

Evidence for ecological release over a fine spatial scale in a lizard from the White Sands formation

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When a population experiences relaxation of selective pressures due to reduced predation or competition, it may undergo ecological release. Ecological release often manifests as increased niche breadth and trait variation, as individuals have the opportunity to exploit a wider variety of resources. At the recently-colonized White Sands dune formation in New Mexico, lizards from white sand habitat have fewer predators and competitors than their dark soil counterparts, and show evidence of ecological release compared to dark soil lizards. To determine whether the dynamics of ecological release also play out over an even finer habitat gradient, we studied southwestern fence lizards in the center of the White Sands dune formation and the narrow ecotone between White Sands and the surrounding dark soil habitats. We predicted that lizards from the central dunes would exhibit ecological release in terms of broadened resource use compared to lizards from the ecotone. We first conducted avian surveys in both the central dunes and ecotone habitats to measure abundance, richness and diversity of avian species that could act as lizard predators. Next, we measured microhabitat-scale resource use by comparing perch selection of lizards in both habitats. Finally, we measured landscape-scale resource use by quantifying home range sizes and daily distances traveled by lizards in both habitats. We found that central dunes lizards used a greater diversity of perch types, and had greater variation in both home range size and daily distances traveled, than ecotone lizards. There were fewer predatory bird species in the central dunes than on the ecotone, and there was a tendency for fewer predation events in the central dunes than on the ecotone. Our results demonstrate that ecological release is detectable over a fine habitat gradient, such as between the center of a recently-colonized habitat and its ecotone with the surrounding ecosystem.

Ecological release occurs when a population experiences a relaxation of selection pressures such as predation or competition (MacArthur and Wilson 1967, Lister 1976, Yoder et al. 2010, Emery and Ackerly 2014). Theory predicts that at the population scale, ecological release takes the form of increased density (MacArthur et al. 1972), broadened niche breadth (MacArthur and Wilson 1967), and/or increased trait variation because selection against extreme phenotypes is relaxed (Bolnick et al. 2007). Because ecological release often manifests as rapid ecological and evolutionary change following relaxation of selection pressures (Cox and Ricklefs 1977, Losos and DeQueiroz 1997, Bolnick et al. 2010), it can potentially lead to diversification, speciation, and adaptive radiation (Harmon et al. 2008, Parent and Crespi 2009, Yoder et al. 2010, Des Roches et al. 2011).

Ecological release can be particularly evident in recently-colonized habitats, which present opportunities for colonizers to exploit new niches and to escape previous selection pressures (Harmon et al. 2008, Parent and Crespi 2009). One such newly-colonized habitat, the White Sands dune formation in New Mexico, provides an excellent opportunity to study ecological release. The gypsum dunes of White Sands were formed in the last 7000 years (Kocurek et al. 2007) and contrast sharply with adjacent areas of dark

soil habitat. Three lizard species (southwestern fence lizard *Sceloporus cowlesi*, lesser earless lizard *Holbrookia maculata* and little striped whiptail *Aspidoscelis inornata*) have colonized the White Sands formation and exhibit parallel evolution of white coloration that provides camouflage on the light substrate (Rosenblum 2005, 2006, Rosenblum et al. 2010). In addition to differences in dorsal coloration, white sand populations of *S. cowlesi* differ from their dark soil counterparts in social signal coloration (Robertson and Rosenblum 2009), body size and shape (Rosenblum and Harmon 2011), social behavior (Robertson and Rosenblum 2010), and anti-predator behavior (Robertson et al. 2011, Des Roches et al. 2014). Moreover, white sand *S. cowlesi* exhibit evidence of ecological release when compared to dark soil counterparts (Des Roches et al. 2011, 2015).

