

RAPID ADAPTATION IN A NOVEL ECOSYSTEM:
EVOLUTIONARY ECOLOGY OF WHITE SANDS LIZARDS

A Dissertation

Presented in Partial Fulfillment of the Requirements for the
Degree of Doctorate of Philosophy

with a

Major in Biology

in the

College of Graduate Studies

University of Idaho

by

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May 2014

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Abstract

The species of lizards that inhabit White Sands, New Mexico provide an ideal system in which to study evolutionary and ecological interactions. Characterized by 250 square miles of gypsum sand dunes, White Sands formed in the last two to seven thousand years. Three lizard species, the Lesser Earless Lizard (*Holbrookia maculata*), the Southwestern Fence Lizard (*Sceloporus cowlesi*), and the Little Striped Whiptail (*Aspidoscelis inornata*) colonized White Sands since its formation and today exhibit blanched colouration, unlike their closely related dark-coloured counterparts inhabiting the surrounding Chihuahuan Desert. As both a geologically young and novel ecosystem, White Sands provides a setting for studying ecological and evolutionary changes in its colonist species.

In my dissertation, I examined the ecological implications of morphological differences between White Sands and dark soils lizards and investigated the current dynamics of ecological population dynamics and natural selection on White Sands lizard populations. In Chapter I, I introduced the geological history of White Sands and the biological history of its lizard inhabitants. In Chapter II, I examined whether White Sand lizards show evidence of ecological release. Specifically, I found that there are fewer potential competitor and predator species in White Sands and the three resident species exhibit density compensation. Furthermore, one of the White Sands species, *S. cowlesi*, demonstrates expansion of resource use by using a greater variety of perch types than in dark soils habitats. In chapters III and IV, I explored whether ecologically relevant morphology, performance, and resource use showed evidence of ecological release and directional selection. In particular, I found that two species White Sands lizards have longer legs than their dark soils counterparts, but this does not influence their sprint speed as much as their behavioural response to a simulated predator. In addition, all three species consume a greater number of prey species in White Sands than in

dark soils; however, only *A. inornata* eats significantly harder prey, and only *H. maculata* has expanded the variability of its diet in White Sands. Finally, in Chapter V, I investigated the changes in population demographics and selection on ecologically important traits in two species, *S. cowlesi* and *H. maculata* on the White Sands ecotone over two to three years. I found extreme differences in the ratio of juveniles to adults, growth, dispersal distances, and potential selection on traits between the two species over time.

Acknowledgements

A PhD is at once an intellectually, logistically, and emotionally challenging endeavour. Mine in particular could not have been possible without the personal support I received in all of these aspects. I first and foremost thank my mother, Katie O'Brien, who may not be a scientist, but loves me as one. I thank my father, Edward Des Roches, who may actually read my dissertation from cover to cover... and then have remarkably insightful questions afterwards. I thank my sister Danelle Des Roches, who has become such a good friend to me in the past few years, and Carly Richardson and Kristen Wigton for reminding me where home is. I especially thank my field assistants, many of whom are authors on these chapters and the corresponding papers (in alphabetical order): Michaela Brinkmeyer, Knut Hovertson, Jacqueline Howells, Isaiah Hoyer, Travis Morgan, Karen Pohl, and Jack Torresdal. You have quite literally taught me more than anyone else in these past few years. I would like to thank my friends and graduate student colleagues at the University of Idaho, in particular, Manasi Kanuga, Jeremy Yoder, Denim Jochimsen, Kayla Hardwick, Travis Hagey, and Katie Shine; and at the University of California, Berkeley, including Karina Klonoski, Maddie Girard, Alex Krohn, and Tom Poorten. Thank you to the postdocs, Jeanne Robertson, Jamie Voyles, Christine Parent, Jeanine Resfinder, and Eveline Diepeveen, who have been so supportive and such great female role models, I would also like to thank Leithen M'Gonigle, for help with the Bayesian models that unfortunately did not make it into this dissertation, but will in future publications. Thank you to all the other members of the Rosenblum and Harmon labs for general support and specific feedback. Thank you to Joan Stimpson for being a friend in Alamogordo, and making living there so much easier. Thank you to the White Sands National Monument, White Sands Missile Range, Jornada Long-term Ecological Research Station and

New Mexico Department of Game and Fish for providing field permits. In particular thank you to Doug Burkett, Patricia Culter, and Ed Garcia for organizational field help and to Doug Bustos and all the wonderful park rangers at the White Sands National Monument. Thank you to Holly Wichman for being such a grounded female role model. Thank you to Kristi Accola for keeping me on track, but more importantly for her love, patience, and photocopies. Finally, thank you to my advisors, Luke Harmon and Erica Rosenblum who have supported me in every single aspect of my journey.

To everyone above and so many more, thank you for showing me that friendship is nested within every important relationship.

Funding for my work was provided in part through a National Science Foundation CAREER grant to EBR (DEB-1054062) and the University of Idaho Department of Biological Sciences. Funding to me specifically was provided via Natural Science and Engineering Research Council of Canada PGS-M and PGS-D fellowships, an American Society of Ichthyologists and Herpetologists Gaige grant, an American Museum of Natural History grant, and several University of Idaho Travel and Student Grant Program grants. All live animal work was conducted with relevant Animal Care and Use Committee permits (University of Idaho, Protocol #2010-48).

Dedication

I dedicate my dissertation

to my field assistants, and in loving memory of Karen Pohl,
to my mom and dad, who let this biologist grow,
and to the little dragons, who put up with everything.

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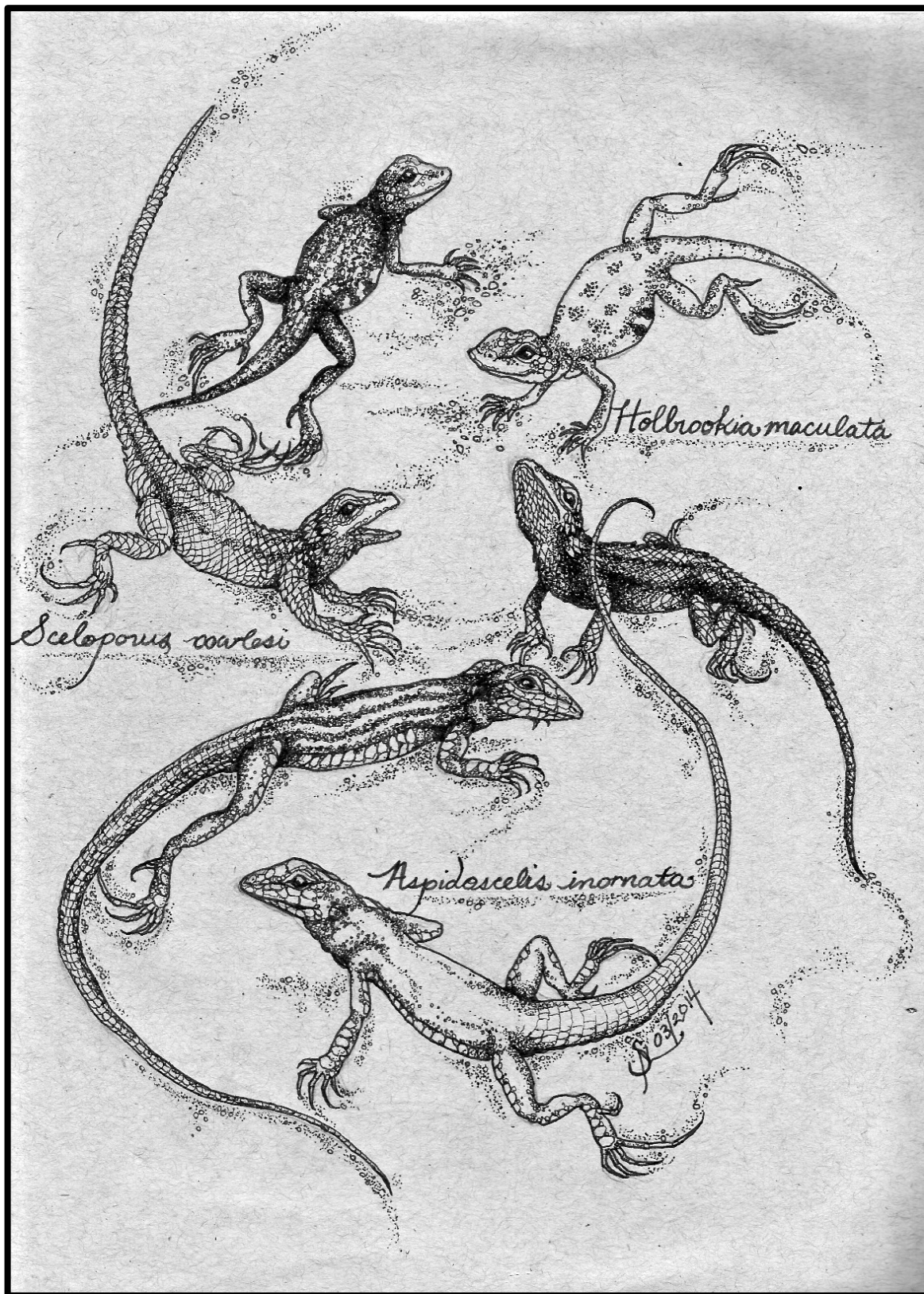


Illustration I: The three species of White Sands lizards and their dark soils counterparts: the lesser earless lizard (*Holbrookia maculata*), southwestern fence lizard (*Sceloporus cowlesi*), and the little striped whiptail (*Aspidoscelis inornata*)

CHAPTER I

INTRODUCTION TO THE STUDY SYSTEM: A 250 MILLION YEAR NATURAL HISTORY OF WHITE SANDS AND ITS LIZARD INHABITANTS

Dedicated to my father, who has an appreciation for geology and the great timing of things.

The picture afforded in this expanse of white sand is unlike anything known. The white environment has produced a notable effect upon the limited animal life of the sands, and zoologists look to this natural laboratory for possible answers to questions bearing upon adaptation [...]. Yet it is not the scientific interest alone which justifies the reservation of this unique bit of the American scene. The loveliness of its white and green, the cleanliness of its vast expanse, and its appeal to the lover of the unexplored and desolate mark it as an area to which will go those discerning travelers who would see Nature's masterpieces.

Carl P. Russell
 Chief, Eastern Museum Division,
 National Park Service,
 National Geographic Magazine August 1935

When I first arrived at White Sands five and a half years ago, I was struck by the distinctiveness of the place. Like a great inland gypsum lake, the White Sands ecosystem contrasts sharply with the surrounding Chihuahuan desert scrubland. The transition, or ecotone, between the dark soils of the Chihuahuan flatlands and the towering white dunes is so abrupt in sections along the border that one might jump from one ecosystem to the other. At other places, the transition is more like a gradual intertidal zone – with waves of sand slowing to a crawl, ever heading southeast with the prevailing wind. And all across the shallow ripples of white to the west, to the highest 13 metre (42 foot) dunes to the east, three species of lizards bask, run, forage and survive: the Eastern Fence Lizard (Iguanidae: *Sceloporus cowlesi*), the Lesser Earless Lizard (Iguanidae: *Holbrookia maculata*), and the Little Striped Whiptail (Teiidae: *Aspidoscelis inornata*). These three species are the only

lizard species that inhabit White Sands, despite upwards of thirty others with populations in the surrounding desert.

White Sands as a place of geological and biological convergence

The natural history of White Sands began at the close of the Permian, 250 million years ago, when the seven continents were clustered together as the supercontinent Pangaea, and the first reptiles evolved (Erwin 1990). At that time, a vast and shallow tropical sea covered what is now the American Southwest. Previous drying of this Permian sea caused the massive deposition of gypsum rock, which would eventually be the source of the mineral that makes up White Sands today (Kocurek *et al.* 2007, Szyrkiewicz *et al.* 2010). The end of the Permian was also characterized by the extinction of nearly all life on earth (see Benton and Twitchett 2003). Two groups of animals replaced the previously dominant terrestrial vertebrate fauna of diverse amphibians and proto-mammals. One was a new group of “synapsids,” characterized by one paired hole in the skull and ancestral to modern mammals. The other was the “diapsids,” characterized by two paired holes in the skull and ancestral to modern birds, snakes, and lizards (Erwin 1990).

The next 250 million years saw the break-up of Pangaea, the formation of the North American Rocky Mountains and the divergence of the major clades of lizards. During the Triassic through Cretaceous, the very same tectonic subduction that forced the Rocky Mountains to rise also caused the uplift of the marine gypsum rocks in southern New Mexico to form the Sacramento and San Andreas Mountains (Szyrkiewicz *et al.* 2010). About 170 million years ago the Iguanids (including the *Sceloporus* and *Holbrookia* genera) diverged from other lizard clades including the Teiids (including the *Aspidoscelis* genus; Vidal and

Hedges 2005, Castoe *et al.* 2010, Kumar *et al.* 2011). These two lineages continued to evolve, ultimately giving rise to many of the modern lizard families. By the end of the Cretaceous, 65 million years ago, both Iguanids (Augé 2007) and Teiids (Krause 2008) had reached widespread distributions across North America. Today, these clades can be distinguished by major differences in feeding ecomorphology and foraging mode. Teiids, which rely on chemoreception using their forked tongue, will actively pursue prey and forage on the move (Cooper 1995). Iguanids, on the other hand, rely on tongue prehension and visual cues for foraging (Vidal and Hedges 2009).

During the Tertiary, 65 – 1.8 million years ago, the seven continents reached their current configuration, great basins formed across North America, and the Iguanids and Teiids diversified in the arid regions of the south. Thirty million years ago, the San Andreas Fault formed, and upwellings of magma tore apart the earth's crust across western North America (Atwater 1970). By this time, the ten genera of the Teiidae family had diverged, all of which likely had South American origin except *Aspidoscelis*, which had origins in North America (Giugliano *et al.* 2007). The Iguanid family Phrynosomatidae, which now represents the most species-rich lizard family in North America, likely originated in arid regions of this continent (Wiens *et al.* 2013). The Phrynosomatidae clade diverged into two major subfamilies, the Phrynosomatinae (including the *Holbrookia* genus) and the Sceloporinae (including the *Sceloporus* genus), around 55 million years ago (Wiens *et al.* 2013). By ten million years ago, the Rio Grande Rift formed large basins including what is now the 16,800 square-kilometer (6,500 square mile) Tularosa Basin. Finally, the modern genera of *Holbrookia* and *Sceloporus* first appear ten million years ago (Wiens *et al.* 2013) and *Aspidoscelis* appear 20 million years ago (Giugliano *et al.* 2007).

During the last ice age (24,000 to 12,000 years ago), the Tularosa Basin received substantial rainfall and therefore was inaccessible to any lizard population. Rainwater runoff from exposed gypsum in the Sacramento and San Andreas Mountains flushed the mineral into what was then a massive inland lake called Lake Otero (Lucas and Hawley 2002). When the ice age ended, the southwest desert eventually returned to its arid state and the slow evaporation of the lake left behind vast gypsum deposits in the Tularosa Basin. The drying of Lake Otero around 12,000 years ago represents the earliest point local lizard populations could have recolonized the basin.

Although geological evidence can provide a timeframe for white sand dune formation in the Tularosa Basin, it is impossible to know for sure when the three species of lizards colonized, and whether they did so repeatedly. The white sand dunes began to develop no earlier than 7,000 years ago, with gypsum deposition occurring as recently as in the last 2,000 (Langford 2003, Kocurek *et al.* 2007). The possibility of ongoing migration confounds estimation of the timing and frequency of colonization by the three White Sands lizard species. Evidence from mitochondrial DNA shows that *Sceloporus cowlesi* probably experienced a bottleneck upon colonization, yet retained relatively high levels of genetic diversity (Rosenblum *et al.* 2007). Furthermore, the genetic structure of the modern White Sands *S. cowlesi* indicate that they are still experiencing movement of genes from populations inhabiting the surrounding dark-soil Chihuahuan Desert (Rosenblum 2006). White Sands *Holbrookia maculata* populations, however, show high genetic structure, indicating very limited dispersal and gene flow from dark-soils populations (Rosenblum 2006). Finally, *Aspidoscelis inornata* populations on White Sands show the lowest levels of genetic structure

suggesting a relatively recent colonization from the surrounding desert followed by a major population expansion or high levels of ongoing migration (Rosenblum 2006).

White Sands as a land-locked island

In their seminal book on island biogeography MacArthur and Wilson (1967) described two major determinants of island biodiversity: island area and distance from the mainland. Island area is important because organisms dispersing from the mainland are more likely to encounter a large island than a small island. Furthermore, larger islands are more likely to have more diverse geography, thus more diverse niche space available for colonizing organisms. Both these factors contribute to a positive relationship between island size and number of species. Distance from the mainland is important for the straightforward reason that dispersal becomes increasingly less probable with increasing distance. If the space between the island and the mainland is inhospitable to organisms, it follows that islands closer to the mainland are more likely to be colonized than those further away. Thus, there is a negative relationship between island distance and number of species. Clearly, other island characteristics are determinants of community composition. Oceanic islands do not sit on continental shelves and are often formed by volcanoes far from the mainland. They may be so ecologically disparate from the closest landmass that even colonists that do make it may not have adaptations that allow them to persist. Alternatively, continental islands form when rising sea levels create a barrier between the mainland and a section of land, and are characteristically closer to the mainland both in distance and ecology.

But what if the island of interest is a 250 square mile unique geological formation nested *within* the surrounding “mainland”? In ecology, the term “island” is extended to any

patch of ecosystem that is geologically and ecologically distinctive or isolated from the surrounding environment (MacArthur and Wilson 1967). Like many continental islands (e.g. Islay, Scottish Isles, 239 square miles), which became separated from the mainland gradually, the distinctiveness of White Sands ecosystem accumulated slowly, and physical distance was never an actual barrier to colonization. On the other hand, like many young oceanic islands (e.g. Fernandina Island, Galapagos, 248 square miles), White Sands is relatively desolate and ecologically very “distant” even from its immediate surroundings.

The relative isolation and uniqueness of islands means that pressures of natural selection on populations can be very different than they are in the surrounding ecosystem. After formation, many islands (especially oceanic) are ecologically desolate, containing few species and open niche space. Unoccupied niches combined with low abundance of antagonist species represent an *ecological opportunity* for colonists that do manage to reach the island (see Lister 1976, Harmon *et al.* 2008, Parent and Crespi 2009, Yoder *et al.* 2010). In other words, there is a reduction in selective pressures from other species competing for resources and from predators reducing survival. The absence of competitors and predators combined with abundant resources often results in colonists experiencing *ecological release*, which may take the form of niche expansion (i.e. using a greater variety of resources, see MacArthur and Wilson 1967, Lister 1976), density compensation (i.e. population growth, see MacArthur *et al.* 1972, Case 1975), and increased trait variability (i.e. more extreme phenotypes survive, see Bolnick *et al.* 2007). Ecological opportunity and ecological release are often cited as the precursor for rapid diversification of colonizing lineages on islands, and even as precursors to adaptive radiations. Examples of adaptive radiations that likely occurred as a result of an ecological opportunity include Caribbean land birds (Cox and Ricklefs 1977), freshwater

threespine stickleback (Schluter 1993), Caribbean anolis lizards (Losos and DeQueiroz 1997), Indian Ocean day geckos (Harmon *et al.* 2008), and Galapagos land snails (Parent and Crespi 2009) Paradoxically, island ecosystems may simultaneously present increased directional selection pressures on some traits, for example, towards increased body size in Galapagos marine iguanas (Wikelski and Trillmich 1997), pelvic reduction in freshwater stickleback (Schluter *et al.* 2010), and dwarfism in island sloths (Anderson and Handley 2002). If the new habitat is drastically different from the ancestral ecosystem, then only those individuals with certain trait values may survive and reproduce.

Like many islands, White Sands presents a selective environment that is distinctive from the surrounding ecosystem. The island-like uniqueness is obvious from afar, where White Sands could be mistaken for a stark-white lake surrounded by brown soil. Up close, the three lizard species have denser populations than outside White Sands, which suggests ecological release and a possible reduction in selection pressures. However, these species also show remarkable convergence towards blanched white colouration, which is considerably different from the dark brown colour of their closest ancestors and may indicate the importance of directional selection for crypsis on the gypsum sand.

The major questions of my dissertation pertain to the topics of ecological release and natural selection. In Chapter II, I examined whether White Sand lizards show evidence of ecological release. Specifically, I found that there are fewer potential competitor and predator species in White Sands and the three resident species exhibit density compensation. Furthermore, one of the White Sands species, *S. cowlesi*, demonstrates expansion of resource use by using a greater variety of perch types than in dark soils habitats. In Chapters III and IV, I explored whether ecologically relevant morphology, performance, and resource use showed

evidence of ecological release and directional selection. In particular, I found that two species White Sands lizards have longer legs than their dark soils counterparts, but I did not find evidence that this influenced their sprint speed as much as their initial behavioural response to a simulated predator. In addition, all three species consume a greater number of different prey species in White Sands than in dark soils; however, only *A. inornata* eats significantly harder prey, and only *H. maculata* expanded the variability of its diet in White Sands compared to dark soils. Finally, in Chapter V, I investigated the changes in population demographics and selection on ecologically important traits in two species, *S. cowlesi* and *H. maculata* on the White Sands ecotone over two to three years. I found extreme differences in the ratio of juveniles to adults, growth, dispersal distances, and potential selection on traits between the two species over time.

The geological history of White Sands goes back as far as the lineage of lizards itself. However, the mysteries of its biological past are as recent as the last few thousand years. White Sands represents a remarkable convergence not only of replicated colonization and adaptation, but also of the earth's physical and biological history. Rarely have geology and ecology intersected in such recent times that we as biologists have the opportunity to study the very beginning stages of colonization and community assembly. Indeed, to say that White Sands is a natural laboratory is an understatement: it is both a laboratory and a time machine that enables those of us lucky enough to glimpse the dynamic beginnings of evolution in a young ecosystem.

