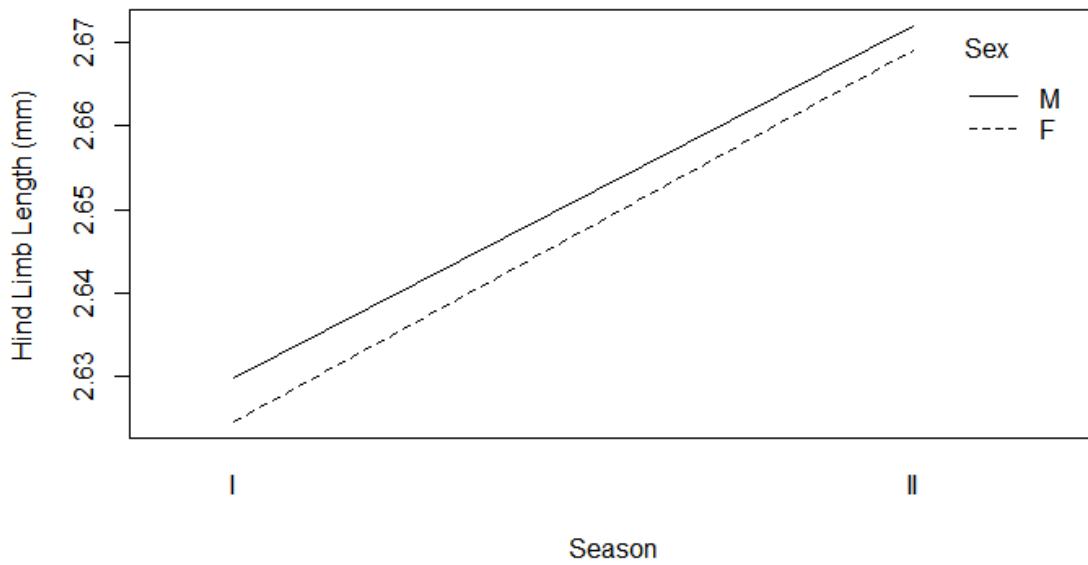


Figure 8. Hind limb length over season I (mating season, May-June) and season II (non-mating season, August) between the sexes. Lizards have longer hind limbs in season II than in season I (ANOVA, F value= 13.41 p=0.003).

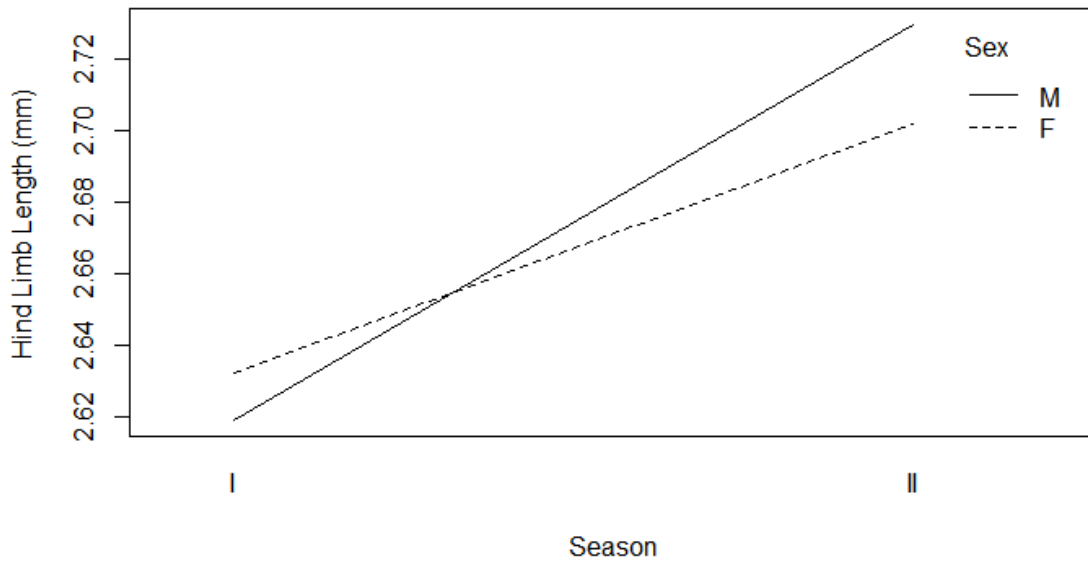


Figure 9. Hind limb length over season I (mating season, May-June) and season II (non-mating season , August) between the sexes for recaptures. Recaptures have longer hind limbs in season II than in season I (ANOVA, F value= 9.28, =0.004).