In addition to the dramatic and well-documented differences between the dark soil and white sand habitats, there is also habitat variation within the White Sands dune formation. In the center of the White Sands formation (hereafter 'central dunes'), high dunes are separated by sparsely vegetated interdune areas. The interdunes are characterized by small, low-growing plants (e.g. alkali sacaton grass *Sporobolus airoides*, jointfir *Ephedra torreyana*, soapbush yucca *Yucca elata* and dwarf juniper *Juniperus communis*). In

contrast, substrate on the edge of the White Sands formation (hereafter 'ecotone') is intermediate in color between the central dunes habitat and the surrounding dark soil habitat (Rosenblum 2006). Two of the three lizard species on the White Sands formation, *S. cowlesi* and *A. inornata*, display dorsal coloration on the ecotone that is intermediate between individuals from the central dunes habitat and the surrounding dark soil habitat (Rosenblum 2006). The ecotone supports a greater diversity of plant species in addition to those found in the central dunes (e.g. cottonwood *Populus deltoides wislizenii*, sumac *Rhus trilobata* and soapbush yucca), and exhibits increased complexity of vegetation structure compared to the central dunes. Natural history observations also suggest that the ecotone supports more predatory reptile and avian species than the central dunes. Specifically, eastern massasaugas *Sistrurus catenatus*, gopher snakes *Pituophis catenifer*, greater roadrunners *Geococcyx californianus* and American kestrels *Falco sparverius*, are regularly observed on the ecotone, but only very rarely in central dunes habitat (Des Roches and Rosenblum unpubl.). Together, these lines of evidence suggest that selection pressure due to predation may be relaxed in the central dunes compared to the ecotone.

Given previous evidence (i.e. increased density and broadened perch use; Des Roches et al. 2011) that ecological release has occurred in white sand *S. cowlesi*, the purpose of this study was to determine whether ecological release is also detectable over the finer habitat gradient between the ecotone and center of the White Sands formation. We first conducted point count surveys for avian predators on the ecotone and in the central dunes. We then compared habitat use at the microhabitat and landscape scales between lizards from the ecotone and the central dunes. At the microhabitat scale, we compared type and characteristics of perches selected by lizards in both habitats. At the landscape scale, we measured home range size and daily distances traveled by lizards in both habitats using radio-telemetry, a method that has not previously been feasible for species as small as *S. cowlesi*. We predicted that central dunes lizards would exhibit greater variation than ecotone lizards in habitat use at both spatial scales, which would indicate ecological release in the central dunes. Also, because the study species is the smallest lizard radio-tracked to date, a secondary objective was to assess the efficacy of transmitter attachment and radio-telemetry for species of this size.

Material and methods

Study sites and species

We studied the southwestern fence lizard *Sceloporus cowlesi* (formerly *S. undulatus*, Wiens et al. 2010), at four sites in White Sands National Monument, Otero County, New Mexico (Fig. 1). The two ecotone sites were in the leading edge of the dune field, where the dune habitat encroaches on the surrounding dark soil habitat; lizards in the ecotone were sampled on white sand substrate immediately adjacent (10–500 m) to the dark soil habitat. The two central dunes sites were in interdune areas ca 5 km into the center of the White Sands formation. Visual encounter surveys have

demonstrated no difference in abundance of *S. cowlesi* between the ecotone and the central dunes (Des Roches unpubl.).

Avian surveys

To identify potential avian predators in the ecotone and central dunes, we conducted point count surveys during May and June 2009 (as in Des Roches et al. 2011). We conducted point counts (Ralph et al. 1993) every 200 m, for 3 min at each point, along a 2000-m road transect in each habitat. Only birds identified within approximately 100 m of the observation point, and only species that were likely predators of lizards, were included in analyses. To test for differences in avian predators between the ecotone and central dunes habitats, we calculated the total abundance of bird species along each transect and compared the average over three surveys. We also calculated total species richness and total species diversity for each habitat type. We tested for differences in avian species abundance, richness, and diversity between the ecotone and central dunes sites using Student's t-tests.