Figures

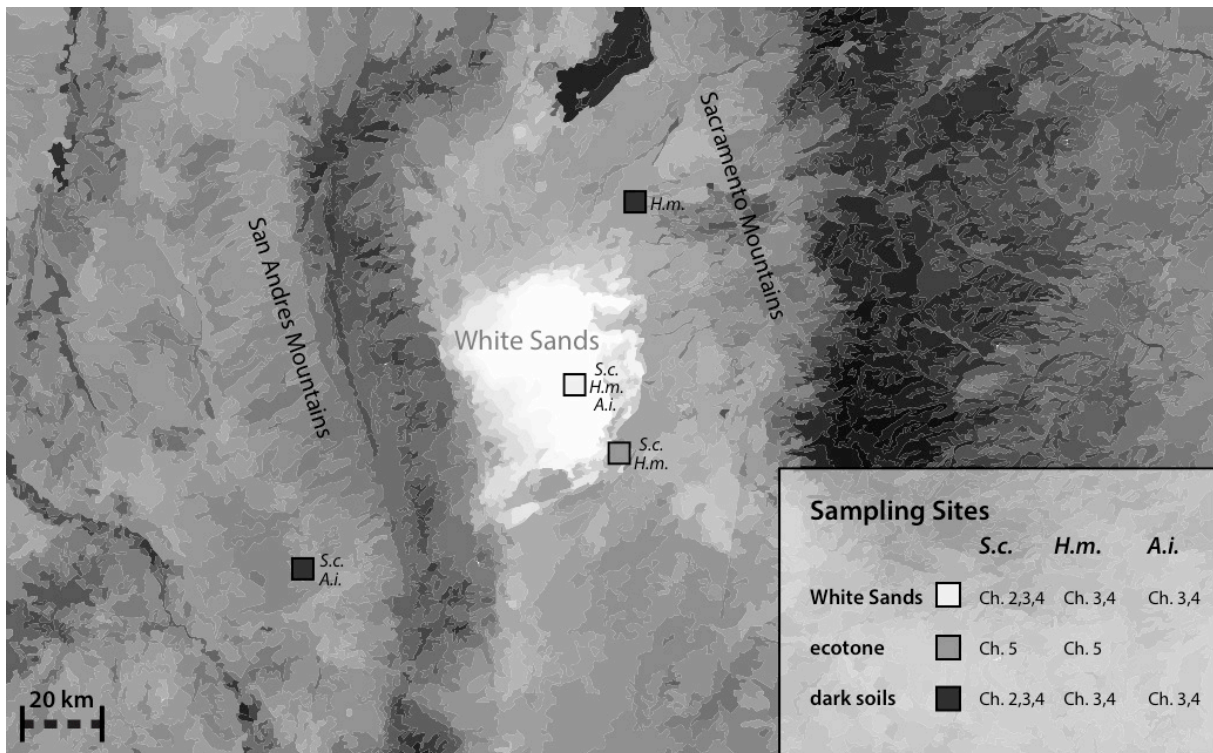


Figure 1.1: Sampling locations for three species: *Sceloporus cowlesi* (*S.c.*), *Holbrookia maculata* (*H.m.*), and *Aspidoscelis inornata* (*A.i.*) in White Sands, ecotone, and dark soils sites.

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Illustration II: Dark soils southwestern fence lizards (*Sceloporus cowlesi*) on a soap tree yucca (*Yucca elata*) at the Jornada Long Term Ecological Research Station.

CHAPTER II

ECOLOGICAL RELEASE IN WHITE SANDS LIZARDS

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Published in 2011, *Ecology and Evolution*, 1: 571-578.

Abstract

Ecological opportunity is any change that allows populations to escape selection from competition and predation. After encountering ecological opportunity, populations experience *ecological release*: enlarged population size, broadened resource use, and/or increased morphological variation. We identified ecological opportunity and tested for ecological release in three lizard colonists species of White Sands, New Mexico (*Sceloporus cowlesi*, *Holbrookia maculata*, and *Aspidoscelis inornata*). First we provide evidence for ecological opportunity by demonstrating reduced species richness and abundance of potential competitors and predators at White Sands relative to nearby dark soils habitats. Second, we characterize ecological release at White Sands by demonstrating density compensation in the three White Sands lizard species and expanded resource use in White Sands *S. cowlesi*. Contrary to predictions from some models of ecological release, we observed directional trait change but not increased trait variation in *S. cowlesi*. Our results suggest that ecological opportunity and ecological release can be identified in natural populations, especially those that have recently colonized isolated ecosystems.

Introduction

Ecological opportunity occurs when selection pressures on a population are relaxed due to a reduction in competition and/or predation (see Simpson 1949, Lister, 1976, Harmon et al., 2008, Parent and Crespi, 2009, Martin and Pfennig, 2010, Yoder et al., 2010). A number of ecological and evolutionary changes, collectively referred to as *ecological release*, can occur rapidly after a population encounters ecological opportunity (MacArthur and Wilson 1967, Cox and Ricklefs 1977, Azuma 1992, Losos and DeQueiroz 1997, Bolnick et al. 2004, Yoder et al. 2010). Colonizing a new environment can be one type of ecological opportunity (Harmon et al. 2008, Parent and Crespi 2009), but ecological release can also follow the extinction of antagonists (Sepkoski 1981, Niklas et al. 1983), or the evolution of a key trait (Ehrlich and Raven 1964, Farrell 1998, Salzburger et al. 2005).

Examples of ecological opportunity and ecological release often appear in the context of adaptive radiation, especially on islands and other isolated systems (Cox and Ricklefs, 1977, Schluter 1993, Losos and DeQueiroz, 1997, Harmon et al. 2008, Parent and Crespi 2009, Losos 2010). However, we can also observe the consequences of ecological opportunity and ecological release in natural systems that do not precede adaptive radiations. For example, we can look for ecological opportunity when the evolution of a key adaptive trait has allowed a subset of species to colonize a new habitat.

Previous researchers have identified three important characteristics of ecological release following ecological opportunity. Colonists may exhibit: 1. *density compensation* (the new habitat can support more individuals in the absence of predation and interspecific competition, MacArthur et al. 1972, Case 1975), 2. *broadened resource use* (antagonists that restrict niche width are absent, MacArthur and Wilson 1967, Lister 1976), and 3. *increased*

trait variation (decreased selection against individuals with extreme morphological characteristics, Bolnick *et al.* 2007).

We identified ecological opportunity and tested for three characteristics of ecological release in recent lizard colonists of White Sands, New Mexico. White Sands provides a replicated natural "experiment" in which to test for rapid ecological and evolutionary changes (Rosenblum 2006, Rosenblum and Harmon 2011). Three lizard species, the Eastern Fence Lizard (*Sceloporus cowlesi*), the Lesser Earless Lizard (*Holbrookia maculata*) and the Little Striped Whiptail (*Aspidoscelis inornata*) colonized the recently formed gypsum sand dunes in the last 2000 to 6000 years (Kocurek *et al.* 2007). The three species have evolved white colouration in parallel, a key trait that allows them to camouflage with the stark white sands (Rosenblum 2006). The evolution from an ancestral dark pigmentation to blanched colouration has a genetic basis in all three species (Rosenblum 2005, Rosenblum *et al.* 2010). Because of its recent formation and novel selective environment, we hypothesize that White Sands represents a case of ecological opportunity and its resident lizards have undergone ecological release.

We looked for evidence of ecological opportunity in White Sands and examined whether lizard colonists experienced the three proposed components of ecological release. To identify ecological opportunity, we surveyed lizard communities in White Sands and ancestral dark soils habitats. We predicted that White Sands would have lower species richness and fewer potential predators and competitors. We then compared the three components of ecological release between White Sands and dark soils lizards. First, we predicted that reduced richness and abundance of predators and competitors would result in increased population sizes of the three White Sands species relative to their dark soil counterparts.

Second, we predicted expanded resource use at White Sands as measured by perch choice (an important component of the ecological niche) focusing on *S. cowlesi*. Third, we predicted greater morphological variation as measured by elements of body shape related to resource use in White Sands *S. cowlesi* compared to conspecifics in dark soils.

Materials and Methods

Identifying ecological opportunity

To identify ecological opportunity, we compared species richness and relative abundance of communities in both White Sands and surrounding dark soils habitats to determine if the number of potential antagonists (predators and competitors) of our focal species differed. We conducted field surveys in the gypsum dunes of White Sands National Monument, Otero County, New Mexico, and in a typical dark soils blue-gramma grass and yucca-mesquite scrubland at Jornada Long-term Ecological Research Station, Doña Ana County, New Mexico (Figure 1.1, “Ch. 2”). We measured species richness and relative abundance of the lizard communities in each habitat by performing visual encounter surveys (Campbell and Christman 1982) from May to June 2009. During each survey, two observers walked in the same direction approximately 20 meters apart for 30 minutes. We conducted the survey procedure three times in a given habitat each day for four days (a total of 12 surveys per habitat). Each observer identified and counted all animals observed within a 6-meter corridor. We totaled the species richness for each observer on each day and used these totals as replicates for statistical analyses. We compared species richness and relative abundance (ln transformed) of all individuals between White Sands and dark soils using Welch’s t-tests.

We also conducted avian surveys to identify potential bird predators along a 2000-meter road transect. We conducted point counts every 200 meters for a total of 3 minutes each, counting only birds identified within approximately 100 meters from the observation point. To test for differences in avian predators between White Sands and dark soils, we totaled the abundance of birds along each transect and compared the average over three surveys. We only counted birds that have been observed directly to prey on lizards or have close relatives that do so. We tested the difference in abundance of these potential bird predators using Welch's t-tests.

Testing for ecological release

We tested the three different components of ecological release in White Sands lizards: density compensation, broadened resource use, and increased morphological trait variation. First, to test for density compensation, we used the results from the surveys described above to compare the abundance (total number of individuals) of each of the three focal lizard species in White Sands and dark soils. We compared abundance between White Sands and dark soils using Welch's t-tests (which do not require the assumption of equal variances).

Second, to test for broadened resource use, we used perch selection as a proxy for resource use of *S. cowlesi*. Perch selectivity is closely related to several components of the ecological niche in lizards including diet, competition, mating behaviour and predation (Schoener 1974). To determine *S. cowlesi* perch selection and to test whether perch use differed between the different habitats, we compared perch availability and perch use in White Sands and dark soils (see Rand 1964, Campbell and Christman 1982, Harmon *et al.*

2007). We quantified habitats from May to June in 2009 and observed lizards during their most active times of day (between 08:00 and 13:00, and 16:00 and 19:00). We measured perch use for 55 lizards in White Sands, and 39 lizards in dark soils. We characterized the surrounding microhabitat of lizards at the exact location we first sighted them and recorded the following parameters: perch height, diameter and distance to nearest vegetation (in meters), and canopy cover (percentage as a visual estimate to the nearest 5%). We also categorized perch surface into one of three broad categories: exposed surfaces (not associated with vegetation), yucca (often preferred by *S. cowlesi*), or other non-yucca shrub/tree (association with mesquite, creosote, sage-brush and other leafy vegetation). For each lizard, we also measured perch characteristics for a random point not associated with a lizard. The random point was found by using a random number generator to select a distance between one and twenty meters and a direction between 0 and 360 degrees. We performed log linear models to test whether lizards select perches proportionally to their availability, non-randomly, or non-randomly and differently across habitats (Heisey 1985, Manly *et al.* 1993). We also compared other aspects of microhabitat (perch diameter, perch height, and canopy cover) using Welch's t-tests.

To further analyze differences in *S. cowlesi* perch use across habitats, we simulated the perches that dark soil lizards might use in White Sands given their calculated selectivity indices (Manly *et al.* 1993). We calculated the expected perch use of a lizard with a given selectivity for a habitat type using the Heisey formula (Heisey 1985):

$$p_i = \frac{\alpha_i A_i}{\sum_{i=1}^n \alpha_i A_i}$$

Where n is the number of perch types, p_i is the expected probability that perch type i is used, α_i is its availability (in White Sands) and A_i is the lizard selectivity for that perch category. We calculated the expected probabilities and then drew random lizard perches (“simulated” dark soil lizards) with the same sample size as our empirical data. We then computed the Shannon diversity index (Shannon 1948) of simulated dark soils lizards 1000 times to generate a null distribution. We compared the simulated null distribution to the Shannon diversity index of actual lizard perch use in White Sands to calculate a P-value.

To test whether morphological traits change in mean or variance in White Sands *S. cowlesi* we measured eight aspects of body shape following Melville *et al.* (2006) (shoulder-elbow, elbow-wrist, longest forelimb toe, hip-knee, knee-ankle, longest hindlimb toe length, snout vent length, head depth, head width, tail length, and pelvic width) for 20 White Sands and 18 dark soils lizards. To determine the most important axes of variation for the set of related morphological characteristics we performed a principal components (PC) analysis on the ln-transformed measurements. We compared mean body shape across habitats using MANOVA followed by post-hoc ANCOVAs on each individual variable controlling for body size. We then used Levene’s test to examine whether the variance differed between White Sands and dark soils lizards for each of the first four principal components. All analyses were conducted in R (R Development Core Team 2011).

Results

Identifying ecological opportunity

White Sands contained fewer potential predators and competitors than the surrounding dark soils habitat and thus met a key criterion for ecological opportunity. There was no difference between the total number of lizards (of all species) between White Sands and dark soils (Figure 2.1, Welch's t-test: $t = 0.4$, $P > 0.05$). Species richness, however, was nearly significantly higher in dark soils (Figure 2.2, Welch's t-test: $t = 2.2$, $P = 0.05$). During our surveys, we observed three lizard species at White Sands (*Aspidoscelis inornata*, *Holbrookia maculata*, and *Sceloporus cowlesi*), compared to six lizard species in dark soils (*Aspidoscelis inornata*, *Aspidoscelis neomexicanus*, *Aspidoscelis tessellatus*, *Sceloporus cowlesi*, *Uta stansburiana* and *Gambelia wislizenii*). Note that although *H. maculata* is present at dark soils (Rosenblum 2006), we did not observe this species during our regular surveys at dark soils. We observed no additional lizard species at White Sands outside regular surveys but we documented an additional four lizard species in dark soils outside regular surveys (*Crotaphytus collaris*, *Phrynosoma cornutum*, *Aspidoscelis tigris* and *Sceloporus magister*).

Total abundance of potential avian predators was higher along our dark soils transect than our White Sands transect (Welch's t-test: $t = 3.2$, $P = 0.03$). During our surveys we observed the Northern mockingbird (*Mimus polyglottos*), the Common raven (*Corvus corax*), the Swainson's hawk (*Buteo swainsoni*) and various flycatchers (Tyrannidae). However, there were several key avian predators of lizards that we did not observe in either habitat during our surveys [e.g., the Loggerhead shrike (*Lanius ludovicianus*, Reid and Fulbright 1981), American kestrel (*Falco sparverius*, Craig and Trost 1979, McLaughlin and Roughgarden 1989) and the Greater roadrunner (*Geococcyx californianus*, Audsley *et al.* 2006)].

Testing for ecological release

Our surveys showed evidence of density compensation in White Sands on the community level. As stated, the combined abundance of all lizards at White Sands was equivalent with that in dark soils even though species richness was significantly lower. Moreover, the combined abundance of the focal species was significantly greater in White Sands compared to dark soils (Figure 2.1, Welch's t-test: $t = -3.3$, $P = 0.002$). The population sizes of each species were not significantly different between habitats when we analyzed each species separately (Welch's t-test: all $P > 0.5$)

Sceloporus cowlesi perch use was non-random and significantly different between White Sands and dark soils. First, lizards selected their perches non-randomly in each habitat, that is, not proportionately to perch availability (Figure 2.3, Log linear model, perch*selectivity: $F_{11,7} = 13.7$, $P \ll 0.001$). Second, lizard selected their perches differently between White Sands and dark soils (Figure 2.3, Log linear model, perch * selectivity * location: $F_{11,4} = 48.1$, $P \ll 0.001$). Therefore, White Sands and dark soils *S. cowlesi* differed in their perch use in a way that is not simply a reflection of perch availability in each of the two habitats.

Our simulation results demonstrated that White Sands lizards had especially diverse perch use. To control for differences in availability between the two habitats we compared a simulation of dark soils *S. cowlesi* perch use in White Sands to actual White Sands lizard perch use. We found that given their selectivities, if dark soil lizards were in White Sands, they would use a more restricted range of perches than White Sands lizards (randomization test, Shannon diversity $H = 1.1$, $P = 0.0001$).

Perches selected by lizards in White Sands versus dark soils differed significantly in diameter, height, canopy cover, and distance from vegetation. White Sands lizards used perches with significantly larger diameter (Welch's t-test: $t = -3.4$, $P = 0.002$), whereas dark soils lizards used perches that were significantly higher (Welch's t-test: $t = 10.5$, $P < 0.0001$) and with more canopy cover (Welch's t-test: $t = -2.9$, $P = 0.005$). Most of the perch characteristics that we measured were more variable for White Sands lizards including perch diameter (Levene test: $F = 8.4$, $P = 0.005$), canopy cover (Levene test: $F = 6.9$, $P = 0.01$) and distance from vegetation (Levene test: $F = 6.0$, $P = 0.02$), but not perch height (Levene test: $F = 0.4$, $P > 0.5$).

Our principal component analysis of morphology showed a difference in mean trait values across habitats but no evidence of increased trait variance in White Sands lizards. We observed a difference in means across populations for morphological traits (MANOVA: Wilks' $\lambda = 0.6$, $P = 0.04$). Specifically several fore- and hind- limb measurements differed between White Sands and dark soils *S. cowlesi* (ANCOVA: habitat effect, all $P < 0.05$, body size effect, all $P < 0.05$, habitat by body size interaction, all $P > 0.05$). All other morphological variables (e.g. head and body dimensions) were related to body size but did not differ across habitats (ANCOVA: habitat effect, all $P > 0.05$). For variance, the first principal component, which corresponded primarily to body size, was actually more variable for dark soils lizards (Levene Test: $F = 17.8$, $P < 0.01$), but this was due to a bimodal distribution of sizes in the dark soils population and likely reflects the presence more sub-adults in this population during the sampling period. PC2 to PC4 were not significantly different in variance between dark soils and White Sands individuals (Levene Test: all $P > 0.1$) demonstrating no evidence of increased trait variance in either habitat.

Discussion

There is potential for ecological opportunity in many recently formed, isolated or novel environments (MacArthur and Wilson 1967, Cox and Ricklefs 1977, Schluter 1993, Losos and DeQueiroz 1997, Harmon *et al.* 2008, Parent and Crespi 2009). As with many cases of ecological opportunity, the invasion of White Sands by three species of desert lizards coincided with the evolution of a key trait (Ehrlich and Raven 1964, Farrell 1998, Salzburger *et al.* 2005): blanched colouration that allowed substrate-matching. The successful colonization of the novel White Sands habitat set the stage for ecological opportunity and release.

One of the hallmarks of ecological opportunity is reduced predation and competition, and indeed we found fewer potential antagonists at White Sands. Our surveys demonstrated that the reptile community of White Sands is species poor (Figure 2.2) including only three lizard species (*S. cowlesi*, *H. maculata* and *A. inornata*). Up to 35 different reptile species inhabit the dark soils habitat (see Degenhardt *et al.* 1996). In our dark soil surveys, we directly observed six species, including species that overlap in prey use with *A. inornata* [e.g. *Aspidoscelis neomexicanus* and *Aspidoscelis tessellatus* (Dixon 1966, Scudday and Dixon 1973)] and *S. cowlesi* and *H. maculata* [e.g. *Uta stansburiana* (Dixon 1966)]. We also observed *Gambelia wislizenii* in our dark soils surveys, which is a known predator of all three focal species (Little and Keller 1937, Gehlbach 1956). Outside regular surveys, we recorded four additional lizard species in dark soils that either share food resources with or predate on the three focal species [i.e., *Phrynosoma cornutum*, (Pianka and Parker 1975), *Crotaphytus collaris* (Little and Keller 1937), *Aspidoscelis tigris* (Pianka 1970), and *Sceloporus magister* (Parker and Pianka 1973)]. We did not observe any snakes during our surveys. In general,

snakes rarely enter the central dunes of White Sands (McKeever *personal communication*), but various snake species [e.g., rattlesnakes (Holycross *et al.* 2002) and gopher snakes (Rodriguez-Robles, 2002)] are common in dark soils habitat and are known to predate on the focal lizard species (Little and Keller, 1937).

We also found reduced numbers of bird antagonists at White Sands. Specifically, we saw fewer avian predators (including mockingbirds, flycatchers, larger hawks and ravens) at White Sands compared to dark soils habitat. Although the diet of these species has not been studied at White Sands *per se*, they may be important predators of lizards. For example, species of mockingbirds and flycatchers occasionally feed on *Anolis* lizards in the dry season in the tropics (Wunderle 1981), Swainson's hawks include desert lizards as a large part of their diet (Giovanni *et al.* 2007), and common ravens opportunistically forage on small reptiles (Steihl and Trautwein 1991). Avian visual predators, such as the American kestrel, Loggerhead shrike and Greater roadrunner were absent from our surveys in both dark soils and White Sands, however, we saw foraging roadrunners outside regular surveys as well as their tracks in our dark soils site. The lack of kestrels and shrikes in our observations is consistent with documentation that both have recently experienced steady population declines in North America (Hobson and Wassenaar 2001, Smallwood *et al.* 2009).

We found evidence that ecological opportunity in White Sands has led to two of the three main components of ecological release in its lizard inhabitants: density compensation and broadened resource use. The combined populations of all three White Sands lizard species showed density compensation, that is, an increase in population size after colonization. Although we observed density compensation only at the level of the entire lizard community, our results follow MacArthur *et al.* (1972) who suggested that density compensation might

occur on the community scale if the total number of individuals on island populations is equivalent to that of the mainland population. At White Sands, the combined abundance of the focal species was significantly greater in White Sands compared to dark soils (Figure 2.1), and the total lizard community abundance was equivalent across habitats even with lower species richness at White Sands (Figure 2.2). Additionally, *H. maculata* was absent from our surveys in dark soils habitat where the three focal species are widely distributed and rarely overlap in one location (Rosenblum 2006, *personal observation*). Indeed, White Sands is one of the few locations in New Mexico with large overlapping populations of all three species. The large population sizes of the three focal species at White Sands likely reflects the reduction of predators and competitors.