DISCUSSION

I found that microhabitat selection has a relationship with sex and season but not with morphology. There were relationships between sex and percent foliage cover selection and brightness across seasons and sexes which may indicate that breeding behavior is a driving force of variation in behavioral and morphological characteristics the ecotone of White Sands. Previous research demonstrates that there is a correlation between aspects of morphology and microhabitat selection for diurnal lizards (Calsbeek and Irschick 2007). My study shows no evidence of this that microhabitat selection is not directly correlated with morphology for the population of *S. undulatus* on the ecotone of White Sands. Microhabitat selection for many species can be influenced by numerous factors, including season, sex, age, morphology, resource opportunity, mating, predator evasion and temperature regulation (Calder 1973, Jaksic et al. 1980, Leber 1985, McIvor 1988, Baltz et al. 1991, Losos 1993).

Microhabitat selection, sex, and season

Percent foliage cover differed between both sexes and seasons. In the breeding season, females were found under more cover than males, while in the non-breeding season, females were found under less cover than males. This trend is similar to previous studies which suggest that during the breeding season, males risk more exposure to predators in order to find a mate (Stamps 1983, Baltz et al. 1991, Cooper 2003). Females may be less likely to risk exposure to predators during mating season due to reduced locomotor ability from carrying eggs, and so may be further away from cover after laying eggs in season II (Cooper 1990, Losos 1993).

Although some species of lizards have adapted morphologies that correspond with specific microhabitat use, I did not find any relationships between morphology and microhabitat use for *S. undulatus* on the ecotone (Calsbeek and Irschick 2007). Perhaps other factors such as breeding pressures, interspecific and intraspecific competition, and temperature regulation play a more important role than morphology in how an individual selects their microhabitat on the ecotone (Calder 1973, Jaksic et al. 1980, Leber 1985, McIvor 1988, Baltz et al. 1991, Losos

1993). No study has determined if microhabitat use varies with predator abundance, species abundance, or habitat availability between the ecotone, White Sands, and the dark soiled Chihuahuan desert, thus it is difficult to determine the driving force behind microhabitat selection.

Morphology, sex, and season

There was a significant correlation between brightness and sex across breeding season (season I) and non-breeding season (season II), which suggests that variation in brightness may be driven by breeding pressures. Diurnal reptiles may experience longer-term, seasonal fluctuations in brightness (Watkins 1997). In my study I found that females were brighter than males in both seasons. Perhaps males and females present different coloration to attract a mate, for example brighter females may be more attractive than darker females (Watkins 1997). However, these interactions between brightness and sex were not significant when I conducted the same analyses using only recaptured individuals over season which suggests that lizards do not change in brightness significantly over time.

There was a significant correlation between snout-vent length and season and hind limb length and season. Both males and females had longer bodies in season II than in season I. This trend was also significant within the recapture group, suggesting that all the lizards may have grown over the two seasons I sampled. This is plausible as individuals that I caught may not have all reached their full adult size.

Limitations and future directions

The main limitation of this study is that the data was taken only on the ecotone during one summer. In order to determine how lizards are adapting to their environment as a population and as individuals, studies must be conducted throughout the year over many years on the ecotone, White Sands, and the Chihuahuan dark soils. Long term studies would increase information on both the plasticity of recaptured individuals and measure trends in variation for populations on the three ecosystems.

Furthermore, experiments determining the strength and effects of natural selection (observing which individuals survive and reproduce and which die prior to recapture) as well as experiments on sexual selection will be important in assessing influences on changes in behavior and phenotype. Understanding the influences on variation in the novel ecotone environment will help to clarify the relationship between ecology and phenotypic adaptation in transition zones.

CONCLUSIONS

I found correlations between brightness and sex, and between percent foliage cover over perch and sex. The relationship between percent foliage cover over perch and sex changed during the breeding season and non-breeding season. This study also showed a lack of correlation between morphology and microhabitat use within the ecotone population. Finally, these findings reveal how novel environments are important locations for studying speciation because they create a backdrop for the examination of speciation as it occurs in response to ecological variation.

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REFERENCES

- Baltz, D.M., B. Vondracek, L.R. Brown, and P.B. Moyle. 1991. Seasonal changes in microhabitat selection by Rainbow Trout in a small stream. *Transactions of the American Fisheries Society* 120: 166-176.
- Calsbeek, R., and D.J. Irschick. 2007. Selection on morphology, performance and habitat use in island lizards. *Evolution* 61: 2493-2503