Microhabitat scale: perch characteristics and type

For sit-and-wait foragers such as *S. cowlesi*, perch use is directly tied to many aspects of the ecological niche, such as acquisition of prey, shelter and mates (Schoener 1974). We compared perch use and selectivity by *S. cowlesi* in ecotone and central dunes sites to determine whether ecological release was detectable between habitat types. We performed habitat quantification in May and June 2009, during lizard activity periods (08:00 to 13:00, and 16:00 to 19:00). We measured perch use for 19 lizards at the ecotone site and 55 lizards at the central dunes site. We recorded the following microhabitat characteristics for the exact location at which we first sighted each individual: perch type (on exposed ground, in or under a tree or shrub, on a yucca plant, or on non-yucca herbaceous vegetation); perch height and diameter; distance to nearest vegetation; and canopy, shrub, herbaceous and litter cover (visually estimated percentage to the nearest 5%). To generate comparable data points that represented perch availability, we also measured these same characteristics for a random point not associated with a lizard. To select a random point associated with each lizard capture location, we used a random number generator in R (<www.r-project.org>) to select a distance between 1 and 20 m and a direction between 0 and 360 degrees.

Landscape scale: home range and distance traveled

We captured adult male *S. cowlesi* by hand or slipknot noose at the ecotone (n = 12) and central dunes (n = 10) sites in May and June of 2013 and 2014. We weighed and measured each individual (snout–vent length and tail length). We then used a few drops of fast-drying superglue to attach a radio-transmitter directly to each lizard's dorsal surface. We positioned transmitters along the midline directly over the anterior limb girdle, with the 7.5 cm antenna pointing posteriorly along the center of the tail. We gently held the transmitter in place for two minutes while the glue

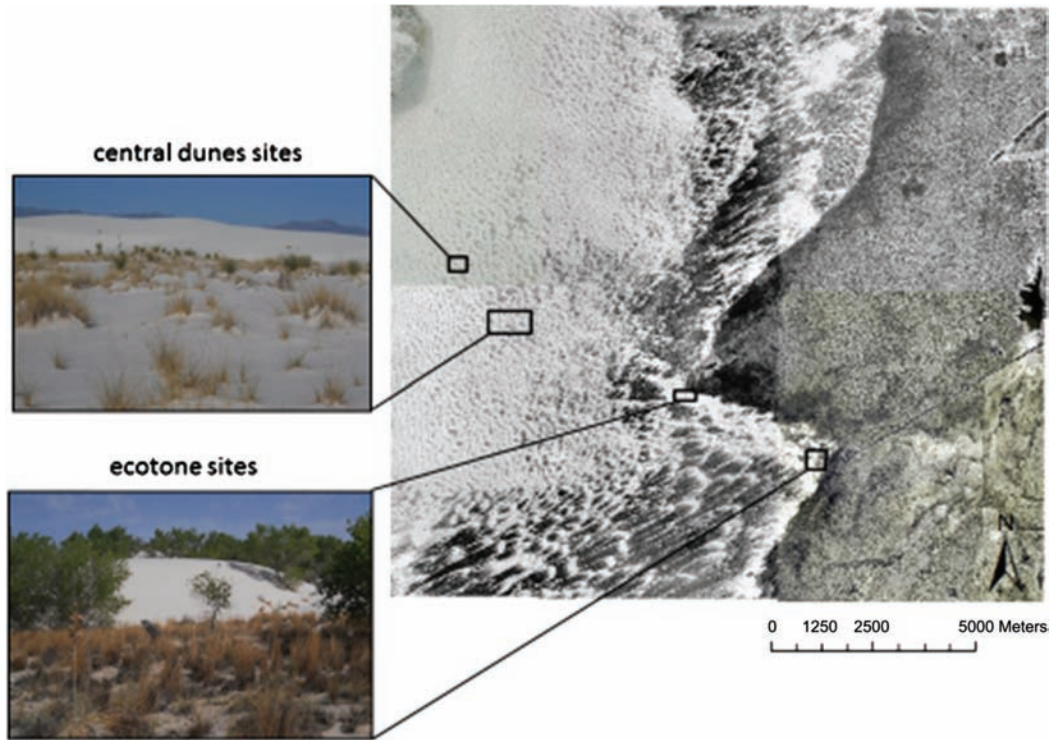


Figure 1. White Sands National Monument, Otero Co., New Mexico, showing study sites in the ecotone and central dunes formation (photos by J. Refsnider). The dark soil habitat surrounding the White Sands formation is visible on the right side of the aerial photograph.