Niche expansion, a key component of ecological release, was also evident in White Sands *S. cowlesi* in the form of broadened perch selection. We documented expanded resource use (i.e., change in niche width) by comparing perch availability and selectivity in this species. Perch use represents a key component of the ecological niche of sit and wait foragers such as *S. cowlesi*. Indeed, many *Sceloporus* species will defend their perches from both intraspecific (Martins 1993, Haenel *et al.* 2003, Robertson and Rosenblum 2010) and interspecific competitors (Dunham 1980). Preferable perches could be those that offer better predator evasion (e.g. Stamps 1983), access to better food resources (e.g. Schoener 1975), and prominent sites for display (e.g. Pounds and Jackson 1983). As we predicted, in both habitats, *S. cowlesi* did not select perches randomly (i.e., according to their availability). Moreover, in White Sands, *S. cowlesi* used more variable perches and partitioned available perches more evenly than in those in dark soils (Figure 2.3). In both habitats, *S. cowlesi* frequently perched on yuccas, which were relatively rare (see also Hager 2001). In White Sands, however, lizards

selected perches that were exposed or associated with non-yucca shrubs or trees just as often as they selected yucca perches (Figure 2.3). The wider variety of perch diameter, distance from vegetation and canopy cover used by White Sands lizards was a consequence of their more diverse perch use. Further research is needed to understand the ecological mechanism for shifts in perch use across habitats. It is possible that dark soils lizards perched almost exclusively on yucca stalks high above the ground to avoid ground predators (Schoener *et al.* 2001, Losos *et al.* 2004) or as a result of resource partitioning with interspecific competitors occupying lower perches (see Schoener 1974, Losos *et al.* 1993). Similarly it is possible that because White Sands *S. cowlesi* forage at the base of vegetation (Dixon 1966), they prefer perches where food is nearby to those higher off the ground. A comparative analysis of the diet of lizards in both habitats would demonstrate whether perch use affects this aspect of the ecological niche.

Although density compensation and broadened resource use provide convincing evidence for ecological release in White Sands lizards, we did not observe increased trait variation. Although frequently associated with the concept of ecological release, increased trait variation was not a condition of ecological release in its original definition (MacArthur and Wilson 1967) and is rarely documented in natural populations (Schluter 2000). As such, the absence of high morphological diversity in White Sands *S. cowlesi* does not negate the importance of ecological release as an evolutionary process in White Sands. Mechanistically, the lack of increased trait variation in White Sands could be explained in several ways. First, the increased niche breadth that characterizes ecological release can occur without increased trait variation. For example, directional change in trait values may itself be a response to more variable resource availability. Here we report a directional shift in *S. cowlesi* limb

morphology across habitats that may allow more flexibility in perch use (Irschick and Losos 1998). Similarly, the directional change towards broader heads in other White Sands lizard species (i.e., *H. maculata* and *A. inornata*, Rosenblum and Harmon 2011) may enable lizards to add harder prey to their diet (Herrel *et al.* 2001). Second, increased trait variation may be the final step in ecological release (Yoder *et al.* 2010) and White Sands populations may be too young to have reached that final stage. Finally, colonization by a small number of individuals in a novel habitat could initially reduce genetic diversity (see Templeton 1979) thus reducing trait variation.

We have demonstrated that the White Sands lizards have experienced ecological opportunity in their novel habitat. White Sands is species poor, ecologically distinct from the surrounding dark soil desert, and contains only a few species with the key adaptations necessary for survival. For White Sands lizards, ecological release manifests as density compensation and broadened resource use, but not as increased morphological variation within species. We stress that the study of ecological opportunity and release should not be restricted to cases where diversification, speciation, and adaptive radiation have occurred. Likely, there are many undocumented cases of ecological release in nature that can shed light on the ecological and evolutionary changes that occur following colonization of novel habitats.

Tables

perch characteristic	mean +/- standard error		P-value	
	dark soils	White Sands	Welch's t-test	Levene test
diameter (mm)	6 +/- 1.4	19 +/- 2.7	= 0.002	= 0.005
height (mm)	157 +/- 8.3	40 +/- 7.3	< 0.0001	= 0.54
canopy cover (%)	8 +/- 2.4	18 +/- 2.7	= 0.005	= 0.001
distance from vegetation (mm)	0 +/- 0	40 +/- 13.6	= 0.005	= 0.02

Table 2.1: Summary of differences between perch characteristics used by lizards in dark soils and White Sands habitats showing mean and standard error as well as P-values for differences in means (Welch's t-tests) and differences in variances (Levene's tests).

Figures

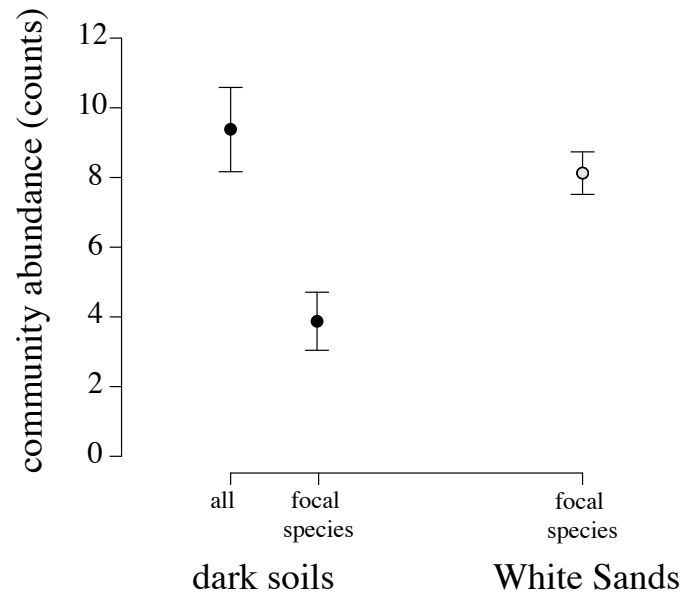


Figure 2.1: Total lizard community abundance per transect for all species and focal species in dark soils and White Sands for different sample dates. Error bars represent standard error of the mean.

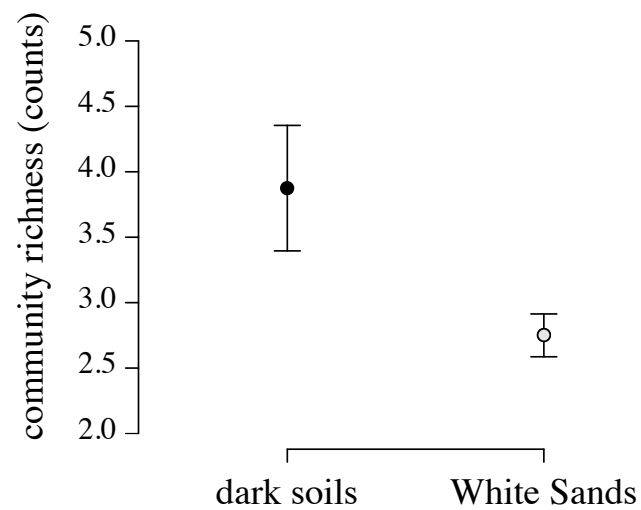


Figure 2.2: Total lizard community richness per transect in ancestral dark soils and White Sands for different sample dates. Error bars represent standard error of the mean

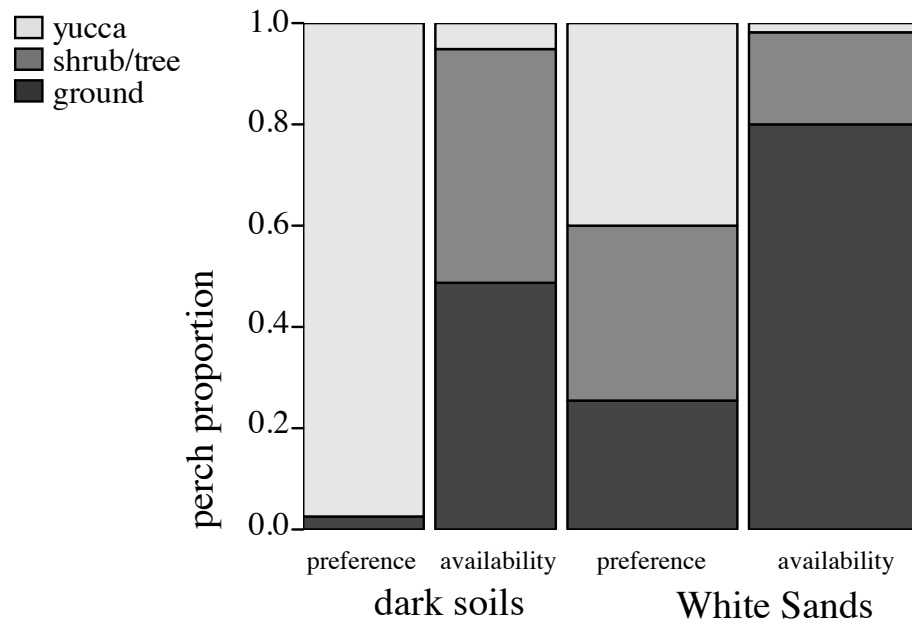


Figure 2.3: *S. cowlesi* perch preference compared to availability in ancestral dark soils and White Sands habitats. Column width corresponds to sample size in each location.

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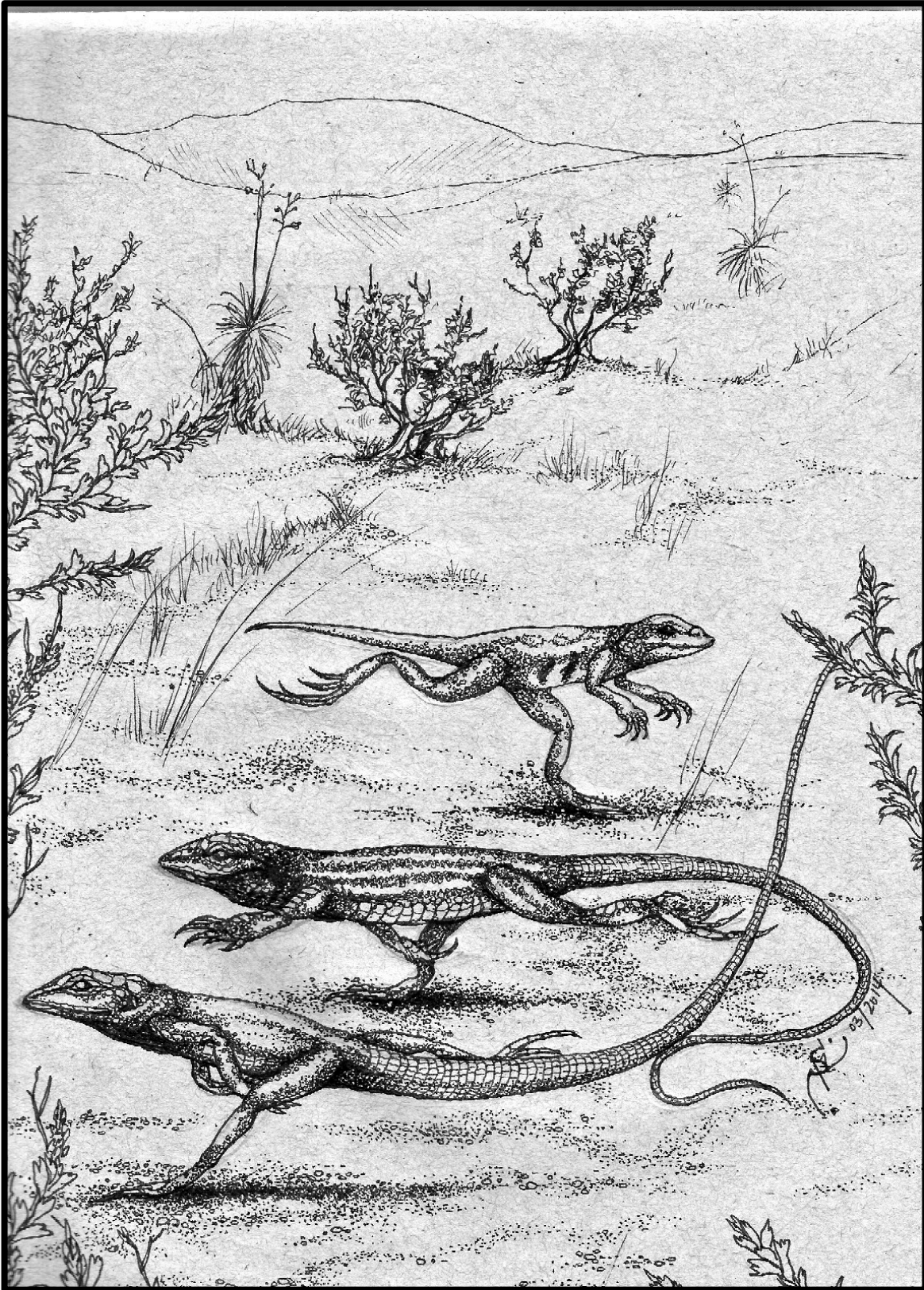


Illustration III: Lesser earless lizard (*Holbrookia maculata*) and little striped whiptails (*Aspidoscelis inornata*) sprinting on white sand substrate among soaptree yucca (*Yucca elata*) and purple bursage (*Ambrosia dumosa*)

CHAPTER III

BEYOND BLACK AND WHITE:

DIVERGENT BEHAVIOUR AND PERFORMANCE IN THREE RAPIDLY EVOLVING LIZARD SPECIES AT WHITE SANDS

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Published in 2014, *Biological Journal of the Linnean Society*, 111(1), 169-182.

Abstract

Determining which traits enable organisms to colonize and persist in new environments is key to understanding adaptation and ecological speciation. New environments can present novel selective pressures on colonists' morphology, behaviour, and performance, collectively referred to as *ecomorphology*. To investigate ecomorphological change during adaptation and incipient ecological speciation, we measured differences in morphology (body shape and size), behaviour (startle response), and performance (sprint speed) in three New Mexican lizard species: *Holbrookia maculata*, *Sceloporus cowlesi*, and *Aspidoscelis inornata*. Each species is represented by dark morphs, which are cryptic on the dark soil of the Chihuahuan Desert, and white morphs, which are cryptic on the gypsum substrate of White Sands. For each species, we determined the effects of morphology and startle response on sprint speed on matched and mismatched substrate. For two of the three

species, white morphs had larger body size and longer limbs. However, we found no statistical evidence that these morphological differences affected sprint speed. Colour morphs also exhibited different escape responses on the two substrates: in all species, dark morphs were less likely to immediately sprint from a simulated predator on white sand. As a result, escape response had a significant effect on sprint speed for two of the three species. Not surprisingly, all lizards sprinted faster on dark soil, which was probably due to the lizards' more immediate escape response and the higher compaction of dark soil. The relationship between escape response and sprint performance across the dark soil and white sand habitats suggests that behavioural differences may be an important component of adaptation and speciation in new environments.

Introduction

Determining the morphological and behavioural traits that enable organisms to successfully colonize and persist in novel environments is crucial to understanding both adaptation (Losos *et al.* 1997, Reznick and Ghalambor 2001) and ecological speciation (Orr and Smith 1998, Rundle and Nosil 2005, Schluter 2009). The three main aspects of ecomorphology – morphology, behaviour, and performance – affect the survival of an organism through interactions with the surrounding environment (Galis 1996, Irschick 2002). Morphology and behaviour interact to influence performance in different habitats (Arnold 1983, Galis 1996, Calsbeek and Irschick 2007), which in turn can strongly affect fitness (Arnold 1983). As such, performance is an important and ecologically relevant link between the phenotype and the environment (Irschick 2003).

Squamates have been the focus of many ecomorphological studies because of their impressive ecological, morphological and behavioural diversity (Garland and Losos 1994). Results from field and laboratory experiments on squamates typically support a link between morphology, performance, and habitat use. For example, in many groups, including phrynosomatid, lygosominid, and anoline lizards, longer-limbed lizards sprint faster (Bonine and Garland 1999) especially in open habitats (Melville and Swain 2000) and on broad perches (Losos 1990). Similarly, limb reduction and elongated bodies have evolved multiple times in squamates and are correlated with increased speed through dense vegetation (Wiens *et al.* 2006). However, some studies show that morphology does not always correlate predictably with performance in different habitats: although certain morphological traits appear to have evolved for habitat-specific performance, phylogenetic analyses sometimes fail to support particular adaptive hypotheses (Jaksic *et al.* 1980, Vanhooydonck and Van Damme 1999).

Behavioural shifts can play a crucial role during adaptation to new environments. On entering a new habitat, behavioural changes often precede morphological adaptations (West-Eberhard 1989). Microhabitat selection, for example, can buffer organisms from environmental changes that otherwise would exert strong selective pressure on morphology (Bogert 1949, Coyne *et al.* 1983, Duckworth 2009, Huey *et al.* 2003), which is known as behavioural inertia (Huey *et al.* 2003). Behavioural shifts can also expose organisms to novel selective environments, a process termed behavioural drive (Mayr 1963). When behaviours are heritable, behavioural drive can promote evolutionary change in morphological, physiological, or ecological traits (Bateson 1988, Wcislo 1989, West-Eberhard 1989) and may even contribute to speciation (Duckworth 2009).

Certain behaviours may be especially important for the success of colonists in new environments. Different antipredator strategies adopted by colonists can determine whether they survive post-colonisation (Schwarzkopf and Shine 1992, Vanhooydonck and Van Damme, 1999). For example, lizards will avoid habitats in which they perform poorly (Irschick and Losos 1999) and alter antipredator behaviour depending on their immediate surroundings (Vanhooydonck and Van Damme 1999). Although the most common escape strategy for a startled lizard is to move towards a refuge (Greene 1988), its behaviour and morphology may prevent detection altogether, for example, through substrate matching (Losos *et al.* 2002, Schulte *et al.* 2004). For lizards already detected by a predator, the inability to flee may be fatal. As such there can be strong selection for the fastest individuals that immediately respond to a predator by sprinting (see Husak 2006). Because sprint speed is often heritable and can influence fitness (e.g. Husak 2006, Husak *et al.* 2006, Miles 2004), it is frequently used to measure performance in different habitats.

The geologically and ecologically unique White Sands dune field in New Mexico provides a setting for the integrated study of recent and ongoing selection on morphology, behaviour, and performance. White Sands formed approximately 6000 years ago (Kocurek *et al.* 2007) and represents a novel habitat for three lizard species (*Holbrookia maculata*, *Sceloporus cowlesi*, and *Aspidoscelis inornata*). The White Sands populations evolved from lizards inhabiting the surrounding Chihuahuan dark soil desert scrubland, and there is dramatic divergence in dorsal colour between White Sands and dark soil individuals (Rosenblum and Harmon 2011). All three species have evolved blanched colouration on White Sands, which presumably allows them to better match their surrounding white substrate (Rosenblum *et al.* 2010). Additionally, two of the three species (*H. maculata* and *A. inornata*)

show parallel directional shifts in body shape with white morphs having longer legs and broader heads (Rosenblum and Harmon 2011). These morphological shifts may be a result of selection in a novel habitat with different microhabitat and substrate characteristics (Des Roches *et al.* 2011). Soil compaction, for example, affects the speed of sprinting animals and lizards, among other species, will often evolve longer limbs to increase performance on looser soils (Ding *et al.* 2011). Finally, dark and white morphs show divergence in certain behavioural characteristics (e.g. Robertson and Rosenblum 2010). Most relevant to the current study are differences in anti-predator response with white morphs of *S. cowlesi* being more wary (i.e. they retreat more), but less vigilant (i.e. they allow the approaching observer to get closer before retreating) than dark morphs (Robertson *et al.* 2011). Nevertheless, previous research has not examined these putative morphological and behavioural differences in the context of the performance of these different colour morphs.

We compared aspects of morphology, escape behaviour, and sprint performance between dark and white morphs of the three species from the dark soil desert and White Sands, respectively. First, we examined morphological differences between dark and white morphs. We expected our findings to correspond in general with the findings of Rosenblum and Harmon (2011), specifically, white morphs having longer legs in both *H. maculata* and *A. inornata*, but not *S. cowlesi*. Second, we conducted an experiment in natural conditions to determine whether startle response behaviour and sprint performance differed between morphs on matched and mismatched substrate. In terms of startle response, we formulated two alternate hypotheses both based on the finding that white and dark morphs have diverged in behavioural characteristics in different habitats (Robertson and Rosenblum 2010). If lizards are aware of their level of substrate matching, matched lizards will remain still, apparently

cryptic to a predator, whereas mismatched lizards will sprint immediately from a simulated predator. Alternatively, we hypothesize that matched lizards may be more familiar with their native background, and sprint immediately. In terms of performance, we hypothesize that selection has led to optimal performance for all lizards in their native habitats. As a result, matched lizards will in general sprint faster than mis-matched lizards on either substrate. Finally, we tested whether morphological differences and/or startle response behaviour were predictive of sprint performance. We hypothesized that if white *H. maculata* and *A. inornata* had longer legs, this morphology would allow them to sprint faster in general, and specifically on white sand substrate (Ding *et al.* 2011). Furthermore, we hypothesized that larger lizards would sprint faster, regardless of species and substrate. We also hypothesized that startle response would strongly influence performance in terms of sprint speed, with individuals that immediately sprint when startled achieving a greater speed. By simultaneously examining morphology, behaviour, and performance of three different species that have undergone parallel evolution, we provide an example of replicated ecomorphological change in a new environment.

Materials and Methods

Sampling

We captured lizards in New Mexico from 12 May to 9 July 2010 between 07:30 and 13:30. For each habitat, we had three different collection sites (Figure 1.1, “Ch. 3”). We collected 20 dark *S. cowlesi* and 19 dark *A. inornata* from a blue-gramma grassland and yucca-mesquite scrubland at Jornada Long-term Ecological Research Station, Doña Ana County. We collected 15 dark *H. maculata* from a similarly vegetated Bureau of Land

Management site northeast of the White Sands Missile Range, Otero County. We collected 15 white *H. maculata*, 18 white *S. cowlesi*, and 18 white *A. inornata* from the White Sands National Monument, Otero County. We alternated collecting efforts between dark soils and White Sands sites to control for possible seasonal changes. Because we were not comparing ecomorphology among the species, we tested one species at a time, each within the span of up to two weeks. We used only adult male lizards, which we collected by hand or with pole and slipknot noose, with the exception of two dark *A. inornata* we obtained from pitfall traps. We performed trials the day following capture after all lizards were housed in controlled temperature and light conditions overnight. We returned all lizards to the capture site the day following the trials. Because soil density affects the speed of sprinting animals (Ding *et al.* 2011), we measured soil compaction at dark soils and white sands sites using a pocket penetrometer (Korff and McHenry 2011). The results from twenty random compaction measurements at each site demonstrated that soil compaction did not differ significantly between dark soils and white sands (Wilcoxon Rank Sum Test: $Z = 1.8$, $p = 0.07$ from 100,000 random permutations of the data), however there was a trend toward white sand having lower compaction.