- Calder, W.A. 1973. Microhabitat selection during nesting season of hummingbirds in the Rocky Mountains. *Ecology* 54: 127-134.
- Cooper, W.A. 1990. Locomotor impairment and defense in gravid lizards (*Eumeces laticeps*): behavioral shift in activity may offset costs of reproduction in an active forager. *Behavioral Ecology and Sociobiology* 27: 153-157.
- Darwin, C. 1859. *On the Origin of Species*. London, England. John Murray.
- Des Roches, S., J. M. Robertson, L. J. Harmon, and E. B. Rosenblum. 2011. Ecological Release in White Sands Lizards. *Ecology and Evolution* 10: 571-578.
- Haenel, G.J., L.C. Smith, B.H. John-Alder, and C. Guyer. 2003. Home-Range Analysis in *Sceloporus undulatus* (Eastern Fence Lizard) Spacing Patterns and the Context of Territorial Behavior. *Copeia* 1: 99-112.
- Hager, S. 2001. Microhabitat use and activity patterns of *Holbrookia maculata* and *Sceloporus undulatus* at White Sands National Monument, New Mexico. *Journal of Herpetology* 35: 326-330.
- Jaksic, F.M., H. Nunez, F.P. Ojeda. 1980. Body proportions, microhabitat selection, and adaptive radiation of *Liolaemus* lizards in central Chile. *Oecologia* 45: 178-181.
- Jones, S. M., and D. L. Droge. 1980. Home range size and spatial distributions of two sympatric lizards (*Sceloporus undulatus*, *Holbrookia maculata*) in the Sand Hills of Nebraska. *Herpetologica* 36:127-133
- Kocurek, G., M. Carr, R. Ewing, K. G. Havholm, Y. C. Nagar, and A. K. Singhvi. 2007. White Sands Dune Field, New Mexico: age, dune dynamics and recent accumulations. *Sediment. Sedimentary Geology* 197: 313-331.
- Leber, K.M. The influence of predatory decapods, refuge, and microhabitat selection on Seagrass communities. 1985. *Ecology* 66: 1951-1964.
- Losos, J. B., J. C. Marks, and T. W. Schoener. 1993. Habitat use and ecological interactions of an introduced and a native species of anolis lizard on Grand Cayman, with a review of the outcomes of Anole introductions. *Oecologia* 95:525-532.
- Losos, J.B. 2010. Adaptive Radiation, Ecological Opportunity, and Evolutionary Determinism. *The American Naturalist* 175: 623-639.
- Macdonald, G.J.F. 1953. Anhydrite-gypsum equilibrium relations. *American Journal of Science* 251: 884-898.

- Melville, J. and R. Swain. 2000. Evolutionary relationships between morphology, performance and habitat openness in the lizard genus *Niveoscincus* (Scincidae : Lygosominae). *Biological Journal of the Linnean Society* 70: 667-683.
- Melville, J., L. J. Harmon, and J. B. Losos. 2006. Intercontinental community convergence of ecology and morphology in desert lizards. *Proceedings of the Royal Society B*. 273:557–563.
- McIvor, C.C., W.E. Odum. Food, predation risk, and microhabitat selection in a marsh fish assemblage. 1988. *Ecology* 69: 1341-1351.
- R Development Core Team. 2011. R: a language and environment for statistical computing. R foundation for Statistical Computing, Vienna, Austria.
- Rice, W.R., and G.W. Salt. 1990. The evolution of reproductive isolation as a correlated character under sympatric conditions: experimental evidence. *Evolution* 44: 1140-1152.
- Robertson, J., K. Hoversten, M. Grundler, T. Poorten, D. Hews, E. B. Rosenblum. 2011. Colonization of novel White Sands habitat associated with changes in lizard anti-predator behavior. *Biological Journal of the Linnean Society* 103 :657-667.
- Rosenblum, E.B., L.J. Harmon. 2011. “Same same but different.”: Replicated ecological speciation at White Sands. *Evolution* 65: 946-960.
- Rosenblum, E.B., H. Rompler, T. Schoneberg, and H.E. Hoekstra. 2010. Molecular and functional basis of phenotypic convergence in white lizards at White Sands. *Proceedings of the National Academy of Sciences* 107: 2113-2117.
- Rosenblum, E.B. 2006. Convergent evolution and divergent selection: Lizards at the White Sands ecotone. *American Naturalist* 167: 1-15
- Rundle, H.D., P. Nosil. 2005. Ecological Speciation. *Ecological Letters* 8: 336 -352.
- Schluter, D. 1993. Adaptive radiation in sticklebacks – size, shape, and habitat use efficiency. *Ecology* 74:699–709
- Site Atlas. 2011. Siteatlas.com
- Stamps, J. A. 1983. The relationship between ontogenetic habitat shifts, competition and predator avoidance in a juvenile lizard (*Anolis aenus*). *Behavioral Ecology and Sociobiology* 12:19–33.
- U.S. National Park Service, 2013. White Sands, New Mexico. <http://www.nps.gov/whsa>
- Watkins, G.G. 1996. Intersexual signaling and the functions of female coloration in the tropidurid lizard (*Microlophus occipitalis*).