hardened. We then placed the lizard in a plastic terrarium in the shade for a further five minutes to ensure the superglue was completely dry before releasing the lizard at the site of capture. Transmitters weighed 0.35 g, which was 4.3–5.8% of lizard body mass. Prior to attachment, we painted transmitters using acrylic paint to match lizards' dorsal coloration.

Due to the small size of the transmitters, battery life was necessarily limited. To maximize the number of locations attainable during the 2–3 week life of the transmitters, we located lizards twice daily using ground-based radio-telemetry. We were always able to track lizards to the plant in which they were sheltering, even when the lizard was not visible (e.g. buried in sand or motionless in a dense leaf mass), by slowly circling completely around the plant and ensuring the radio signal was strongest from within the plant. At each radio-location, we recorded the geographic coordinates of the lizard using a handheld GPS unit and averaged 100 points for an accuracy of < 5 m. We also recorded whether or not the lizard was visible to estimate detectability.

Statistical analyses

We conducted statistical analysis using SAS 9.3 (SAS Inst.) and R (< www.r-project.org >). For the microhabitat scale analyses, we first compared characteristics of used perches between the ecotone and central dunes sites using Welch's t-tests. To test the hypothesis that ecological release in the central dunes would lead to broadened resource use in that habitat, we compared the variance in characteristics of used perches between sites using Levene's tests. For both study sites, we calculated selection indices for each of the four perch

types (Manly et al. 1993). We then used separate log-linear models to determine whether lizards were using perch types randomly (i.e. in accordance with their availability) or selecting them non-randomly at each study site. We also used a log-linear model to determine whether lizards selected perch types differently in ecotone versus central dunes habitat.

Finally, to compare breadth of perch use between the ecotone and central dunes habitats while controlling for differences in perch availability, we compared a simulation of ecotone lizard perch use in central dunes habitat to actual perch use in the central dunes (following Des Roches et al. 2011). The purpose of this analysis was to predict how ecotone lizards (based on their empirically-assessed perch use) would select perches in central dunes habitat (based on the availability of perch types in the central dunes) in order to directly compare diversity of perch use in the two habitats while controlling for differences in perch type availability. Using the selection indices calculated for ecotone lizards and the availability of each perch type in central dunes habitat, we calculated the expected perch use of ecotone lizards in central dunes habitat using the Heisey formula (Heisey 1985). We then simulated ecotone lizard perch use in central dunes habitat 1000 times by drawing 55-lizard samples, with each perch type having the expected probability of use based on the Heisey formula calculation. We calculated the Shannon diversity index (Shannon 1948) for each of the 1000 samples to generate a null distribution. Finally, we compared the Shannon diversity index of actual perch use by central dunes lizards to this simulated null distribution to calculate a p-value. Importantly, this method assumes that the selection indices of perch use for ecotone lizards would not change in central dunes habitat.

For the landscape scale analyses, we plotted radio-locations on 2009 digital orthophotographs in ArcMap 10.1. For each individual, we estimated home range size by creating a minimum convex polygon (Mohr 1947) using minimum bounding geometry (hull type). We also measured the minimum straight-line distances traveled by each individual over each 24-h period to estimate daily distance traveled. We estimated detectability of each lizard by calculating the proportion of radio-locations during which the individual was visible to researchers. We tested for differences in home range size and detectability between ecotone and central dunes lizards using Welch's t-tests. We used one-way analyses of variance in the MIXED procedure (SAS Inst.), with individual identity as a random effect, to test for between-population differences in daily distance traveled. Finally, to test the hypothesis that ecological release in the central dunes would lead to broadened resource use in that habitat, we compared the variance in home range size and daily distance traveled between the two habitats using Levene's tests. We also estimated individual niche breadths by calculating each lizard's Shannon diversity index for perch use from the repeated observations of each individual obtained during radio-telemetry. We then compared mean individual niche breadths between the two habitats using Welch's t-tests.