Morphology

We measured the following morphological characteristics for each lizard: body weight using a Pesola spring scale, snout-vent-length (SVL), interlimb length (from posterior insertion of forelimb and anterior insertion of hindlimb), pelvic width, fore and hindlimb length (from shoulder to tip of longest toe), rear toe length (from heel to tip of longest toe), and tail length (only individuals with intact tails were included) using a clear plastic ruler, and

pelvic width using handheld calipers. We first compared morphological traits unadjusted for allometric differences in SVL between dark and white morphs using Welch's t-tests. We then compared traits between morphs controlling for the effect of SVL by performing ANCOVAs on the trait of interest against SVL, colour morph, and the interaction between SVL and colour morph. In all cases, measurements were ln-transformed prior to analysis. We performed all statistical tests in R (R Development Core Team 2012).

Escape behaviour

To test escape response behaviour of the two colour morphs on different substrates, we constructed an outdoor racetrack on the edge of the dune fields of White Sands National Monument. Racetracks are frequently used to measure escape behaviour and performance of lizards (Bauwens *et al.* 1995, Robson and Miles 2000, Vanhooydonck and Van Damme 2001) and other vertebrates (e.g. Huey *et al.* 1981, Llewelyn *et al.* 2010) because ecological variables (such as substrate) can be manipulated, animals can be confined, and conditions can be made similar to the natural environment. The racetrack, which we made from 47 cm aluminum flashing, consisted of two side-by-side sections, each approximately 0.3 m wide by 2 m long. We dug the track into the ground and lined it with plastic sheeting to prevent intermixing of the treatment substrate with the local substrate. One section contained dark soils and one contained white gypsum sand (approximately 15 cm deep) collected from dark soil and White Sands sites, respectively. We ran trials on the day following capture between 08:30 and 12:00 when ambient temperatures were 30 to 35 °C. We tested lizards on each substrate, alternating which they performed on first. Individuals had an interval of at least 30 minutes between trials, during which time we kept them at constant temperature in plastic

cages in indirect sunlight. Before each trial, we recorded each individual's internal body temperature using a cloacal probe to ensure they were within their normal active temperature range. The active body temperature range of for our focal species are: *H. maculata*: 30-39 °C (Dixon 1967, Sena 1978, Hager 2000), *S. cowlesi*: 30-40 °C (Crowley 1985, Pinch and Claussen 2003), *A. inornata*: 37-39 °C (Medica 1967, Schall 1977).

For each trial, we induced a single lizard to run from one end of the racetrack starting from standstill. Because sudden movements initiated by a human observer can elicit a startle-response in reptiles (Cooper *et al.* 2009), we rapidly moved a feather duster behind each lizard to simulate a predator. We recorded all trials using a Canon VIXIA HFR10 HD video camera mounted perpendicularly on a tripod over the racetrack. We later determined startle response from the video recordings. We defined startle response as the initial behaviour within the first three seconds of the duster first coming in to view of the camera. Although some studies use a simple dichotomous categorization of response (e.g. flee or fail, Fuiman and Cowan 2003), others categorize a variety of responses relevant to natural escape behaviour in the field (Bauwens and Thoen 1981). Still others account for differences between fleeing towards or away from a refuge, or remaining immobile (Amo *et al.* 2003). For each lizard, we categorized startle response as one of the following: *fail* (did not move), *intermediate* (moved slowly or in bursts), or *sprint* (sprinted immediately, in any direction). We used chi-squared tests to determine whether dark and white morphs differed in startle response on dark soil and white sand substrate (R Development Core Team 2012).

Sprint speed

After recording initial startle response, we measured lizard sprint speed using the same experimental set-up described above. However, we excluded *failed* individuals from analysis of sprint speed only if they did not generate useable sprint data, which decreased our sample size for *H. maculata* and *S. cowlesi*. We placed measuring tape in the track so that at least 1.5 m were visible in the viewfinder and videotaped all trials at 30 frames/second. For each trial, we startled the lizard with the duster at one end of the track until it ran the full length at least 5 times or tired, a standard procedure for small reptiles (Huey *et al.* 1981, Losos 1990, van Berkum 1986). Because some lizards only sprinted once, we used only the first full sprint over approximately 80 cm. We used ProAnalyst software to compute maximum sprint speed, which we calculated as the furthest distance covered over a specified time interval of two frames, or 0.06 seconds (e.g. Martin and Avery 1998). Our procedure is comparable to methods using spaced photocells to record sprint speed, which measure the shortest time interval taken by an individual to move across a certain distance (Kohlsdorf *et al.* 2004, Losos 1990). We calibrated the program with the centre-most 10 cm of the measuring tape in the racetrack. We then manually tracked the tip of each individual lizard's nose through the field of view, which generated movement data across an x-y field. We calculated the resulting speed by dividing the distance between two (x,y) coordinates over two frames by elapsed time (= 0.06 seconds). The maximum sprint speed for each individual was the largest displacement within two frames (see Martin and Avery 1998). To determine whether lizards performed better on 'matched substrate' (i.e. white morphs on white sand, dark morphs on dark soil), we used two-way ANOVAs to test for the effects of colour morph and/or substrate on sprint speed.

Finally, for each species, we evaluated the effects of morphology and response behaviour on sprint performance of the two colour morphs on the two substrates. First, we used general linear models to test the effects of morphology on sprint speed, including colour morph and substrate as fixed effects. Here, we only tested morphological variables that were significantly different between colour morphs after controlling for SVL. Second, we tested the effects of startle response on sprint speed including colour morph and substrate as fixed effects. Because body temperature can strongly affect sprint speed (Pinch and Claussen 2003), and we used the same individuals for trials on both substrates, we ran all linear models including body temperature as a covariate and individual as a random effect. However, since neither of these variables significantly influenced the outcomes of our models, we have presented our results without these variables.

Results

Morphology

Overall, we found that white morphs were significantly larger in two of the three species (*H. maculata* and *A. inornata*). Once adjusting for SVL, some morphological traits remained significantly different. Specifically, dark *S. cowlesi* had longer rear toes and forelimbs, and white *A. inornata* had longer rear toes and hindlimbs. We outline these results separately for each species below.

Either body size, shape, or both differed between colour morphs for each species. White *H. maculata* were significantly larger than dark morphs in terms of both SVL and weight. White morphs also had longer hindlimbs, and larger pelvic width, but were not significantly different from dark morphs in forelimb, interlimb, and rear toe length. Hindlimb

length and pelvic width scaled with size, and were no longer significantly different between colour morphs when we controlled for SVL by including it in the model. Forelimb, rear toe, and interlimb length all scaled with SVL but did not differ between colour morphs. Finally, dark morphs had longer tails than white morphs, even when controlled for SVL (all results presented in Table 3.1).

Dark and white *S. cowlesi* were not significantly different in size in terms of either SVL or weight. However, dark morphs had longer hindlimbs and rear toes but were not significantly different from white morphs in forelimb length, interlimb length, and pelvic width. Hindlimb, rear toe, and forelimb length correlated with SVL, and were still significantly longer in dark morphs when we controlled for SVL. Interlimb length and pelvic width also correlated with SVL, but remained non-significant after controlling for SVL. Tail length was correlated with SVL, and as with *H. maculata*, dark morphs had longer tails when controlled for SVL (Table 3.1).

White *A. inornata* were significantly larger than dark *A. inornata* in both SVL and weight. They also had longer hindlimbs, rear toes, forelimbs, and larger interlimb length and pelvic width. Forelimb, interlimb length, and pelvic width scaled with body size and did not remain significantly different between morphs when we corrected for SVL. Although hindlimb and rear toe were significantly correlated with SVL, they were still significantly larger in white morphs when we controlled for SVL. Tail length was not significantly different between colour morphs of *A. inornata* from the two habitats and was not correlated with SVL (Table 3.1).

Escape behaviour

Startle response to a simulated predator varied depending on species, substrate, and colour morph. On dark soil substrate, *sprint* was the most common response for all lizards, regardless of species and did not differ significantly between colour morphs (Figure 3.1, Chi Squared test: *H. maculata*: $X^2_2 = 5.4$, $P > 0.05$, *S. cowlesi*: $X^2_2 = 0.03$, $P > 0.05$, *A. inornata*: $X^2_1 = 0.5$, $P > 0.05$). On white sand substrate however, startle response varied depending on species and colour morph. For *A. inornata*, dark and white morphs did not differ significantly in startle response, with nearly all individuals sprinting immediately after stimulation (Figure 3.1 f, $X^2_1 = 1.3$, $P > 0.05$). However, for both *H. maculata* and *S. cowlesi*, colour morphs exhibited significantly different startle responses (Figure 3.1, *H. maculata*: $X^2_2 = 7.2$, $P = 0.03$, *S. cowlesi*: $X^2_2 = 8.1$, $P = 0.02$). Specifically, on white sand substrate nearly 50 percent of dark morphs of *H. maculata* and *S. cowlesi* entirely failed to move from their starting position. The tendency for dark morphs to remain immobile on white sand substrate was particularly notable because the same individuals would respond by sprinting when tested on dark soil substrate. In some cases, these failed dark morphs eventually sprinted on white sand substrate and we were able to record their maximum speed.

Sprint speed

For all three species, maximum sprint speed was significantly correlated with substrate and colour morph. In general, lizards sprinted faster on dark soil substrate (Figure 2, two-way ANOVA: *H. maculata*: $F_{1,51} = 15.2$, $P > 0.001$, *S. cowlesi*: $F_{1,57} = 6.9$, $P = 0.01$, *A. inornata*: $F_{1,70} = 4.2$, $P = 0.04$). Colour morph also influenced sprint performance. Both white *H. maculata* and *A. inornata* sprinted faster than their dark counterparts (Figure 3.2a and c, *H. maculata*:

$F_{1,51} = 4.1, P = 0.05$, *A. inornata*: $F_{1,70} = 7.6, P = 0.008$). In *H. maculata*, this effect was driven mainly by superior performance on white sand substrate (Figure 3.2a). On the other hand, dark *S. cowlesi* sprinted faster than white individuals, especially on dark soil substrate (Figure 3.2b, $F_{1,57} = 4.3, P = 0.04$). In all cases, there were no significant interactions between substrate and colour morph (all $P > 0.05$).

We found no evidence that morphological differences between colour morphs influenced sprint speed in any species when our models included colour morph and substrate. In *H. maculata*, only SVL differed between morphs (see above) but there was no significant relationship between SVL and sprint speed (general linear model: SVL effect: $F_{1,47} = 0.6, P > 0.05$, substrate effect: $F_{1,47} = 15.0, P < 0.001$, morph effect: $F_{1,47} = 4.7, P = 0.03$, all interactions: $P > 0.05$). In *S. cowlesi*, hindlimb, rear toe, and forelimb differed between colour morphs but did not affect sprint speed (morphological characters' effect: $F_{3,45} = 1.3, P > 0.05$, substrate effect: $F_{1,58} = 7.8, P < 0.01$, morph effect: $F_{1,58} = 0.8, P > 0.05$, all interactions: $P > 0.05$). Likewise, in *A. inornata*, SVL, hindlimb and rear toe length differed between colour morphs, but had no effect on sprint speed (morphological characters' effect: $F_{3,58} = 0.3, P > 0.05$, substrate effect: $F_{1,58} = 4.7, P = 0.03$, morph effect: $F_{1,58} = 2.0, P > 0.05$, all interactions: $P > 0.05$).

Sprint speed was significantly influenced by startle response in *S. cowlesi* and *A. inornata*, but not in *H. maculata*. In the first two species, startle response affected speed but did not interact with colour morph or substrate (Table 3.2, *S. cowlesi*, response effect: $F_{2,49} = 15.1, P \ll 0.0001$, *A. inornata*, response effect: $F_{1,67} = 4.5, P = 0.04$, all interactions: $P > 0.05$). In both *S. cowlesi* and *A. inornata*, individuals that exhibited the response *sprint* achieved a greater sprint speed than those categorized as either *intermediate* or *fail* (which did not

significantly differ from one another). In *H. maculata*, however, startle response did not significantly affect the relationship among sprint speed, colour morph, and substrate (three-way ANOVA: response effect: $F_{2,44} = 1.3$, $P > 0.05$, all interactions: $P > 0.05$). Within each species, initial body temperature did not vary greatly. Furthermore, in all cases where we included initial body temperature as a covariate, it did not significantly affect sprint speed.

Discussion

The parallel phenotypic evolution of the White Sands lizard species provides an opportunity to study comparative ecomorphology during rapid adaptation. Our current and previous work (Rosenblum and Harmon 2011) demonstrate divergence in body size and shape between dark and white lizard morphs inhabiting the dark-brown quartz soil desert and gypsum White Sands dunes, respectively. However, we found no evidence of these morphological differences affecting sprint performance on dark soil and white sand substrates in an experimental context. Instead, we found that behavioural differences had important consequences on performance. Specifically, startle response to a simulated predator differed between dark and white morphs on different substrates and was predictive of maximum sprint speed in two species. Our results underscore the link between behaviour and performance post-colonization of novel habitats.

Morphology

The most notable difference in morphology between dark and white lizards was in body size of *H. maculata* and *A. inornata*. In both species, white morphs were significantly larger in SVL and body weight. Most other traits (limb length, pelvic width, interlimb length)

scaled allometrically with body size, and thus were larger in white morphs. Differences between the morphology of colour morphs may be a result of drift in small isolated populations, phenotypic plasticity, or natural selection on heritable traits, as discussed below.

Phenotypically plastic responses to ecological, physiological, or life history pressures may explain differences in morphology between morphs. First, because size is indeterminate in these species, white lizards may be larger because they are older (Shine and Charnov 1991). Specifically, reduced predation in White Sands (Des Roches *et al.* 2011, Robertson *et al.* 2011) may allow lizards to live longer (e.g. Sebens 1987). Second, higher resource availability could promote faster development (Stamps *et al.* 1998) and lower interspecific competition at White Sands (Des Roches *et al.* 2011, Robertson *et al.* 2011). Increased body size resulting from competitive release has been shown for the brown anole, *Anolis sagrei*, individuals in areas of higher resource availability and lower species richness grow faster and are larger than those from adjacent resource-poor areas (Schoener and Schoener 1978).

Morphological differences between morphs could also be due to natural selection, given the dramatic differences between dark soils and White Sands habitats. For example, some trait differences between morphs remained significant even after correcting for body size. It is possible that such traits have adaptive significance if they are heritable. For *S. cowlesi*, white morphs had shorter forelimbs, hindlimbs, and longest rear toes. Natural selection for shorter limbs in white *S. cowlesi* may follow from our observation that this species uses a wider variety of perches at White Sands (Des Roches *et al.* 2011). In studies of both *Anolis* and *Sceloporus* species, reduced limb size allows for increased “surefootedness” on an increased variety of perches (Losos and Sinervo 1989, Sinervo and Losos 1991). Conversely, we observed longer hindlimbs and longest rear toes of white *A. inornata*. We

expect this difference is correlated with alternate ecological strategies in the two species (i.e., shorter limbs for surefootedness in the arboreal *S. cowlesi* and longer limbs for speed in the terrestrial *A. inornata*). However, our data do not provide evidence that longer limbs in *A. inornata* correlated with faster speed in either habitat (see discussion below). Finally, both white morphs of *H. maculata* and *S. cowlesi* had shorter tails, irrespective of body size. Various studies have shown that tail length affects locomotion, for example, better climbers often have longer tails (Jaksic *et al.* 1980) and better sprinters often have shorter tails (Li *et al.* 2011). Still, the relationship between locomotion and tail length is not as well established as it is with other morphological traits (Buckley *et al.* 2010). Some researchers have argued that tail length is more variable and easily affected by external influences, such as temperature (Buckley *et al.* 2010). In both *Sceloporus* (Buckley *et al.* 2010) and *Lampropholis* (Qualls and Shine 1998), individuals incubated at higher temperatures had shorter tails, and a larger body size. Interestingly, this is similar to the trend we observed in our study, where lizards from the cooler White Sands habitat were also more likely to be larger with shorter tails (see Hager 2000). More research is needed to discern whether morphological shifts at White Sands are due to heritable change and how they affect performance and fitness.

It is important to note that our study focused on paired comparisons between one White Sands and one dark soils population for each species. Differences among studies in which specific dark soils populations were sampled may explain the minor discrepancies between our study and previous morphological comparisons, (which pooled samples from different localities by habitat type, (i.e. Rosenblum and Harmon 2011). Future work with broad sampling across many dark soil sites but without pooling by habitat type will provide a more general understanding of morphological variation at this spatial scale.

Escape behaviour

The most unexpected result of our study was the variation of startle response between dark and white morphs. Specifically, we found that many dark *H. maculata* and *S. cowlesi* sprinted on dark soil substrate but failed to sprint on white sand substrate where they were mismatched. Our result is surprising because substrate matched species such as sculpin (Houtman and Dill 1994), and sit-and-wait lizard foragers (including *H. maculata* and *S. cowlesi*) commonly adopt an immobile strategy to enhance crypsis when faced with a predator (Huey and Pianka 1981). Other species such as the yellow-legged frog (*Rana muscosa*) will exhibit more alert behaviour when they are mismatched and when threatened, quickly escape to cover (Norris and Lowe 1964). In our study, lizards that stood out against the white sand background remained motionless when stimulated. Surprisingly, the same individuals would sprint immediately when startled on dark soil substrate, as would white individuals on white sand substrate. It is possible that quantitative differences between dark soil and white sand substrates influence escape response. For example, gypsum has a lower thermal capacity (Weast 1986). Another intriguing possibility is that the observed differences in startle responses reflect a change in sensory perception in White Sands due to the higher reflectivity of gypsum. Geckos (*Sphaerdactylus macrolepis*) from populations inhabiting dark habitats better detect motion in dimmer light, whereas those from light habitats perform better in brighter light (Nava *et al.* 2009). Similarly, difference in light conditions between White Sands and dark soils habitats, for example the higher reflectivity (Wheeler *et al.* 1994) of the former, may have led to evolved differences in visual acuity in the lizard species. Regardless of the specific mechanism underlying the response differences, failure of mismatched lizards to sprint could be maladaptive when faced with a predator. These behavioural shifts may have

played important role during adaptation to the new White Sands environment. Indeed, appropriate startle response behaviour may have been a crucial adaptation preceding morphological adaptation. Further work is needed to determine the relevance of this response in a natural setting and whether it represents an actual genetic change under selection.

Sprint speed

Our prediction that sprint speed would be different on white sands and dark soils substrates was met. In general, for all species and both colour morphs, performance was better on dark soil substrate. Our results were not surprising considering that other studies have shown a relationship between sprint performance and substrate type (Ding *et al.* 2011, Kohlsdorf *et al.* 2004). Our test of soil compaction demonstrated a trend towards looser soil in White Sands, which has also been shown in other studies (Hager 2001). The limbs of a running lizard sink deeper into loose substrate, such as sand. The larger the foot surface area, the less penetration and more propulsive force (Ding *et al.* 2011). Thus, evolution of longer feet or toes is a common adaptation for sprinting in sandy habitats (Ding *et al.* 2011, Kohlsdorf *et al.* 2001, Melville and Swain 2000). However, even lizards that are loose sand specialists, such as the Zebra-tailed lizard (*Callisaurus draconoides*), still sprint faster on harder ground (Ding *et al.* 2011).

Our data also supported our prediction that the two colour morphs would show differences in sprint speed. However, the patterns we observed were not parallel across species. In the two more ‘terrestrial’ species (rarely observed on vegetation), *H. maculata* and *A. inornata*, white morphs sprinted faster than their dark counterparts. For *H. maculata*, this effect was driven mostly by white morphs being faster than dark morphs on white sand

substrate. For *A. inornata*, white morphs were faster than dark morphs on both substrate types. In the more arboreal species, *S. cowlesi*, dark morphs were faster sprinters, but only significantly so on dark soil substrate. Although there are alternative, non-adaptive mechanisms (e.g. phenotypic plasticity or genetic drift) for increased sprint speed in the more terrestrial white sands species, one possibility is that natural selection for faster sprint speed has been stronger in *H. maculata* and *A. inornata* because they spend more time foraging and basking on the exposed substrate than does *S. cowlesi* (Medica 1967, Hager 2001).

Our results did not provide evidence for a relationship between sprint speed and morphology. Research in other systems has shown that morphological adaptation in lizards is often related to performance in specific habitats (Losos 1990, Bonine and Garland 1999, Melville and Swain 2000, Kohlsdorf *et al.* 2001, Goodman 2009), yet, morphological change does not always accompany ecological divergence (Jaksic *et al.* 1980, Vanhooydonck and Van Damme 1999). For example, in our study, white *H. maculata* and *A. inornata* were faster sprinters, but faster speed was not associated with their larger body size or longer limbs. If morphology is related to performance at White Sands, there are several reasons why we may not have uncovered this link. It is possible that morphological variation is related to a performance trait that we did not measure, for example, endurance (e.g. for anoles, Calsbeek and Irschick 2007). It is also possible that we may have lacked power to detect subtle effects of morphological variation on sprint speed (considering the reduced sample size after we removed failed individuals). Finally, differences in running kinematics, such as stride length and speed (Irschick and Jayne 1999) and muscle physiology (Garland *et al.* 1995) may explain the subtler relationship between morphology and sprint performance. Further research using a larger sample size of lizards induced to run longer distances, and including direct

measurement of kinematics and muscle physiology may elucidate the less apparent effects of morphology on performance.

Although we had no evidence that sprint speed was correlated with morphology, sprint speed was predicted by initial startle response. In both *S. cowlesi* and *A. inornata*, individuals that failed or walked initially were slower sprinters. In these species, individuals that exhibited the response *sprint* achieved a greater speed. However, startle response did not significantly influence sprint speed in *H. maculata*, perhaps due to low statistical power after removing failed individuals. As discussed above, lizards can adopt alternative antipredator strategies such as crypsis or sprinting (for a comparison of these strategies see Schwarzkopf and Shine 1992). Studies of other species including the keeled earless lizard (*Holbrookia propinqua*) and the water skink (*Eulamprus typanum*) demonstrate that individuals avoid sprinting (Cooper 2003) and adopt crypsis (Schwarzkopf and Shine 1992) as an anti-predator tactic when their running is impeded (i.e. they have lost tails or are gravid). Although the lizards in our study did not have such extreme morphological impediments, running may be more difficult on white sands substrate and thus lead to shifts in anti-predator tactics. Future work in the White Sands system will be needed to understand the link between initial escape tactic and running performance in both experimental and natural contexts.