Results

Avian surveys

We found greater abundance (10.7 DF, $t = 5.8$, $p < 0.001$), richness (11.4 DF, $t = 6.7$, $p < 0.0001$), and diversity (10.0 DF, $t = 4.7$, $p < 0.001$) of avian predators in the ecotone compared to the central dunes.

Microhabitat scale

Most characteristics of perches used by lizards were similar in the ecotone and central dunes (Table 1). However, perches used in the ecotone had more shrub (Welch's $t = 18.2$, $p = 0.0001$) and litter (Welch's $t = 10.5$, $p = 0.004$) cover than perches used in the central dunes.

Lizards selected perches non-randomly in both the ecotone and the central dunes habitats (ecotone: 3 DF, $\chi^2 = 9.3$, $p = 0.03$; central dunes: 3 DF, $\chi^2 = 11.97$, $p < 0.01$), and perch selection also differed between the two habitats (1 DF, $\chi^2 = 5.79$, $p = 0.016$). That is, lizard selectivity for perch types differed significantly from availability of perch types. Lizards in both the ecotone and the central dunes sites selected yuccas more than would be expected based on their availability (indeed, while yuccas occurred in the ecotone sites, none were sampled at the random non-lizard sites during habitat quantification), and they selected herbaceous vegetation and exposed ground less than expected based on availability. However, based on availability, lizards in the ecotone selected perches in shrubs/trees less than expected, whereas central dunes lizards selected perches in shrubs/trees more than expected. Notably, 5.8 times more shrub/tree habitat was available in the ecotone than in the central dunes, but ecotone lizards used shrub/tree habitat only half as frequently as did central dunes lizards (Fig. 2). Finally, our simulation of ecotone lizard perch-use in central dunes habitat, which controlled for differences in availability of perch types between the two habitats, showed that central dunes lizards had more diverse perch use than ecotone lizards (randomization test, Shannon diversity $H = 1.30$; $p = 0.001$; Fig. 2). That is, based on perch selection of each population in its home habitat, central dunes lizards demonstrated greater diversity of perch use than ecotone lizards are predicted to use if placed in central dunes habitat.

Landscape scale

We radio-tracked 10 male *S. cowlesi* in central dunes habitat (four in 2013 and six in 2014) and 12 in the ecotone (eight in 2013 and four in 2014), and obtained 8–20 radio-locations per individual (mean 16) from which home ranges were constructed (Fig. 3). Lizards in the two habitats did not differ in either mean home range size (Welch's $F_{1,10.4} = 1.31$, $p = 0.28$) or mean daily distance traveled ($F_{1,146} = 0.19$, $p = 0.66$). However, variance in both home range size (Levene's test, $F_{1,20} = 6.48$, $p = 0.02$) and daily distance traveled (Levene's test, $F_{1,166} = 6.58$, $p = 0.01$) was greater in central dunes habitat than in ecotone habitat (Fig. 4). Despite

Table 1. Characteristics of perches used by *Sceloporus cowlesi* in sites in the center (central dunes) and edge (ecotone) of the White Sands dune formation (means \pm standard deviation), and comparison of means and variances between populations. Asterisks denote characteristics that differ significantly between the ecotone and white sands populations.

	Ecotone (n = 19)	Central dunes (n = 55)	Comparison of means	Comparison of variances (Levene's test)
Perch height (cm)	40.5 \pm 55.9	39.8 \pm 54.5	Welch's $t = 0.0$ $p = 0.96$	$F_{1,72} = 0.0$ $p = 0.97$
Perch diameter (cm)	14.2 \pm 10.1	18.2 \pm 19.6	Welch's $t = 0.7$ $p = 0.40$	$F_{1,41} = 0.6$ $p = 0.45$
Dist to cover (cm)	13.4 \pm 18.6	39.5 \pm 100.7	Welch's $t = 3.4$ $p = 0.07$	$F_{1,72} = 1.3$ $p = 0.26$
Shrub cover (%)*	27.1 \pm 12.8	12.1 \pm 14.9	Welch's $t = 18.2$ $p < 0.001$	$F_{1,72} = 0.5$ $p = 0.48$
Herb. cover (%)	10.0 \pm 10.7	8.2 \pm 9.2	Welch's $t = 0.4$ $p = 0.51$	$F_{1,72} = 0.4$ $p = 0.52$
Litter cover (%)*	12.6 \pm 8.4	5.9 \pm 5.7	Welch's $t = 10.5$ $p = 0.004$	$F_{1,72} = 5.0$ $p = 0.03$
Canopy cover (%)	16.6 \pm 23.2	18.7 \pm 20.1	Welch's $t = 0.1$ $p = 0.72$	$F_{1,71} = 0.5$ $p = 0.49$

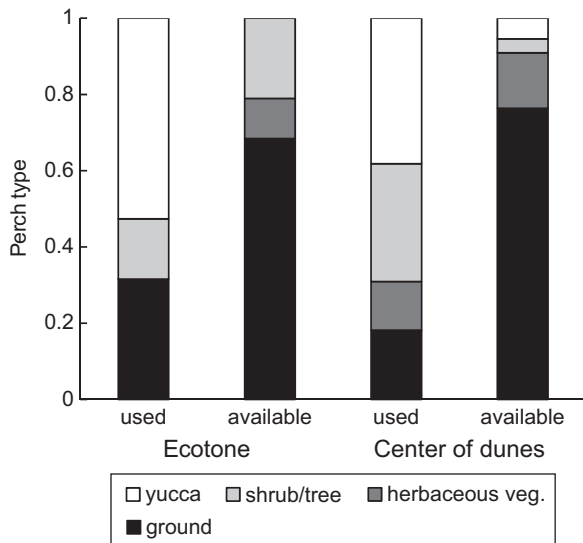


Figure 2. Proportional use and availability of *Sceloporus cowlesi* perch types in ecotone and central dunes sites measured at White Sands National Monument.

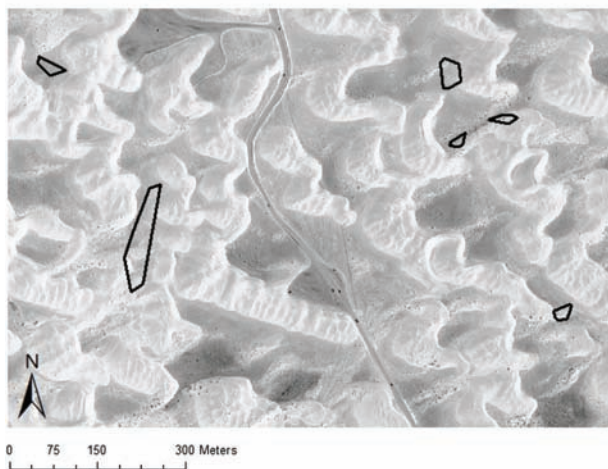


Figure 3. Home ranges (measured as minimum convex polygons) of male *Sceloporus cowlesi* in ecotone (A) and central dunes (B) habitat at White Sands National Monument.