Interactions among morphology, behaviour, and performance have been studied in a diversity of animals including insects (e.g. Betz 2002), fish (e.g. Huber *et al.* 1997), mammals (e.g. Aguirre *et al.* 2002), and lizards (e.g. Vanhooydonck and Van Damme 2001, Schulte *et al.* 2004, Irschick *et al.* 2005). The White Sands system, colonized recently and independently by three lizard species, provides an opportunity to study these ecomorphological interactions in a comparative framework. Our results underscore the relationship between behaviour and

performance across the White Sands ecotone, while deemphasizing the importance of morphological differences post-colonisation of a new habitat. More generally, the results of our study underscore the importance of future research that integrates analysis of adaptive morphology, behaviour, and performance in the study of organisms invading and persisting in new habitats.

Tables

species	trait	t-test				ANCOVA			
		raw measurement		SVL effect		variable effect		interaction effect	
		t	P	F	P	F	P	F	P
<i>H. maculata</i>	SVL	-3.5	= 0.001	N/A	N/A	N/A	N/A	N/A	N/A
	weight	-2.8	= 0.008	92.3	< 0.001	0.000	= 1.0	0.09	= 0.8
	forelimb	-1.8	= 0.08	55.1	< 0.001	1.6	= 0.2	0.08	= 0.8
	hindlimb	-2.0	= 0.05	46.6	< 0.001	0.3	= 0.6	0.000	= 1.0
	rear toe	-0.5	= 0.6	11.1	= 0.002	1.2	= 0.3	0.1	= 0.7
	pelvis	-3.9	= 0.001	92.5	< 0.001	1.2	= 0.3	3.4	= 0.07
	interlimb	-1.3	= 0.2	16.0	< 0.001	0.4	= 0.5	0.05	= 0.8
	tail	3.0	= 0.007	1.5	= 0.2	11.2	= 0.002	0.002	= 1.0
<i>S. cowlesi</i>	SVL	-0.11	= 0.9	N/A	N/A	N/A	N/A	N/A	N/A
	weight	1.1	= 0.3	185.8	< 0.001	8.7	= 0.006	6.5	= 0.02
	forelimb	1.4	= 0.2	43.6	< 0.001	4.6	= 0.04	1.2	= 0.3
	hindlimb	2.6	= 0.02	51.0	< 0.001	16.8	< 0.001	5.3	= 0.03
	rear toe	3.2	= 0.002	6.0	= 0.02	12.7	= 0.001	2.4	= 0.1
	pelvis	0.7	= 0.5	37.9	< 0.001	1.1	= 0.3	1.2	= 0.3
	interlimb	-0.5	= 0.6	52.8	< 0.001	0.4	= 0.5	0.1	= 0.7
	tail	1.9	= 0.07	11.5	= 0.003	5.5	= 0.03	0.9	= 0.4
<i>A. inornata</i>	SVL	-4.6	< 0.001	N/A	N/A	N/A	N/A	N/A	N/A
	weight	-7.1	< 0.001	65.7	< 0.001	20.4	< 0.001	0.02	= 0.9
	forelimb	-3.2	= 0.003	25.0	< 0.001	0.06	= 0.8	0.08	= 0.7
	hindlimb	-6.7	< 0.001	26.2	< 0.001	15.7	< 0.001	2.4	= 0.1
	rear toe	-8.3	< 0.001	14.9	< 0.001	31.9	< 0.001	3.1	= 0.09
	pelvis	-4.8	< 0.001	76.2	< 0.001	1.8	= 0.2	1.1	= 0.3
	interlimb	-4.9	< 0.001	44.8	< 0.001	2.9	= 0.09	1.3	= 0.3
	tail	-1.4	= 0.4	1.2	= 0.3	0.3	= 0.6	N/A	N/A

Table 3.1: Differences in morphological traits between lizards from dark soils and White Sands sites, both not controlled (raw measurements, using Welch's t-test) and controlled (using ANCOVA) for snout-vent-length (SVL). All measurements were natural log transformed. Negative test statistics denote the trait of interest was larger in White Sands morphs. Two-way interactions for *Aspidoscelis inornata* tail length could not be calculated since several lizards lacking tails were excluded from the analysis.

species	test used	substrate effect	colour morph effect	morphology ¹ effect	behaviour effect
<i>H. maculata</i>	2-way ANOVA	15.17***	4.11*	N/A	N/A
<i>S. cowlesi</i>		6.87*	4.28*	N/A	NA
<i>A. inornata</i>		4.19*	7.57**	N/A	NA
<i>H. maculata</i>	ANCOVA	14.10***	4.74*	0.063	N/A
<i>S. cowlesi</i>		7.78**	0.82	1.26	N/A
<i>A. inornata</i>		4.67*	2.02*	0.31	N/A
<i>H. maculata</i>	3-way ANOVA	7.88**	1.90	N/A	1.28
<i>S. cowlesi</i>		11.83**	5.89*	N/A	15.10***
<i>A. inornata</i>		2.98	4.91*	N/A	4.50*

Table 3.2: The effects of morphology and escape behaviour on sprint performance for dark and white colour morphs of three species on dark soil and white sand substrates. The results of a 2-way ANOVA describes the combined effects of substrate and colour morph on sprint speed. The results of an ANCOVA and 3-way ANOVA show the effects of morphology and startle response, respectively on this relationship.

¹Only morphological characteristics that differed between white and dark morphs were tested: SVL for *Holbrookia maculata*, forelimb, hindlimb, longest toe for *Sceloporus cowlesi*, SVL, hindlimb, longest toe for *Aspidoscelis inornata*.

- * P < 0.05
- ** P < 0.01
- *** P < 0.001

Figures

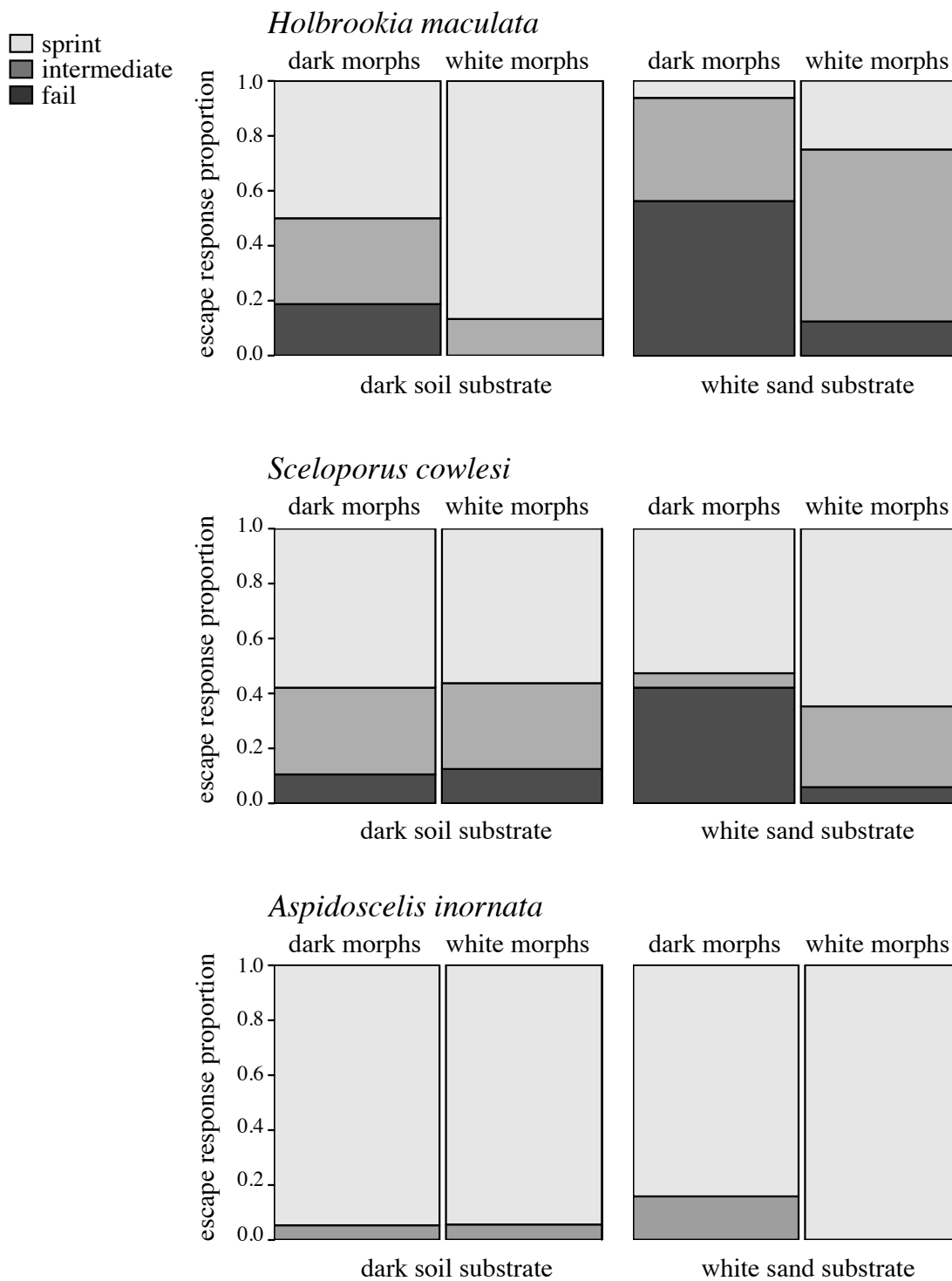


Figure 3.1: Differences in startle response for three species presented with a simulated predator: a. *Holbrookia maculata*, b. *Sceloporus cowlesi*, c. *Aspidoscelis inornata* on dark soil (left) and white sand (right) substrate. Within each panel, response of dark and white morphs are shown on the left and right, respectively.

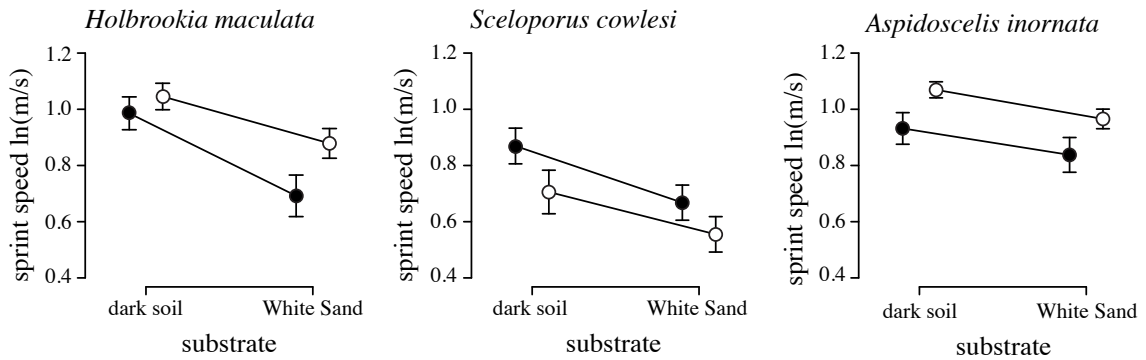


Figure 3.2: Average maximum sprint speed for three species: a. *Holbrookia maculata*, b. *Sceloporus cowlesi*, c. *Aspidoscelis inornata* on dark soil (left) and white sand substrate (right). Within each panel, dark and white circles represent average sprint speed for dark and white morphs, respectively. Points are connected to illustrate the parallel trend for all species to sprint faster on dark soil substrate. Error bars represent standard error of the mean.

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Illustration IV: Little striped whiptail (*Aspidoscelis inornata*) consuming a termite (*Reticulitermes flavipes*)

CHAPTER IV

ECOLOGICAL RELEASE AND DIRECTIONAL CHANGE IN WHITE SANDS

LIZARD TROPHIC ECOMORPHOLOGY

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Submitted to *Functional Ecology*, March 2014

Abstract

Following colonization, selection can lead to changes in trophic ecomorphology. Specifically, the morphological and performance traits that influence diet determine how colonists interact with a new resource base. Resource shifts may result in dietary change of colonists and therefore, the evolution of ecomorphological adaptations such as changes in bite force, head, and body size. To understand the drivers and dynamics of ecomorphological change after colonization we studied prey availability, diet, performance, and morphology in three lizard species (*Aspidoscelis inornata*, *Holbrookia maculata*, and *Sceloporus cowlesi*) in the novel environment of White Sands, NM. For each species we compared White Sands individuals to conspecifics inhabiting the surrounding "dark soils" Chihuahuan desert habitat. The White Sands habitat had higher prey species richness, increased breadth of prey orders, and a higher percentage of hard-bodied prey than the dark soils habitat. Although similarities in resource use across the three species in White Sands indicated parallel responses to a shared environment, we found differences among species in performance and morphology

traits. Specifically, differences in average hardness of prey in the diet, bite-force, head size and body size demonstrate that the three species have responded differently to a shared shift in their environment. White Sands presents a snapshot of the early stages of community assembly in a novel ecosystem. Some dietary shifts in the three species were predictable and reflect a common environment. Differences among species may reflect constraints due to ecological and/or evolutionary history.

Introduction

Colonization of novel ecosystems can provide a rare glimpse into patterns of rapid ecological and evolutionary change in new environments. When multiple colonist species encounter a novel, shared environment, how they interact with their new surroundings may be as variable as their individual evolutionary histories. Colonists' ecomorphology - the interaction between morphology and performance (Galis 1996, Irschick 2002) - may determine whether they survive, persist, and adapt to their new ecosystems. If colonists persist, how selection acts on aspects of their ecomorphology will depend on numerous factors including resource availability and presence of other interacting species.

Both the ecological and evolutionary history of colonists will influence their likelihood of effectively exploiting resources and surviving in a new environment (Simberloff 1978, Parsons 1982, Lodge 1993, Reznick and Ghalambor 2001). If colonist populations do survive, new selection pressures may influence their course of evolution in a number of ways. Directional selection can lead to the evolution of different mean trait values that optimize fitness in the new resource environment (see Thompson 1998). Alternatively, lack of antagonist species (competitors and predators) and availability of resources in a novel

environment may result in reduced selective pressures and thus ecological release (Losos and De Queiroz 1997, Yoder *et al.* 2010). Ecological release is likely to allow increased variation of resources used, which may or may not translate into increased variance of trait values (Lister 1976a, Lister 1976b, Bolnick *et al.* 2007). Finally, fluctuating selection or phenotypic plasticity of traits related to resource acquisition may result in very little change in the ecomorphology of colonist species.

The morphological and performance traits that influence diet will determine how colonists interact with a new resource base. Recently available resources may result in dietary change of colonists and therefore, the evolution of ecomorphological adaptations (e.g. Schluter and Grant 1984, McPhail 1993, Herrel *et al.* 2008). Performance traits, such as bite force, provide a link between morphological traits - like head shape - and fitness (Arnold 1983, Galis 1996, Calsbeek and Irschick 2007). There is substantial variation in morphological and performance traits that affect trophic ecology both within and among species (e.g. Wainwright 1991, Irschick 2002). In lizards for example, individuals with larger heads have a more powerful bite and take less time to handle hard-bodied prey items like beetles and ants (Herrel *et al.* 2001, Verwajen, Van Damme and Herrel 2002, Kaliontzopoulou *et al.* 2012, Sales *et al.* 2012). Although large-headed individuals may be able to incorporate bigger and harder prey in their diet (Herrel *et al.* 2001, Verwajen *et al.* 2002), they may experience trade-offs in prey capture velocity (Herrel *et al.* 1999). Head size often scales allometrically with body size (e.g. Meyers, Herrel and Birch 2002, Herrel and O'Reilly 2006), which itself can be under selection (Calsbeek and Smith 2007). Head size and bite force can also be influenced by sexual selection (i.e. male-male aggression, Husak *et al.*

2006). As a result, selection may take many forms when influencing the morphological and performance traits that link resource use to trophic ecomorphology.

Here, we focus our attention on three lizard species that coexist in the unique gypsum dune field of White Sands, New Mexico (Rosenblum 2006). The three species, *Aspidoscelis inornata* (the Little Striped Whiptail), *Holbrookia maculata* (the Lesser Earless lizard), and *Sceloporus cowlesi* (the Southwestern Fence Lizard, formerly *S. undulatus*, Wiens *et al.* 2010) are the most abundant reptile species inhabiting the sparsely vegetated dunes. These three species have broad distributions across the Chihuahuan desert and are only distantly related to each other. In the 6,000 years since the White Sands dunes formed (Kocurek *et al.* 2007), the three species have established dense local populations (Des Roches *et al.* 2011). The most striking convergently evolved adaptive trait exhibited by all three species at White Sands is cryptic blanched colouration. However, previous research has demonstrated differences in behaviour (Robertson *et al.* 2011), performance (Des Roches *et al.* 2014), habitat use (Des Roches *et al.* 2011), body shape and size (Rosenblum and Harmon 2011) between White Sands lizards and their conspecifics in the surrounding Chihuahuan scrubland. Because White Sands and dark soils lizards demonstrate differences in body size and shape, we hypothesized that morphological shifts could be related to changes in resource availability and resource use in this novel environment.

We examined differences in trophic ecomorphology for the three lizard colonist species of White Sands compared to their dark soils counterparts. Because differences in resource availability between dark soils and White Sands habitats may have caused ecomorphological divergence, we began by first measuring arthropod prey community composition and lizard diet in the two habitats. Specifically, we recorded available arthropod

morphospecies richness, niche breadth, and proportion of hard, intermediate, and soft-bodied prey in both dark soils and White Sands habitats. We then recorded these same metrics for the diet of the three species in each habitat. To determine if significant differences in relevant ecomorphological traits exist between lizards from the two different habitats, we then recorded lizard bite force, head size, and body size.

We predicted differences in prey availability between dark soils and White Sands habitats and correlated changes in lizard diet and ecomorphology. We expected several alternative roles for selection on ecomorphological traits, including the possibility that evolution by natural selection did not produce detectible differences between dark soils and White Sands lizards. First, if directional selection led to ecomorphological change at White Sands, we expected shifts in diet and in morphological and performance traits towards one extreme (e.g. a higher proportion of harder-bodied prey, stronger bite force and larger head size). Second, if ecological release (i.e. relaxed selection) led to ecomorphological change at White Sands, we expected an expansion in lizard diet to include a greater variety of prey types and potentially a greater variation in ecomorphological traits. Finally, if natural selection did not drive ecomorphological shifts in White Sands lizards, we expected to observe either stochastic change, or a lack of change, in performance and morphological traits relative to resource use. Analyzing the relationships among prey availability, diet, performance, and morphology in multiple species in a shared novel environment provides an integrative approach to understanding the dynamics of ecomorphological change after colonization of a new environment.

Materials and Methods

Sampling

We collected lizards in New Mexico from White Sands and dark soils habitats from 12 May to 9 July 2010. For each habitat, we had three different collection sites (Figure 1.1, “Ch. 4”). In White Sands Sites A, B, and C were all located at the White Sands National Monument, Otero County. In Dark Soils, Sites D and E were located at a blue-gramma grassland and yucca-mesquite scrubland at Jornada Long-term Ecological Research Station, Doña Ana County, and Site F was located at a similarly vegetated Bureau of Land Management site northeast of the White Sands Missile Range, Otero County. In White Sands, we collected 18 white *A. inornata* from Site A and B, 15 white *H. maculata* at Sites A and B, and 18 white *S. cowlesi* from Sites B and C. We collected 19 dark *A. inornata* from Site D, 20 dark *S. cowlesi* from Site E, and 15 dark *H. maculata* from Site F. We used only adult male lizards to control for variation in developmental stage and sexual dimorphism. We captured all lizards by hand or with pole and slipknot noose, with the exception of two dark *A. inornata* that we obtained from pitfall traps. Because we were more interested in ecomorphological differences between conspecific morphs than differences across species, we conducted experiments on one species at a time during a 12 to 15 day period, alternating between collection at dark soils and White Sands habitats. We returned all lizards to the capture site the day following their capture.

Prey Availability and Diet

To estimate prey availability, we trapped primarily terrestrial arthropods in all specific locations where we sampled lizards. We placed eight pitfall traps in 1 metre intervals along a

transect in Sites A through C in White Sands habitats and D through F in dark soils habitats. We dug 50 mL Falcon tubes into the ground and filled them with 1 part non-toxic anti-freeze (propylene glycol), 1 part water, and 1-2 mL of biodegradable detergent (to reduce surface tension on the arthropod; see Verwaijen *et al.* 2002). We collected all traps after leaving them continuously open for three days and froze them at -4°C . We then filtered each pitfall sample with distilled water and excluded very large insects (camel crickets, darkling beetles) that exceed the gape size of our focal species and were therefore too large to be included in the diet (DeMarco, Drenner and Ferguson 1985). Because we collected each dark soils lizard species from one site only (either D, E, or F), we summarized prey availability data for each dark soils species from eight pitfall traps. In White Sands, however, we collected each species from two sites, thus prey availability data for each species in this habitat was summarized from sixteen pitfall traps.

To obtain samples of lizard diet, we stomach flushed all caught individuals according to standard methods (Legler and Sullivan 1979). We used a flushing instrument consisting of a 75 mm x 16 g curved stainless steel dosing cannula (Harvard Apparatus, Holliston, MA) attached to a 5 ml plastic syringe. We stimulated each lizard to open its jaws, which we propped open with a small plastic ring cut from a Pasteur pipette. While securing the animal in one hand, we slowly inserted the metal cannula through the digestive tract. We flushed the entire stomach contents with tap water (at the lizard's body temperature) and stored stomach contents in ethanol.

We used pitfall and stomach content samples to estimate the arthropod morphospecies richness, niche breadth, and hardness of available prey and lizard diet. To obtain a rough estimate of species richness, we recorded the number of morphologically distinct species in

each sample. We subsequently dried specimens from each sample in a drying oven for approximately 24 hours at 37 degrees Celsius and weighed them to the nearest 0.001 grams. We recorded total stomach content sample weight for each lizard as the summed weights across each order. Finally, we calculated niche breadth as the inverse of Simpson's Diversity Index:

$$B = \frac{1}{\sum_{i=1}^n p_i^2}$$

where B is niche breadth, N is the sample size, p is the proportion, and i is the resource category, in this case, arthropod order (Edwards *et al.* 2013). We then identified arthropods from pitfall traps and stomach contents to order and separated these out for each sample, while grouping all unidentifiable pieces as “unknown”. Because the force required to crush prey can limit which arthropods are consumed by lizards (Herrel *et al.* 2001, Verwaijen *et al.* 2002, Kaliontzopoulou *et al.* 2012, Sales *et al.* 2012), we categorized arthropod orders into three hardness categories following previous studies (Herrel *et al.* 1999, Aguirre *et al.* 2003): “hard” (Coleoptera, Hymenoptera, Chilopoda), “intermediate” (Hemiptera, Orthoptera), or “soft” (Diptera, Lepidoptera, Isoptera, Aranae, Thysanoptera, larvae of any order, and other rare orders). In addition to sorting arthropods by order and hardness, we further categorized the length of each prey item in each order by size class: extra-small (< 2 mm), small (2 – 6 mm), medium (6 – 12 mm), and large (> 12 mm). In instances where only a portion of an arthropod remained, we estimated the total length based on previously observed prey items. We approximated maximum and average prey hardness per lizard stomach content using the following equations, which estimate overall prey hardness based on length and hardness category (Herrel *et al.* 1999, Aguirre *et al.* 2003):

Hard: $\log_{10}[\text{prey hardness}] = 1.582 * \log_{10}[\text{prey length}] - 1.365$

Intermediate: $\log_{10}[\text{prey hardness}] = 1.780 * \log_{10}[\text{prey length}] - 1.942$

Soft: $\log_{10}[\text{prey hardness}] = 0.997 * \log_{10}[\text{prey length}] - 1.365$

with prey hardness measured in Newtons (N) and prey length in millimeters (mm).

Performance and Morphology

We measured lizard bite performance across all three species from the two habitats using a bite force meter (Herrel *et al.* 1999, Herrel *et al.* 2001). We maintained the lizards at their optimal activity temperature (*A. inornata*: 37-39 °C, *H. maculata*: 31-34 °C, *S. cowlesi*: 33-36 °C, Dixon 1967) in a “basking tank” and recorded their body temperature using a cloacal thermometer before measuring bite force. We used an isometric Kistler force transducer (type 9203, Kistler Inc.) connected to Kistler charge amplifier (model 463A, PCB Piezotronics Inc., New York, NY) to measure bite force (see Herrel *et al.* 2001). We stimulated each lizard to bite down on two metal plates connected to the transducer. While *S. cowlesi* individuals exhibited a typical threat response and opened their mouths to bite without provocation, we had to encourage *A. inornata* and *H. maculata* lizards to open their mouths with a blunted toothpick placed at the edge of their jaw. Once the lizards opened their mouths, they would continuously bite down on the metal plates. For each individual we recorded the maximal value (in Newtons) from five sequential bite force readings.

We measured morphological characteristics for each lizard on the same day as capture, prior to stomach flushing. We measured total body weight (in grams) using a Pesola spring scale and snout-vent-length (SVL), using a clear plastic ruler. We measured three metrics of head shape (in millimetres) using handheld calipers: head depth (highest part of the skull,

midway above eye to below jaw), jaw length (tip of snout to behind lower jaw), and head width (at widest point) using handheld calipers. We condensed these three measures of head shape into one metric, “head size,” which we calculated as the cube root of the product of head depth, jaw length, and head width (Mosimann 1970, Kaliontzopoulou *et al.* 2012). We also calculated head size adjusted for body size by taking the residuals of a linear regression of the natural log-transformed values of head size on body size.

Statistical Analysis

We compared morphospecies richness and niche breadth between habitats (dark soils versus White Sands) and prey base (availability versus diet) using two-way ANOVAs. We then used a two-way MANOVA to test the effects of habitat and use on the percentage of hard, intermediate, and soft-bodied arthropod orders consumed. We used Welch’s t-tests to determine pairwise differences between availability and diet, and between dark soils and White Sands habitats for morphospecies richness, niche breadth, and percentage of hard bodied-prey. Finally, to examine the effects of habitat on the pairwise differences in mean and variance of diet hardness, performance (bite force), and morphology (head and body size) we used Welch’s t-test and Levene’s test, respectively. To meet assumptions of normality, we natural log transformed all data, except proportions of hard, intermediate, and soft-bodied prey, which we arcsine transformed. We performed all analysis in R (R Development Core Team 2013).

Results

Prey Availability and Diet

All metrics of arthropod availability- morphospecies richness, niche breadth, and percentage of soft, intermediate, and hard-bodied prey - differed between dark soils and White Sands habitats. There was significantly higher arthropod morphospecies richness and niche breadth in White Sands compared to dark soils ($P < 0.01$ for sites where each of the three species were collected, Table 4.1, Figure 4.1). In sites where *A. inornata* and *H. maculata* were collected, the percentages of hard, intermediate, and soft-bodied prey were also significantly different between White Sands and dark soils habitats (all $P < 0.05$, Table 4.1, Figure 4.2). However, in sites where *S. cowlesi* was collected, the percentages of hard, intermediate, and soft-bodied prey were only marginally different between habitats ($P = 0.07$, Table 4.1, Figure 4.2).

We found differences between prey availability and diet in all three species and in both habitats. For percentage of hard, intermediate, and soft-bodied prey, diet was significantly different from availability in all three species (all $P < 0.001$, Table 4.1, Figure 4.2). For morphospecies richness, diet differed significantly from availability only for *A. inornata* ($P < 0.01$, Table 4.2, Figure 4.1). For niche breadth diet differed significantly from availability only for *H. maculata* ($P < 0.01$, Table 4.2, Figure 4.1). We also found interaction effects between habitat (dark soils versus White Sands) and prey base (available versus diet) in two of the species. For *A. inornata*, available prey richness was significantly higher than lizard diet richness, but the magnitude of this difference was more extreme in dark soils ($P = 0.02$, Table 4.1, Figure 4.1). For *S. cowlesi*, lizards did not differ significantly in diet breadth between habitats, despite there being a much higher breadth available in White Sands ($P =$

0.01, Table 4.1, Figure 4.1). These particular contrasts are reflected in the pairwise comparisons below.

Pairwise comparisons for morphospecies richness, niche breadth, and percentage of soft, intermediate, and hard-bodied prey revealed similarities and differences between dark soils and White Sands habitats in both availability and diet. Available breadth of arthropod orders and percentage of hard-bodied prey were significantly higher at White Sands across all sites (all $P < 0.05$, Table 4.2, Figure 4.1, Figure 4.2). All White Sands lizard species included higher morphospecies richness in their diets than their dark soils counterparts (all $P < 0.05$, Table 4.2, Figure 4.1). However, niche breadth was only significantly higher in White Sands *H. maculata* ($P = 0.005$, Table 4.2, Figure 4.1), and percentage of hard-bodied prey was significantly higher in White Sands *A. inornata* and *S. cowlesi* (both $P < 0.05$, Table 4.2, Figure 4.2) when compared to their dark soils counterparts. Finally, available morphospecies richness was only significantly higher at White Sands at *H. maculata* sites ($P = 0.01$, Table 4.2, Figure 4.1).

Performance and Morphology

Pairwise comparisons between dark soils and White Sands lizards diet demonstrated that while average prey hardness was higher only in White Sands *A. inornata* ($P < 0.01$, Table 4.3, Figure 4.3), bite force was higher in both White Sands *A. inornata* and *H. maculata* ($P < 0.05$, Table 4.3, Figure 4.3). Furthermore, both *A. inornata* and *H. maculata* had larger absolute head size ($P < 0.0001$, Table 4.3, Figure 4.3) and larger body size ($P < 0.001$, Table 4.3, Figure 4.3). Only in *H. maculata* was head size still larger in White Sands lizards after adjusting for body size ($P = 0.004$, Table 4.3, Figure 4.3). Although *S. cowlesi* demonstrated a

similar trend with White Sands lizards having stronger bite, larger head, and larger body size, they were not significantly different from their dark soils counterparts in these aspects (all $P > 0.05$, Table 4.3, Figure 4.3). Dark soils *S. cowlesi* did, however, show significantly more variation in these performance and morphology characteristics than their White Sands counterparts ($P < 0.01$, Table 4.3, Figure 4.3) but this was not the case for the other two species.

Discussion

When colonizing a new habitat, a population's trophic ecomorphology is influenced by several non-mutually exclusive factors. First, a new resource environment affects which prey are available for colonists to consume. For example, changes in arthropod species richness or diversity may affect trophic ecomorphology. Second, changes in the competitive environment may affect what prey the colonists actually consume. For example the presence or absence of other competing species affects whether colonists experience competitive exclusion or ecological release. Third, species traits - and the potential for evolution of these traits - also affect resource use in a new environment. For example, certain trait values (e.g., stronger bite force and larger head size) may facilitate the use of particular resources or be subject to natural selection. By comparing recent colonists of White Sands with their dark soils conspecifics, we have shown how the trophic ecomorphology of three different species changes in a shared ecological setting.

We found important differences in prey availability between White Sands and dark soils habitats. Specifically, White Sands had higher arthropod species richness, increased breadth of arthropod orders, and a higher percentage of hard-bodied prey. Lower richness and

diversity of arthropods in dark soils habitats is surprising given that there are more species of vertebrates (Des Roches *et al.* 2011) and plants (Emerson 1935) than in White Sands. Our sampling of prey availability was, however, limited to a short time interval and only terrestrial arthropods that fell into traps, so therefore likely does not encompass the breadth of diversity in either habitat. Our limited sampling considered, our results do reflect the influence of a high proportion of hard-bodied hymenopterans (i.e., ants), which we collected at the dark soils sites in large numbers.

All three species showed a similar dietary response to higher arthropod diversity in White Sands. In all cases, White Sands species included a significantly higher richness of arthropod morphospecies in their diet than did their dark soils conspecifics (Table 4.2, Figure 4.1). Although there was a similar trend for all lizard species to have a higher dietary niche breadth in White Sands, this difference was only significant in *H. maculata* (Table 4.2, Figure 4.1). Similarly, all White Sands species had a higher average proportion of hard-bodied arthropods in their diets, but this difference was only significant in *S. cowlesi* and *A. inornata*. The increase in hard-bodied prey in lizard diet at White Sands is consistent with our observation of a higher abundance of coleopterans in that habitat (Figure 4.2). The difference also may be due to the fact that two species of ants (which are hard-bodied) represented such a large portion of available prey in dark soils. Adult lizards, including those studied here, may avoid invasive and toxic fire ants and not include them in their diets (Robbins and Langkilde 2012, Robbins, Freidenfelds and Langkilde 2013).

Although similarities in resource use across the three species in White Sands indicated parallel response to a shared environment, important differences emerged in performance and morphological traits. Specifically, differences between White Sands and dark soils lizards in

the *average* hardness of prey in their diets, bite-force, and head and body size is consistent with patterns of directional selection (*A. inornata*), ecological release (*H. maculata*) or no change in selection (*S. cowlesi*). Below we discuss patterns observed in each species separately to highlight both shared and unique ecomorphological changes in the lizards of White Sands.

Directional change in diet and ecomorphological traits was most pronounced for *A. inornata*. The diet of White Sands *A. inornata* showed the largest increase in percentage of hard-bodied prey compared to their dark soils conspecifics (Table 4.2, Figure 4.2). Furthermore, only in this species was the average hardness of prey in the diet significantly higher in White Sands (Table 4.3, Figure 4.3). The observation that White Sands *A. inornata* included harder prey in their diet was paralleled by an increase in bite force, head size, and body size. Close ties between diet, performance, and morphology are common in lizards as a stronger bite force is often required for consumption of harder bodied and larger prey (Verwaijen *et al.* 2002, Herrel and O'Reilly 2006, Kaliontzopoulou *et al.* 2012). Not surprisingly, head size is closely related to bite force, and lizards with larger heads generally have a stronger bite force and feed on harder prey (Verwaijen *et al.* 2002, Herrel and O'Reilly 2006, Kaliontzopoulou *et al.* 2012).

Differences in head size between dark soils and White Sands lizards are almost entirely due to differences in body size (i.e. when adjusted for body size, head size is no longer significantly different between dark soils and White Sands lizards, Table 4.3). Thus, the consumption of harder prey for White Sands *A. inornata* could be due to increased body size and/or increased availability of harder prey. Several other species of *Aspidoscelis* (e.g. *A. exsanguis*, *A. tessellata*, *A. tigris*, and *A. uniparens*) live sympatrically with *A. inornata* in dark

soils habitats and reach a larger maximum size than *A. inornata*. These congeneric species compete with - and predate on - *A. inornata* outside of White Sands (see Degenhardt, Painter and Price 2005). Thus, the directional shift towards larger body and head size and harder prey in the diet of White Sands lizards may be a consequence of relaxed competition and predation pressures from larger individuals of other *Aspidoscelis* species (Dayan and Simberloff 1998).

Of the three species, *H. maculata* demonstrated the most likely case of ecological release in trophic ecomorphology. Like *A. inornata*, *H. maculata* exhibited directional change in ecomorphological traits and had stronger bite force and larger head and body size in White Sands than in dark soils. Mean prey hardness, however, was not higher in White Sands *H. maculata*, but was significantly more variable. Increased variability in this functional aspect of diet is consistent with increase in dietary niche breadth, which was also significantly different between dark soils and White Sands *H. maculata*. Increases in both niche breadth and in the variability of mean prey hardness in the diet in White Sands *H. maculata* are consistent with models of ecological release (see Van Valen 1965, Lister 1976a, Lister 1976b, Losos and de Queiroz 1997, Yoder *et al.* 2010). Trophic niche expansion could suggest relaxation in selection on White Sands *H. maculata* as a result of absence of competitors (Losos and de Queiroz 1997), predators (Losos and Mahler 2010), and/or increased availability of resources (Roughgarden 1972). Because the White Sands population of *H. maculata* is dense compared to dark soils populations (Des Roches *et al.* 2011), there may have also been a shift towards increased intraspecific competition with individuals diverging in their resource use to minimize overlap with conspecifics, which is also a key component of ecological release (Van Valen 1965).

In addition to changes in diet, White Sands, *H. maculata* showed a directional change in ecomorphological traits (i.e., stronger bite force, larger head and body size). Whether lizards have shifted to consume harder prey on average, like White Sands *A. inornata*, or expanded their resource use to include harder prey in addition to soft prey, like White Sands *H. maculata*, stronger bite force may still be necessary (Schoener 1969, Wilson 1975). Although increased variation in performance and morphology might be expected with ecological release, prior studies have demonstrated that ecomorphological variation often does not accompany expansion of resource use (Bolnick *et al.* 2007). Interestingly, *H. maculata* is the only species of the three to have a larger head size in White Sands, even when adjusted for larger body size (Table 4.3). Considering our finding that these lizards do not consume harder prey on average, head size may have shifted due to genetic drift or may be under selection unrelated to trophic ecomorphology (e.g., due to intraspecific competition for mates via male-male aggression, Herrel *et al.* 1999).

Finally, *S. cowlesi* showed little change in diet between White Sands and dark soils populations, and also did not differ significantly in mean bite force, head size, or body size. Although changes in diet and ecomorphology between dark soils and White Sands *S. cowlesi* were usually in the same direction as the other two species, they were largely non-significant (Table 4.3, Figure 4.3). Niche breadth did not increase significantly, nor did proportion of hard bodied prey or average prey hardness in White Sands compared to dark soil lizard diet. Either selection on aspects of trophic ecomorphology did not lead to significant differences between dark soils and White Sands *S. cowlesi* or we did not detect these differences. Prior research has demonstrated that White Sands *S. cowlesi* has diverged from their dark soils conspecifics in terms of intraspecific communication (Robertson and Rosenblum 2009, 2010),

anti-predator behaviour (Robertson *et al.* 2011), escape behavior (Des Roches *et al.* 2014), and microhabitat use (Des Roches *et al.* 2011). However, dark soils and White Sands *S. cowlesi* are not significantly diverged in traits related to ecomorphology (Rosenblum and Harmon 2011, Des Roches *et al.* 2014), perhaps because it is a generalist insectivore (Stebbins 1985) and trophic specialization is not selected for. In general, evidence from *S. cowlesi* demonstrates that changes in resource availability following colonization of a new habitat may not necessarily drive ecomorphological change.

White Sands is a rare case of a system that presents a snapshot of the early stages of community assembly in a novel ecosystem. Some similarities in the diet across the three species are predictable as they reflect a shared environment. Differences, however, may reflect the constraints of ecological or evolutionary history. Whether selection on ecomorphology changes direction, decreases in magnitude, or does not change at all after colonization, may depend on resource availability, presence of antagonists such as predators and competitors, genetic, and morphological constraints. The distant evolutionary relatedness of these three lizard species (Wiens *et al.* 2010, Rosenblum and Harmon 2011) suggests that differences accumulated over long evolutionary periods can have important impacts on the ecological dynamics of newly assembled ecological communities.

Tables

response	covariate	<i>A. inornata</i>			<i>H. maculata</i>			<i>S. cowlesi</i>		
		R ²	F	P	R ²	F	P	R ²	F	P
richness	habitat	0.34	14.1	< 0.001	0.15	10.5	= 0.002	0.11	6.7	= 0.01
	use		9.4	= 0.003		0.04	= 0.8		1.2	= 0.3
	habitat*use		5.3	= 0.02		0.08	= 0.7		0.8	= 0.4
niche breadth	habitat	0.19	7.0	= 0.008	0.31	20.3	< 0.001	0.15	6.6	= 0.01
	use		1.6	= 0.08		10.7	< 0.01*		1.8	= 0.5
	habitat*use		2.5	= 0.05		0.1	= 0.7		6.5	= 0.01
% hard bodied	habitat	NA	4.2	= 0.01	NA	3.3	= 0.03	NA	2.5	= 0.07
	use		9.5	< 0.001		12.8	< 0.001		7.9	< 0.001
	habitat*use		1.9	= 0.1		1.9	= 0.1		1.7	= 0.2

Table 4.1. Results of a 2-way ANOVA (first two rows) and MANOVA (last row) on the effect of use (availability versus diet) and habitat (dark soils versus White Sands) and the interaction of these two variables on the richness of morphospecies, niche breadth, and the proportion of hard-bodied arthropods for all three species.

response	pairwise comparison	<i>A. inornata</i>		<i>H. maculata</i>		<i>S. cowlesi</i>	
		t	P	t	P	t	P
richness	availability	-0.5	= 0.6	-2.8	= 0.01	-1.2	= 0.3
	diet	-4.4	< 0.001	-2.5	= 0.02	-2.5	= 0.02
niche breadth	availability	-3.2	= 0.004	-5.8	< 0.001	-6.0	< 0.001
	diet	-1.1	= 0.3	-3.1	= 0.005	-0.7	= 0.5
% hard bodied	availability	2.6	= 0.02	3.5	= 0.003	5.6	< 0.001
	diet	-2.7	= 0.01	-1.7	= 0.1	-2.4	= 0.03

Table 4.2. Results of pairwise differences in means (Welch's t-test) between habitats (dark soils versus White Sands) for both availability and diet in morphospecies richness, niche breadth, and percentage of hard bodied prey for all three species.

response	<i>A. inornata</i>		Levene's		<i>H. maculata</i>		Levene's		<i>S. cowlesi</i>		Levene's	
	Welch's t	P	F	P	Welch's t	P	F	P	Welch's t	P	F	P
diet hardness	3.1	= 0.004	0.1	= 0.7	-0.2	= 0.8	5.6	= 0.03	1.7	= 0.1	1.7	= 0.2
bite force	2.5	= 0.02	0.2	= 0.6	-5.4	< 0.001	0.2	= 0.6	-1.1	= 0.3	9.3	= 0.005
head size	-4.6	< 0.001	0.1	= 0.7	-5.2	< 0.001	1.4	= 0.2	-1.1	= 0.3	15.4	< 0.001
adj. head size	-2.5	= 0.4	0.0	= 1.0	-3.0	= 0.004	0.8	= 0.4	-1.8	= 0.09	0.4	= 0.5
SVL	-4.6	< 0.001	0.8	= 0.4	-3.5	= 0.001	0.9	= 0.3	-0.1	= 0.9	10.7	= 0.002

Table 4.3. Results of pairwise differences in means (Welch's t-test) and variance (Levene's test) between habitats (dark soils versus White Sands) in various aspects of diet (diet hardness in N), performance (bite force in N), and morphology (head size and body size in mm) for all three species.

Figures

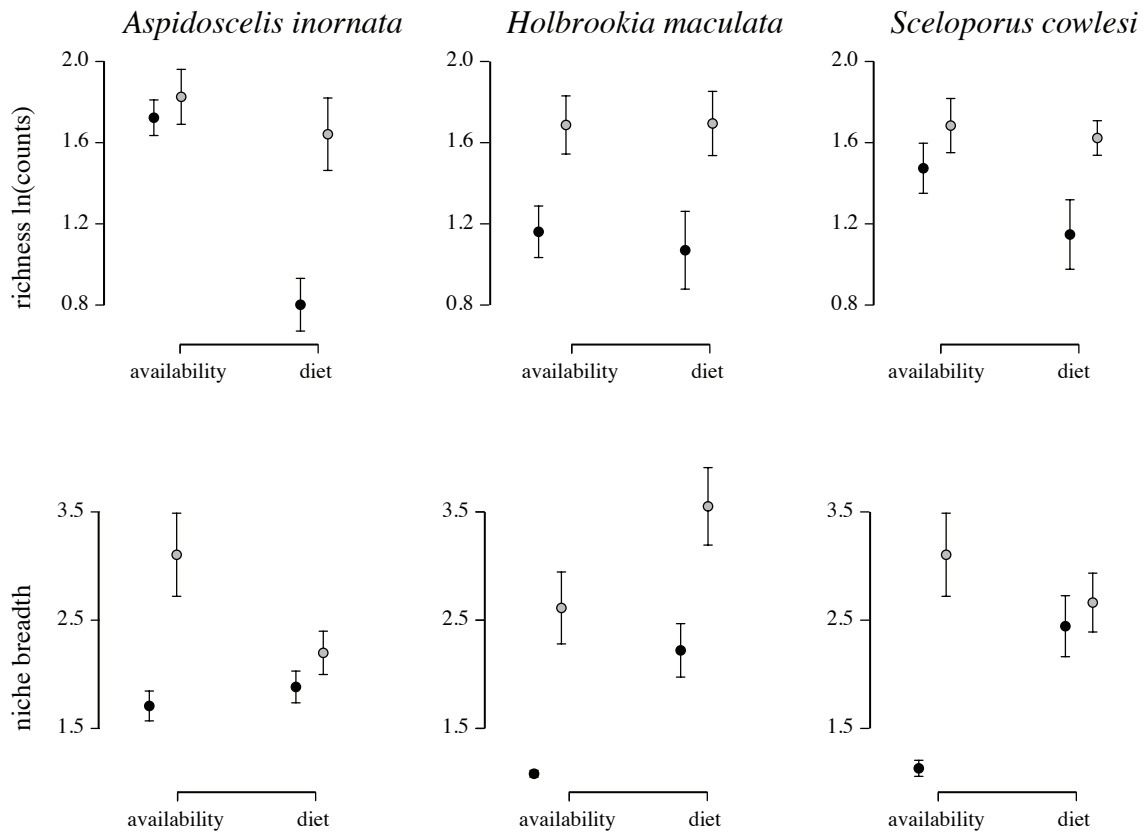


Figure 4.1. Prey availability versus prey use (diet) in the three White Sands lizard species for two metrics of arthropod diversity. The top row shows arthropod richness (number of “morphospecies”) and the bottom row (shows arthropod diversity (1/Simpson’s diversity index)). Dark and light shapes represent mean values from dark soils and White Sands habitats, respectively. Error bars represent standard error of the mean. Results of statistical analysis are displayed in Table 4.1.