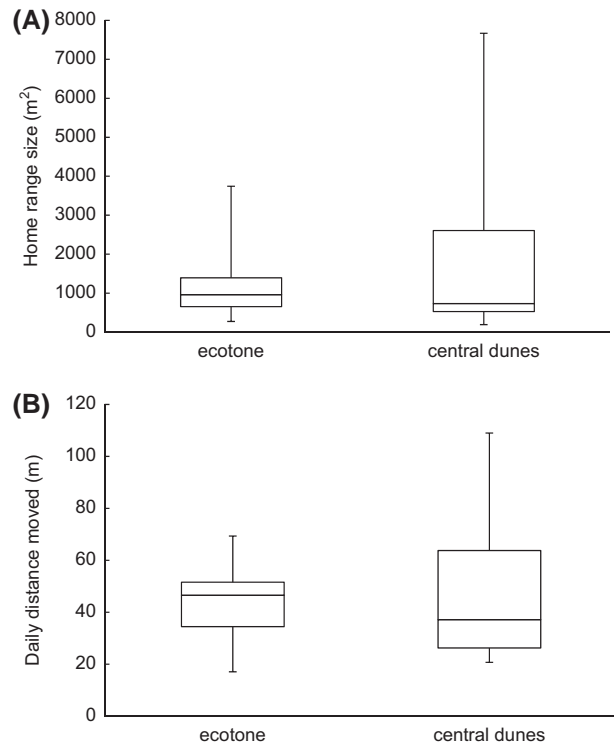


Figure 4. Variation in male *Sceloporus cowlesi* home range size (A) and daily distance traveled (B) was greater in the central dunes than the ecotone.

differences in vegetation structure between the ecotone and central dunes, as described above, detectability of lizards was similar in both habitats (Welch's $F_{1,15,7} = 1.79$, $p = 0.20$). Lizards in the two habitats did not differ in their individual niche breadths in terms of perch use (Welch's $F_{1,20} = 2.29$, $p = 0.14$). Lizard body size was not correlated with home range size ($R^2 = 0.003$, $p = 0.82$).

All radio-marked lizards were alive at the end of the telemetry period in 2013. However, in 2014, we observed two instances of possible predation on ecotone lizards. One individual was tracked to a yucca where it was found impaled on a sharp twig, indicative of predation by a logger-head shrike *Lanius ludovicianus* (Fig. 5). A second individual was observed on the sixth day of tracking, but when we subsequently located the individual's signal in a dense bush, a coachwhip *Masticophis flagellum*, a known lizard predator (Hamilton and Pollack 1956), was observed in the bush. The snake fled from researchers, and the signal was subsequently recovered in a bush 44 m away, after which it never moved again. These two events may suggest a tendency towards higher predation pressure in the ecotone than in the central dunes (χ^2 -test of independence, $\chi^2 = 3.75$, $p = 0.053$).

Discussion

Ecological release has been demonstrated in a variety of taxa following relaxation of selection pressures (Bolnick et al. 2007, 2010, Emery and Ackerly 2014), and is well-studied in the context of colonization events (Losos and DeQueiroz 1997, Des Roches et al. 2011, Des Roches et al. unpubl.).



Figure 5. *Sceloporus cowlesi* killed by a loggerhead shrike (*Lanius ludivicianus*) in ecotone habitat in 2014 at White Sands National Monument. Two predation events were observed on the ecotone while none were observed in central dunes habitat. The intact radio-transmitter is visible on the lizard's back. Photo by S. Des Roches.

In particular, the colonization of oceanic islands often results in ecological release when island populations are compared to ancestral mainland populations (MacArthur et al. 1972, Lister 1976, Cox and Ricklefs 1977, Harmon et al. 2008, Parent and Crespi 2009). Our results demonstrate that ecological release can also be detectable over finer spatial scales, in this case between the center of the White Sands dune formation and the surrounding ecotone.

Our results suggest that predation pressure may be lower in the central dunes compared to the ecotone, establishing the conditions for ecological release (MacArthur and Wilson 1967, Lister 1976, Yoder et al. 2010). Our data demonstrate that the central dunes support a lower diversity of avian predators than the ecotone. Moreover, during the two years of this study, we observed no predation events in the central dunes but two likely predation events in the ecotone. While our observations of predation events are anecdotal, they suggest that selection pressure imposed by predators is higher on the ecotone than the central dunes.