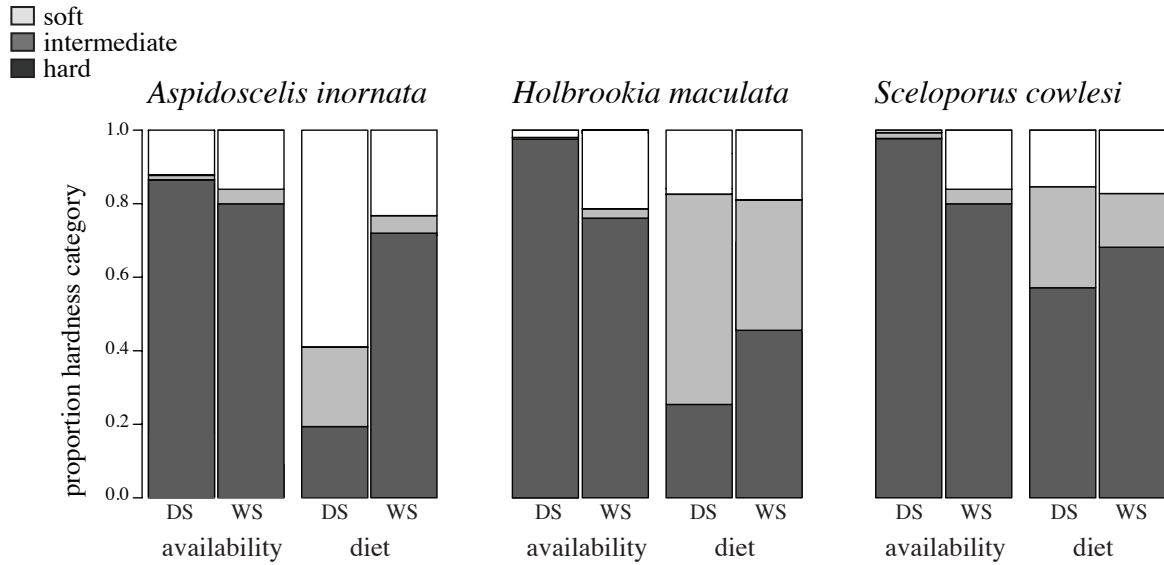


Figure 4.2. Mean percentage of hard, intermediate, and soft prey availability and diet in the three White Sands lizard species. Dark grey, light grey, and white shading correspond to hard, intermediate, and soft-bodied prey, respectively. Results of statistical analysis are displayed in Table 4.2.

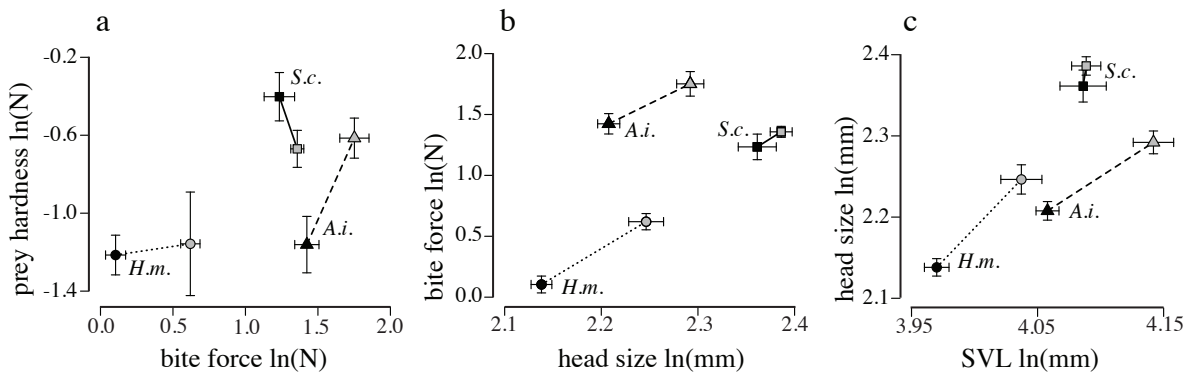


Figure 4.3. Relationships between prey hardness in the diet versus bite force (left), bite force versus head size (centre), and head size versus body size (right) in *Aspidoscelis inornata* (triangles, dashed line), *Holbrookia maculata* (circles, dotted line), and *Sceloporus cowlesi* (squares, solid line). Dark and light shapes represent mean values from dark soils and White Sands habitats, respectively. Error bars represent standard error of the mean. Results of statistical analysis are displayed in Table 4.3.

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Illustration V: Greater roadrunner (*Geococcyx californianus*) and lesser earless lizards (*Holbrookia maculata*) among alkali sacaton grass (*Sporobolus airoides*) at the White Sands ecotone.

CHAPTER V**ECOLOGICAL AND EVOLUTIONARY DYNAMICS OF TWO LIZARD SPECIES
ON THE WHITE SANDS ECOTONE**

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To be submitted as two manuscripts pending another field season in 2014

Abstract

Both ecological and evolutionary characteristics of populations may change drastically following colonization of a novel environment. In particular, population size, sex ratios, recruitment, movement, and immigration from neighbouring populations may vary in conjunction with the changing dynamics of natural selection. Mark-recapture studies (in which researchers mark a subset of a population and then revisit it to monitor changes in demography, survival, and selection) provide an opportunity to understand population dynamics from both an ecological and evolutionary perspective. We conducted a mark-recapture study focused on the ecological and evolutionary dynamics of two species of lizards (*Holbrookia maculata* and *Sceloporus cowlesi*) inhabiting the ecotone between the gypsum dune field of White Sands and the surrounding Chihuahuan desert in New Mexico. White Sands is a young and novel ecosystem and the focal species have colonized and adapted to its gypsum sand dunes in the last few thousand years. We monitored demographic parameters,

trait values, and differential survival of individuals of both species over three years. Specifically, we recorded changes in population density, sex ratios, age class ratios, and movement. We also measured trait values including body size, shape, and condition, and determined whether they were associated with the probability of recapture. In general, the species differed in population density, movement, and traits associated with recapture. However, they were similar in sex and age class ratios, and in the patterns of sex-biased movement over time. Documenting seasonal and yearly changes in two species of lizards at White Sands provides insight on local population dynamics and can inform more complex models of trait-mediated survival.

Introduction

Understanding population demography by monitoring natural populations is important in both ecology and evolution and indeed, provides a link between the two fields. Population size, sex ratios, recruitment, movement, and migration rates are shaped by natural selection (Pradel 1996) and in turn can influence evolutionary dynamics (Lande 1976) especially after colonization of a new ecosystem. Mark-recapture studies provide an opportunity to study population demography and integrate ecological and evolutionary processes. Although for many years researchers used mark-recapture to measure aspects of population ecology (e.g. Petersen 1986, Lincoln 1930, Robson and Regier 1964, Burnham and Overton 1979, Ballinger *et al.* 1981), more recently they have implemented mark-recapture to estimate survival (e.g. Buckland 1982, Lebreton *et al.* 1992) and natural selection (Brodie 1992, Gimenez *et al.* 2006, Gimenez *et al.* 2009, Cam 2009) in the wild.

Mark-recapture was first implemented in the late 1890s (Petersen 1896) and described in the early 1930s (Lincoln 1930) as a technique to measure population demographics, especially abundance, in nature. Since then, countless studies have used mark-recapture methods to estimate changes in population size of animals (Robson and Regier 1964, Burnham and Overton 1979, Ballinger *et al.* 1981) and even plants (see Alexander *et al.* 1997). Most of these studies implement the straightforward Lincoln-Petersen formula, which requires an initial mark event and at least one subsequent capture event. Here, population size is estimated as the product of the number of individuals captured in the first event and the total number captured in the second event divided by the number of individuals captured in both events. (Petersen 1986, Lincoln 1930). The Lincoln-Petersen method does not require researchers to uniquely mark each individual and therefore only provides information on general population parameters including population size (Robson and Regier 1964, Burnham and Overton 1979, Ballinger *et al.* 1981), sex ratios (e.g. Bonnet *et al.* 2002, Nelson *et al.* 2002), age class ratios, and recruitment (e.g. Gennaro 1974, Pradel 1996). If researchers do keep track of individuals, it is possible for to estimate individual growth patterns (Gennaro 1974, Mouden *et al.* 1999, Casale *et al.* 2009), changes in body condition (Burton *et al.* 2009), overall movement (Gennaro 1972, Jones and Droge 1980, Beirinckx *et al.* 2006, Keogh *et al.* 2007), and how these might influence recapture and ultimately survivorship.

Although researchers considered the differential survival of individuals to be a nuisance parameter in early mark-recapture studies (Lebreton *et al.* 1992), it has recently become the focus of models to estimate natural selection (Brodie 1992, Gimenez *et al.* 2006, Gimenez *et al.* 2009, Cam 2009). Because mark-recapture models of natural selection aim to correlate survivorship with specific trait values, they require researchers to uniquely mark

individuals and measure their trait values (see Clobert 1995). The most straightforward of these methods model the probability of recapture against traits of interest (Borchers *et al.* 2002). More complex models (frequentist: see Cam 2009, or Bayesian: see Gimenez *et al.* 2006, Gimenez *et al.* 2009, Kéry and Schaub 2012) incorporate detection probability and movement of individuals, which can confound measures of selection. However, before we can include these demographic factors into mark-recapture models to survival, we must determine how they change over time depending on sex, age, and species of interest (e.g. Vinegar 1975, Rose 1981, Clobert *et al.* 1994, Wells 2000, Massot *et al.* 2003).

The lizards that inhabit White Sands, New Mexico provide an ideal system in which to study the changes in evolution and ecology that occur post-colonization. Characterized by 250 square miles of gypsum sand dunes, White Sands formed in the last two to seven thousand years (Langford 2003, Kocurek *et al.* 2007). As both a geologically young and novel ecosystem, White Sands provides a setting for studying the ecological and evolutionary changes of its colonist species. In White Sands, the three lizard colonists, the Lesser Earless Lizard (*Holbrookia maculata*), the Southwestern Fence Lizard (*Sceloporus cowlesi*), and the Little Striped Whiptail (*Aspidoscelis inornata*) exhibit blanched colouration (Rosenblum 2006, Rosenblum and Harmon 2011) as well as various other behavioural (Robertson *et al.* 2011, Des Roches *et al.* 2011), ecomorphological (Des Roches *et al.* 2014, Des Roches *et al.* in review), and morphological (Rosenblum and Harmon 2011, Des Roches *et al.* 2014, Des Roches *et al.* in review) differences from their closely related dark-coloured counterparts inhabiting the surrounding Chihuahuan Desert. Here we focused on the ecological and evolutionary dynamics of *H. maculata* and *S. cowlesi*. The limited home range sizes of *H. maculata* (Gennero 1974, Jones and Droge 1980, Hulse 1985) and *S. cowlesi* (Jones and

Droge 1980, Hager 2001) as well as their short life spans (Gennero 1974, Vinegar 1975), make these species ideal for mark-recapture.

We performed our study in two sites located along the sharp ecotone between White Sands and the surrounding dark-soil desert for both ecological and evolutionary reasons. First, ecotones are transitional zones that often share biotic and abiotic characteristics of two neighboring ecosystems (see Wiens 1992). For example, although the White Sands ecotone has gypsum substrate, it is more densely vegetated than the heart of the dune field (*pers. obs.*). Second, abrupt ecotones may represent distinctive or intermediate selective environments on a microgeographic scale (Richardson *et al.* 2014). Indeed, the ecotone populations of the three White Sands species show variable genetic structure which partially depends on the level of gene flow from dark-soil populations (Rosenblum 2006). Furthermore, the presence of other reptile and bird species that are common on the ecotone but not in the heart of White Sands (Des Roches, *unpublished data*) may increase local selection due to interspecific competition and predation.

To understand the ecological and evolutionary dynamics of *H. maculata* and *S. cowlesi* on the White Sands ecotone, we monitored demographic parameters, trait values, and survival of marked individuals over three years. Specifically, we recorded population density, changes in sex ratios, age class ratios, and movement. We also measured traits including body size, shape, and condition, and determined whether they were associated with the probability of recapture. By documenting seasonal and yearly changes in ecological characteristics of these two species, we gain an understanding of the population dynamics at the White Sands ecotone and can inform more complex models of trait-mediated survival.

Materials and Methods

Sampling and study sites

We performed mark-recapture on the two lizard species in two sites on the White Sands – Chihuahuan desert ecotone (Figure 5.1). Both sites have white gypsum substrate, but are typically more vegetated and contain a higher density of avian and terrestrial predators than the heart of the White Sands dune field (Des Roches, *unpublished data*). Additionally, both are located on the southeast of White Sands, which is the leading edge of dune movement and exhibits a sharp transition between white gypsum and dark soil substrate. Within each site, we primarily captured lizards in interdune areas (vegetated flat-lands enclosed by three to ten meter-high dunes). Site 1 is composed of four main interdunes and extended approximately 200 meters west into White Sands from its boundary that runs northeast – southwest (total area ~ 10.7 ha, Figure 5.1: bottom-left). Site 2 is substantially larger and composed of six main interdunes and extends approximately 800 meters southwest into White Sands from its boundary running northwest – southeast (total area ~ 45.6 ha, Figure 5.1: bottom right).

We captured adult and juvenile male and female individuals of both species by noose or by hand. We performed all sampling between 07:00 and 15:00, with the majority occurring between 08:30 and 13:00. We returned all lizards during daylight hours after measuring, identifying, or marking them. We sampled in the early (May-June) and late (July-August) activity season to correspond with lizard emergence from, and preparation for, hibernation. For *H. maculata* we had four capture events over three years and for *S. cowlesi* we had three capture events over two years (Table 5.1). Our sampling team consisted of two to four people, and we recorded person-hours spent in each interdune to keep track of sampling effort (see

Supplementary Material: Figure S5.1). To monitor movement of individuals between capture events, we recorded GPS coordinates (using a Garmin GPSMAP 60x and 62 stc) at the point we first sighted each lizard.

Phenotype quantification

We measured morphological characteristics for each lizard on the same day as capture. Because there is substantial variation in phenotype within individuals over time (due to physiological and ontogenetic growth and colour change), we measured traits for all lizards at both the first, and subsequent captures. We recorded body weight (in grams) using a Pesola spring scale. We measured three metrics of head shape (in millimeters) using handheld calipers: head depth (highest part of the skull, midway above eye to below jaw), jaw length (tip of snout to behind lower jaw), and head width (at widest point). We also measured pelvic width (in millimeters) using handheld calipers. We measured all other morphological traits (snout-vent-length, tail length, tail break, interlimb length, fore- and hindlimb length (in millimeters) using ImageJ software (see Meyers et al. 2006) on ventral scans of the lizards. We calculated condition as the residuals of the linear relationship between natural-log transformed weight and SVL. We adjusted all measurements for body size by taking the residuals of the linear relationship between the natural-transformed trait value and SVL. We quantified colour brightness using spectrophotometric readings of the dorsal spine of each individual using a StellarNet EPP2000Cs spectrometer (StellarNet, Tampa, Florida) and calculating the area under the spectral curve of transmission versus wavelength (Endler 1990). Because there was increasing levels of noise and variation in frequency of wavelengths under 500 nm, we used a subset of wavelengths (500 – 700 nm) for this analysis. Finally, we

recorded sex and age class of all individuals. We considered *H. maculata* individuals under 45 mm to be juvenile (Tinkle and Ballinger 1972, Gennaro 1974) and *S. cowlesi* individuals under 50 mm to be juvenile (Vinegar 1975).

Marking, identification, and population size

We uniquely marked each individual of both species with manual injection visual implant elastomer (Northwestern Marine Technology), which has been used effectively to identify reptiles in other mark-recapture studies (Penney et al. 2001). We used up to six different fluorescent colours in four locations on the ventral surface of the lizards such that we could uniquely mark over 1000 individuals of each species. To further help individually identify lizards, we used a combination of photographs and ventral scans when elastomer marks were faint or missing. We used total capture and recapture estimates to calculate population size corrected for small sample sizes (N) and standard error ($S.E.$), respectively (Chapman 1951):

$$N = \frac{(M + 1)(C + 1)}{R + 1} - 1$$

$$S.E. = \sqrt{\frac{(M + 1)(C + 1)(M - R)(C - R)}{(R + 1)(R + 1)(R + 2)}}$$

Where M = number of individuals captured and marked on the first occasion, C = number of individuals captured on the second occasion, and R = number of individuals that were captured on both visits.

Statistical analysis

To statistically evaluate demographic differences between recapture rates, age class, and sex ratios within and between the two species, we used Chi-squared goodness-of-fit tests. For age class and sex ratios, we determined whether the ratio of juveniles to adults and females to males differed significantly across sampling events. For sex ratio specifically, we also evaluated whether the number of females to males significantly departed from a 50:50 ratio. We determined movement by calculating the Euclidean distance between successive GPS coordinates and included individual as a random effect. We then used 2-way mixed-effects ANOVAs to test the effects of sex and species on movement across sampling events. We used Welch's two-sample t-tests to examine the potential differences in growth (changes in SVL) and body condition between age classes and the two sexes. To examine the potential interactive effects between sex or age class and sample period (year or season) on growth and condition, we included these as covariates in 2-way ANOVAS.

To determine whether phenotype was associated with recapture, we tested the relationship between phenotypic trait values and recapture histories for all individuals. For each individual, we used the trait values at the first point of capture and created a presence/absence matrix representing its recapture history. Here, "1" was used to denote a capture, and "0" a failure to capture. The first "1," therefore, represented the initial capture of an individual. To create the matrix, we first noted all "false absences" as instances where an individual was present, absent, then present again (i.e. we failed to detect a present individual), and changed these to presences. Almost half of all the individuals that were captured three or more times contained "false absences." However, most of these occurred during the July-August sampling periods in 2011 (for *H. maculata*) and 2012 (for *S. cowlesi*), which were

survey occasions with considerably lower sampling effort and fewer overall captures (see Supplementary Figure S5.1). As such, this frequency of “false absences” may not reflect our overall sampling efficiency. To estimate recapture proportion, we took the summed number of presences as a fraction of the total number of *potential* presences following the initial capture of each individual. For example, an individual with a recapture history of “1, 0, 1, 1” would have a recapture proportion of $3/3 = 100\%$, an individual with a history of “0, 0, 1, 0” would have $0/1 = 0\%$, and an individual with a history of “0, 1, 1, 0” would have $1/2 = 50\%$. Because the resultant vector of recapture probabilities was not normally distributed, we used a non-parametric Spearman’s Rank Test to evaluate its association with trait values of interest (see Brodie 1992 for a similar analysis).

Finally, we tested the effect of changes in body condition over the activity season on subsequent recapture in following years. In this case, we calculated change in condition as the difference between condition in the beginning versus the end of the activity season (May – August 2011 for *H. maculata*, May – August 2012 for *S. cowlesi*). To simplify analysis, we denoted recapture as either “0” (never captured again) or “1” (captured at least once more) for the following years (2012 and 2013 for *H. maculata*, 2013 only for *S. cowlesi*). We then used general linear models with the binomial link function to test the effect of movement and changes in condition on recapture. We performed all analyses in R (R Development Core Team 2014).

Results

Population demographics

Capture and recapture proportions differed considerably between species. In Site 1, we captured a total of 117 different individuals across four sampling periods over three years and 161 *S. cowlesi* individuals across three sampling periods over two years. In Site 2, we captured a total of 175 *H. maculata* individuals across three sampling periods over two years and 311 *S. cowlesi* individuals across three sampling periods over two years. Although we captured more total *S. cowlesi* than *H. maculata*, the overall percentage of recaptured *H. maculata* at 41.6% was significantly higher and almost double that of *S. cowlesi* at 21.9% (Chi-squared test: $\chi^2_1 = 66.0$, $P \ll 0.0001$).

Disparity between the species in total captures and in recaptures led to significant differences in population size and population density estimates. Because we had shorter sampling periods at the end of the activity season (July-August), we only used the beginning of the activity season (May-June) sampling periods to calculate population size estimates. In general, *S. cowlesi* had a higher population density than *H. maculata* at both sites (Table 5.2). Furthermore, our recapture results indicate that both species had considerably denser populations at Site 1 compared to Site 2 (Table 5.2).