We found evidence of increased niche breadth in central dune lizards relative to ecotone lizards, consistent with a hypothesis of ecological release over a fine spatial scale. Specifically, central dunes lizards used a wider variety of perches than ecotone lizards, even after taking into account differences in perch availability between the two habitats. Perch use in lizards is an important component of the ecological niche and is closely tied to diet, mating behavior, and predator avoidance (Schoener 1974). Although increased dietary niche breadth following ecological release has been

observed across a range of taxa (e.g. including gastropods, teleost fishes, frogs and lizards; Bolnick et al. 2007), increased niche breadth in the form of habitat use is not always observed for lizards in recently-colonized habitats (Losos and DeQueiroz 1997). Therefore, it is particularly noteworthy that we detected a signature of ecological release over such a small spatial scale. An increase in population niche breadth can be due either to all individuals in the population becoming increasingly generalist, or to increased among-individual niche variation (Bolnick et al. 2010). That is, a population that has undergone ecological release may consist of either a group of generalists, all with wide niches, or a range of specialists, each with a narrow niche. Our data suggest that individual niche breadths, in terms of perch use, were not wider in the central dunes than the ecotone. Future research should therefore focus on whether the central dunes population is made up of a range of specialists.

Parallel to the pattern observed at the microhabitat scale, we found that central dunes lizards exhibited greater variation in home range size and daily distance travelled at the landscape scale than ecotone lizards. The increased variation in home range size could be related to a number of different factors. For example, in many *Sceloporus* species, males mate with the females whose home ranges are encompassed by their own, larger home ranges (Ferner 1974), and because the ability of a male to court multiple females increases as the male grows older and larger, the largest males control the largest home ranges (Haenel et al. 2003). In our study, which was conducted during the breeding season, we found no evidence that larger males had larger home range sizes or traveled greater distances. Central dunes lizards may instead be able to travel farther to take advantage of rare or scattered resources because they face decreased predation risk compared to ecotone lizards.

A secondary objective of our study was to assess the efficacy of transmitter attachment and radio-telemetry for the study species. Transmitters and other dataloggers can have negative effects on animal locomotory performance (Lutterschmidt 1994) and survival (Steenhof et al. 2006), particularly due to entanglement in vegetation (Dougill et al. 2000) and the burden of carrying extra weight (Knapp and Abarca 2009). Negative transmitter effects could be especially serious in small lizard species that rely on speed and climbing ability to escape predators. Previous studies on larger lizard species have attached transmitters using a harness design (Warner et al. 2006); however, to minimize weight and the possibility of harnesses causing lizards to become entangled in vegetation, we attached transmitters directly to lizards' skin. While this method meant that lizards continued to carry transmitters past battery failure, the transmitters detached the next time the skin was shed (approximately every three weeks in this species; Jones and Ferguson 1980).

A study of transmitter effects on locomotor performance in iguanas recommended that transmitters weigh no more than 7.5% of lizard body mass to avoid negative effects on climbing, sprint speed, or survival (Knapp and Abarca 2009). The lizards in our study, with body masses of 6.0–8.2 g, are the smallest lizard species radio-tracked to date. The transmitters we used weighed 4.3–5.8% of lizard body mass, and while the duration of our telemetry study was

short, we observed no negative effects (i.e. skin lesions or entanglements in vegetation) of transmitters on lizards. Moreover, we observed three transmitted lizards courting females and two others displaying to unidentified conspecifics, suggesting that the transmitters did not preclude normal social interactions. Our study demonstrates that the transmitters and attachment methods used here were effective and had no observed negative impacts; therefore, our methods should be useful for radio-tracking other small, terrestrial or arboreal lizard species.

We observed fewer predatory bird species in the central dunes than on the ecotone, and there was a tendency towards lower predation pressure in the central dunes than on the ecotone. In addition, we measured broadened resource use at both the microhabitat and landscape scale in *Sceloporus cowlesi* from the center of the White Sands dune formation compared to the ecotone. Our results are consistent with the hypothesis that ecological release has occurred in central dunes habitat, likely because fewer predators are present in the central dunes. Our study demonstrates that ecological release can be detected over a fine habitat gradient, such as between the center of a recently-colonized habitat and its edge.

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