Sex ratio and age class distribution of both species varied with sampling period. Sex ratio varied significantly across all sampling periods for *H. maculata* ($\chi^2_3 = 10.8$, $P = 0.01$), but not *S. cowlesi* ($\chi^2_2 = 2.2$, $P > 0.05$). For sampling periods at the beginning of the activity season the sex ratio was not significantly different from 50:50 for either species ($P > 0.05$). However, sampling periods at the end of the activity season (2011 for *H. maculata*, 2012 for *S. cowlesi*) demonstrated a sex ratio with more females than males for both species (*H.*

maculata: $\chi^2_1 = 4.2$, $P = 0.04$; *S. cowlesi*: $\chi^2_1 = 6.9$, $P = 0.009$, Table 5.2, Figure 5.2). The ratio of juveniles to adults differed significantly across field season for both *H. maculata* ($\chi^2_3 = 37.5$, $P \ll 0.0001$) and *S. cowlesi* ($\chi^2_2 = 10.9$, $P = 0.004$; Table 5.2, Figure 5.2). For both species, the proportion of juveniles was typically lower at the end of the activity season than at the beginning. In *H. maculata*, proportion of juveniles was highest at the beginning of the activity season in 2011 and 2013 as opposed to *S. cowlesi*, where it was highest in 2012.

Movement

Mean yearly movement differed widely between species, and to a lesser extent between the sexes. When we tested the effects of species and sex on movement, we found that *H. maculata* moved significantly further from their point at first capture than did *S. cowlesi* (3-way ANOVA with individual as random effect: species effect $F_{1,9} = 20.8$, $P = 0.001$, Figures 5.3 – 5.4). However, neither sex nor the interaction between sex and species showed significant differences in this model (both $P > 0.05$). When we tested each species separately over the total sampling period (*H. maculata*: 2 years, *S. cowlesi*: 1 year), average male movement (*H. maculata*: mean \pm S.E.: 47.3 \pm 0.2 m, *S. cowlesi*: 15.0 \pm 0.2 m) was higher than average female movement (*H. maculata*: 43.4 \pm 0.3 m, *S. cowlesi*: 12.1 \pm 0.3 m). This comparison was significant in *H. maculata* ($F_{1,119} = 4.67$, $P = 0.03$), however, only marginally so in *S. cowlesi* ($F_{1,80} = 3.57$, $P = 0.06$).

Growth and condition

Yearly growth rate in snout-vent-length was considerably higher for juveniles than for adults in both species. For *H. maculata*, linear juvenile growth rate was significantly higher

than adult growth rate (Welch's t-test: $t_{19,7} = -5.12$, $P < 0.0001$): recaptured individuals that were juveniles upon first capture grew an average of 6.6 ± 3.7 mm, and 64 recaptured adults grew an average of 1.9 ± 1.9 mm over one year. Furthermore, overall yearly growth of both juveniles and adults was significantly higher from 2011 to 2012 compared 2012 to 2013 ($t = 2.8_{24,9}$, $P = 0.02$). For *S. cowlesi*, juvenile growth rate was also significantly higher than adult growth rate ($t = -7.7_{1,9}$, $P = 0.02$): recaptured individuals that were juveniles upon first capture grew an average of 10.0 ± 1.1 mm, and 28 recaptured adults grew an average of 3.2 ± 2.5 mm over one year. We could not calculate a difference in growth by year for *S. cowlesi* as we only sampled this species over a single year.

Body condition varied widely in males and females of both species across years. For *H. maculata* female condition was higher than male condition in 2011, but by 2013 the sexes were of similar condition (Figure 5.5: top-right). Sex of *H. maculata*, but not sampling year, affected condition and there was a marginal interaction effect between the two (2-way ANOVA: Sex: $F_{1,351} = 35.1$, $P < 0.0001$; Year: $F_{1,351} = 0.022$, $P > 0.05$; Sex*Year: $F_{1,351} = 3.5$, $P = 0.06$). Male *S. cowlesi* condition was higher in 2012, but dropped below female condition by 2013. Similarly, *S. cowlesi* sex, but not year had a significant effect on condition (Sex: $F_{1,263} = 9.3$, $P = 0.002$; Year: $F_{1,263} = 0.01$, $P > 0.05$; Sex*Year: $F_{1,263} = 1.6$, $P > 0.05$; Figure 5.5: bottom-right).

Both species showed similar trajectories for male and female condition across the activity season, with female condition decreasing, and male condition increasing (Figure 5.5: left). At the beginning of the activity season, female *H. maculata* condition was higher than male *H. maculata* condition. However, this was opposite in *S. cowlesi* where male condition was higher than female condition. For both species, sex had a small effect on condition, and

sampling time (beginning or end of activity season) had no effect (*H. maculata*: Sex: $F_{1,241} = 3.8$, $P = 0.06$, Month: $F_{1,241} = 0.11$, $P > 0.05$; *S. cowlesi*: Sex: $F_{1,339} = 5.4$, $P = 0.02$, Month: $F_{1,339} = 0.0002$, $P = 0.99$). There was a significant interaction between sex and month for both species, with males increasing, and females decreasing in condition over the activity season (*H. maculata*: Sex*Month: $F_{1,241} = 20.0$, $P < 0.0001$; *S. cowlesi*: Sex*Month: $F_{1,339} = 11.7$, $P = 0.0007$).

Recapture differences

For each species, three of 11 continuous phenotypic traits were significantly correlated with recapture proportion. There was a positive association between recapture proportion and SVL in *S. cowlesi* (Table 5.3), and condition in *H. maculata* ($Z = 1.89$, $P = 0.050$). In *H. maculata*, lizards with both wider and deeper heads (adjusted for SVL) had a higher recapture proportion than those with narrower, shallower heads (Table 5.3). In *S. cowlesi*, longest rear toe (adjusted for SVL) was negatively associated with recapture and wider relative pelvic width was positively associated with recapture (Table 5.3). We did not find evidence for an association between any other traits with recapture proportion.

For *H. maculata* but not *S. cowlesi*, there was an association between change in condition over the activity season and recapture in future years. Specifically, in *H. maculata*, increase in condition over the activity season was positively correlated with recapture (General linear model with binomial link function: $\chi^2 = 4.56$, $P = 0.033$, Figure 5.6). However, this was not the case for *S. cowlesi* ($\chi^2 = 0.26$, $P > 0.05$, Figure 5.6).

Discussion

We evaluated changes in population ecology and dynamics of natural selection in the populations of *H. maculata* and *S. cowlesi* on the White Sands ecotone using mark-recapture techniques. Specifically, we found that the two focal species showed similarities in some population demographics (e.g. sex ratio and movement of the two sexes), but had differences in population density, overall movement, and recapture proportions. Below, we discuss how both ecological and evolutionary factors may have contributed to our observed differences in population dynamics and recapture proportions between the species over time.

Population demographics

We found that *S. cowlesi* had a denser population at the White Sands ecotone than *H. maculata*. Specifically, high levels of *H. maculata* recapture and a lower total capture numbers yielded a density of 6.0 to 18.6 individuals per hectare (for Sites 2 and 1, respectively). Conversely, low levels of *S. cowlesi* recapture, and high total capture numbers yielded a density of 13.8 to 64.5 individuals per hectare (for Sites 2 and 1, respectively). Our estimates of ecotone population density are on the higher end of estimates for each species in the heart of White Sands for *H. maculata* (8.5 individuals/ha) and *S. cowlesi* (9.5 individuals/ha, Hager 2001). Differences in density estimates across study sites, especially for *S. cowlesi*, may indicate considerable variation in lizard population density across White Sands. Furthermore, large differences between the two sites suggest that density may even vary along the ecotone. In addition, lizard movement may have confounded our ability to accurately measure population size, and differences in estimates between the two species may

have had more to do with differences in distances moved between capture events (see discussion in Cam 2009).

Sex ratio was relatively consistent across years, but did change over the activity season. For both species, sex ratio did not deviate from 50:50 in any of the sampling occasions at the beginning of the activity season (May-June). However, at the end of the activity season, we captured significantly fewer males than females of both species (July-August). It is unlikely the bias towards capturing females indicates an actual temporary change in sex ratio in the ecotone populations since proportions went back to 50:50 the next year. Rather, differences in recapture proportions may reflect the changes in activity levels of males and females. For example, male *S. virgatus* are more active than females during the breeding season when they actively court and defend their territories, and this switches after breeding (Rose 1981). As a result, apparent changes in sex ratio may be a result of differences in detectability rather than survival.

Age class ratio varied across the years for both species. The percentage of juveniles in the sampled population ranged from 3 to 29% for *H. maculata* and 4 to 13% for *S. cowlesi*. Generally, the proportion of juveniles was low for sampling dates at the end of the activity season for both species, probably because many juveniles had grown enough over the summer to be classified as adults. Proportion of juveniles to adults was highest in 2011 for *H. maculata* and in 2012 for *S. cowlesi*. Interestingly, in 2012, proportion of *H. maculata* juveniles was considerably lower than for 2011 and 2013, which perhaps suggests either fewer hatchlings the previous year, or low juvenile overwinter survival.

Our results of age class ratios are different from others for *H. maculata* and *S. cowlesi* from dark soil sites. Studies of Eastern New Mexico (Gennaro 1974) and Nebraska (Jones and

Ballinger 1987) populations of *H. maculata* indicate a high turnover in the adult breeding population, which consists of mostly one-year-old lizards. Closely related subspecies of *S. cowlesi* show substantial variation in age-biased mortality across their range and thus also vary in the proportion of juveniles and recruitment (Vinegar 1975). We expect that the true proportion of juveniles is actually higher than our estimates as juveniles are not as conspicuous as their more active and territorial adult counterparts (see Pike *et al.* 2008).

Movement

In general, *H. maculata* moved significantly further than *S. cowlesi* over one year. At an average of 47.3 meters for males and 43.4 meters for females, *H. maculata* movement was over three times further than that of *S. cowlesi* (15.0 meters for males and 12.1 meters for females). Higher movement distance for *H. maculata* is consistent with studies showing their larger home range size (1823 – 3822 m²) compared to *S. undulatus*, which is closely related to *S. cowlesi* (717 – 852 m², Jones and Droge 1980). In both species, males moved further than females, but only significantly so in *H. maculata*. High male movement is not surprising, given that it is closely related to home range size, which is also larger (Gennaro 1972, Jones and Droge 1980) and may be a result of their effort to increase the probability of encountering females (Gennaro 1972). Additionally, male-biased movement is widespread in polygynous lizards (Clobert *et al.*, 1994: *Lacerta vivipara*; Doughty *et al.*, 1994: *Uta stansburiana*; Olsson *et al.*, 1996: *Lacerta agilis*, Massot *et al.* 2003: *Sceloporus occidentalis*) and is often attributed to competition for mates, inbreeding, and kin-competition (see Massot *et al.* 2003).

The combination of large movement distances and high recapture in *H. maculata* and low movement and low recapture in *S. cowlesi* is surprising. We might expect that recapture would be biased towards individuals with low movement that are less likely to move out of

the sampling area (see Cam 2009). One possible explanation is that we failed to recapture the furthest ranging *S. cowlesi* individuals. Broadening the distance surveyed around the original sampling area would increase our chances of detecting far-ranging individuals and allow us to better obtain an estimate of yearly movement.

Growth and condition

Not surprisingly, juvenile lizards of both species grew more than adults across sampling periods. The only other study of *H. maculata* growth rate provides an estimate of 0.26 – 0.10 mm/day for hatchling to one-year-old lizards and 0.02 mm/day for two to three-year-old lizards (Gennaro 1974), which translates to 7.3 mm/year for the slowest growing adult lizard. Our estimates of growth are considerably lower, with average rates of 1.9 to 6.6 mm/year for juveniles and adults, respectively. It is possible that the average growth rate of the ecotone populations of *H. maculata* is actually lower than what is normal for this species. However, discrepancies between our measurements and those of Gennaro (1974) may be a result of the former study recapturing and measuring at shorter intervals during the activity season when lizards are foraging and growing faster. Interestingly, average growth rate for all *H. maculata* individuals was significantly higher over our first sampling year (2011 – 2012) than our second (2012 – 2013). Higher average growth rate in the first year could be a result of a higher proportion of juveniles (29% versus only 5% in the following year), which grow faster. In addition, in the first year, the region was considerably warmer than average (third warmest period in 120 years) and in the second year it experienced drought conditions (sixth driest period in 120 years; National Climate Data Center: www.ncdc.noaa.gov). Low

precipitation results in less arthropod prey for lizards (Dunham 1978) and thus higher competition and reduced average growth rate (Dunham 1980).

We calculated juvenile growth rate for *S. cowlesi* to be 10.0 mm/year and adult growth rate to be 3.2 mm/year. Again, our estimates are lower than those provided by other studies for similar species at 0.30 to 0.12 mm/day (Parker 1994) and probably reflect their frequent sampling only over the activity season when lizards are foraging. Results from other studies show high variation in growth rate for *Sceloporus spp.* with temperature (Andrews *et al.* 2000), latitude (Sinervo and Adolph 1994, Angilletta 2001), altitude (Sinervo and Adolph 1994), and even resource levels (Dunham 1978). Subsequent sampling for of this population across years will allow us to determine whether growth rate changes by year.

Condition changed drastically across sampling occasions for both sexes and species, especially within the activity season. Paradoxically, in *H. maculata* female condition plummeted from 2012 to 2013, while male condition increased, a pattern which was opposite in *S. cowlesi*. Furthermore, male and female condition overlapped in 2013 for *H. maculata*, and in 2012 for *S. cowlesi*. Because condition is an index of body mass to length, either one or a combination of these factors contributes to its change over time. As previously discussed, gravidity of females can strongly influence their weight and might have explained the low condition of female *H. maculata* and high condition of female *S. cowlesi* in 2013. The contrasting interactions between sample year and sex for each species are particularly interesting because of the importance of condition as a measure of foraging success and even fitness (Jakob *et al.* 1996). Thus, these contrasting patterns may be due to differences in selection acting on the two species and sexes.

As expected, females of both species decreased in condition over the activity season (from May-June to July-August). Because females lay eggs during this time (mid-July for both species in White Sands, Dixon 1976), their weight drops considerably, thus decreasing their body condition. In *H. maculata* females, eggs can represent up to 20 percent of total body weight (Droge *et al.* 1982) and for populations of *S. cowlesi* (closely related to *S. cowlesi*) up to 30 percent (Ballinger *et al.* 1981). So while fat deposits may increase over the activity season in both males and females (Droge *et al.* 1982), increase in condition may only be detectible in males.

Recapture differences

Our results showed significant correlations between recapture proportion and certain phenotypic traits. However, because we used simple models of proportion of times recaptured against trait values and did not incorporate detection bias or movement, it is difficult to distinguish survivorship from these confounding factors. Regardless, correlations between recapture and traits are informative and may indicate changes in trait values on a local scale.

In *H. maculata*, individuals that had a higher recapture proportion also had higher condition. We expect a positive correlation between recapture and condition because condition may be a good indicator of overall fitness (Jakob *et al.* 1996, but see Husak 2006) and thus affect survivorship from year to year. In particular, high body mass as a function of SVL (i.e. high condition) suggests foraging success and a competitive advantage necessary for survival and reproduction (Svensson *et al.* 2001). Condition is of crucial importance for overwinter survival (Husak 2006) and lizards tend to gain weight relative to their length especially at the end of the activity season (Haenel and John-Alder 2002).

We also found a positive association between recaptured proportion and size-adjusted head width and depth of *H. maculata*. Because differences in movement or detection due to head size are unlikely, this correlation probably results from differential survivorship. Not surprisingly, White Sands *H. maculata* have significantly broader heads than their dark-soils counterparts, which may indicate the action of directional selection in the past (Rosenblum and Harmon 2011, Des Roches *et al.* in review). Here, our results demonstrate that directional selection may still be acting on head size in this species. Head size is closely linked to bite force in *H. maculata* (Des Roches *et al.* in review). As such, one possible adaptive explanation for increase in head width and depth is that it is a response to an average increase in the hardness of prey consumed at White Sands (Des Roches *et al.* in review). Another explanation may be that larger heads and stronger bite force provide an advantage for males engaging in interference competition (Herrel *et al.* 1999) in the more densely populated White Sands habitat.

In *S. cowlesi*, correlations between recapture proportion and trait values may have been a result of either differences in movement or survivorship. A positive association between SVL and recapture may suggest either lower movement or higher survival of large, adult individuals. In male *Sceloporus* species in particular, there is significant dispersal of juvenile males (Massot *et al.* 2003). Juvenile dispersal may be affected by density of adults in other lizard species (Léna *et al.* 1998). Unfortunately, our low recapture rate of juveniles prevents us from examining the relationship between age class and movement ability specifically. Selection for large body size (e.g especially at high densities, Calsbeek and Smith 2007), or stronger selection on juveniles (e.g. Mantueffel and Eiblmaier 2010) may also explain the positive correlation between SVL and recapture. However, recent studies suggest

that juvenile survivorship in reptiles may be higher than previously predicted and low recapture of young animals is more likely due to biased sampling towards adults or movement of juveniles (see Pike *et al.* 2008).

That recapture of *S. cowlesi* individuals was also associated with shorter rear-toes and larger pelvic width suggests either selection or differential movement tied to locomotory ecomorphology. Both longer toes and narrower pelvic width are correlated with faster sprint speed in other iguanid lizards (Irschick and Jayne 1998), which may influence lizards' ability to disperse further (Christian and Tracy 1981), even out of our sample area. Alternatively, faster sprint speed may reduce a lizard's chances of being recaptured in our study thus biasing our sampling to individuals with shorter toes and wider pelvises.

As with our one-time measurements of condition described above, we also found that increase in condition over the activity season was significantly related to recapture in subsequent years for *H. maculata* but not *S. cowlesi*. A positive association between recapture and change in condition suggests higher survival of *H. maculata* individuals that were able to substantially increase their ratio of body mass to length from May to August. Positive association of condition and survival is expected in light of our other finding that recapture was positively associated with condition and gives more explicit support that high condition is important for overwinter survival (see Husak 2006). Although there was a trend towards a positive relationship between recapture and change in condition in *S. cowlesi*, it was not significant and recaptured individuals had a large variance in change in condition over the activity season. Lack of association may reflect the bias towards recapturing females at the end of the activity season (which lay eggs and decrease in body mass), or the fact that we only had one resampling occasion subsequent to the first activity season.

Changes in population ecology and evolution are intimately linked through time. Ecological characteristics of individuals in populations may influence selection itself, or our ability to detect it. For example, fluctuations in population size, recruitment of juveniles to the breeding population, and differential movement of individuals will all affect local trait values over time. The study of two lizard species co-inhabiting the ecotone of a novel ecosystem allows us to examine these population-level changes in ecology and evolution in a comparative framework. Parallels in ecological and evolutionary dynamics may reflect similarities in the abiotic and biotic environment, whereas differences are likely a result of the individual species' natural history. Although it is difficult to confidently attribute associations between trait values and recapture to differential survival, studying the ecological characteristics of populations allows us to incorporate demographics into more advanced models of selection (e.g. Gimenez *et al.* 2006, Gimenez *et al.* 2009). Ultimately, by tracking ecological and evolutionary change through time, we can discover the mechanics of their interactions – how emergent population characteristics affect trait change, and how evolutionary dynamics influence population demographics.

Tables

sampling occasion	<i>H. maculata</i>			<i>S. cowlesi</i>		
	months of study	Site A	Site B	months of study	Site A	Site B
May-Jun 2011	0	sample	sample	NA	no sample	no sample
Jul-Aug 2011	3	sample	sample	NA	no sample	no sample
May-Jun 2012	12	sample	sample	0	sample	sample
Jul-Aug 2012	NA	no sample	no sample	3	sample	sample
May-Jun 2013	24	sample	no sample	12	sample	sample

Table 5.1: Sampling times for two species (*Holbrookia maculata* and *Sceloporus cowlesi*) in two sites on the White Sands ecotone.

		<i>H. maculata</i>		<i>S. cowlesi</i>	
		Site 1	Site 2	Site 1	Site 2
population size estimate		118 +/- 14 144 +/- 18*	245 +/- 22	498 +/- 144	566 +/- 89
population density (individuals/ha)		15.3 18.6*	6.0	64.5	13.8
recapture / capture**	May-Jun 2011	0 / 45 = 0 %	0 / 96 = 0%	NA	NA
	Jul- Aug 2011	19 / 31 = 61%	42 / 72 = 58%	NA	NA
	May-Jun 2012	21 / 56 = 38%	40/103 = 31%	0 / 46 = 0%	0 / 91 = 0%
	Jul-Aug 2012	NA	NA	13 / 69 = 19%	19 / 139 = 14%
	May-Jun 2013	6 / 55 = 11%	NA	7 / 84 = 8%	23 / 147 = 16%
females : males	May-Jun 2011	49 : 51	48 : 52	NA	NA
	Jul-Aug 2011	71 : 29	62 : 38	NA	NA
	May-Jun 2012	50 : 50	43 : 57	63 : 37	58 : 42
	Jul-Aug 2012	NA	NA	61 : 38	64 : 36
	May-Jun 2013	54 : 45	NA	51 : 49	59 : 41
adults : juveniles	May-Jun 2011	71 : 29	81 : 19	NA	NA
	Jul-Aug 2011	96 : 3	94 : 6	NA	NA
	May-Jun 2012	95 : 5	97 : 3	87 : 13	88 : 12
	Jul-Aug 2012	NA	NA	94 : 6	96 : 4
	May-Jun 2013	74 : 26	NA	94 : 6	NA

Table 5.2: Summary of population demographics (size, density, proportion recaptures, age and sex ratios) for *Holbrookia maculata* and *Sceloporus cowlesi* in two sites over five sampling periods. Population size estimates are presented with +/- standard error. Ratios are presented as percentages. May-June and July-August sampling occasions represent the beginning and end of the activity season, respectively.

*two estimates provided correspond to two different recapture events

**from first recapture

response trait	<i>H. maculata</i>		<i>S. cowlesi</i>	
	Z	P	Z	P
SVL (mm)	0.4	> 0.05	2.2	= 0.03
condition	1.9	= 0.05	1.3	> 0.05
head length (mm)	0.59	> 0.05	-0.5	> 0.05
head width (mm)	2.5	= 0.009	-0.04	> 0.05
head depth (mm)	1.9	= 0.05	0.59	> 0.05
hindlimb length (mm)	-0.2	> 0.05	-1.1	> 0.05
longest toe length (mm)	-0.4	> 0.05	-2.1	= 0.03
forelimb length (mm)	0.5	> 0.05	-1.1	> 0.05
interlimb length (mm)	-0.4	> 0.05	-0.003	> 0.05
pelvic width (mm)	0.5	> 0.05	2.6	= 0.01
spine brightness (counts)	1.4	> 0.05	-0.8	> 0.05

Table 5.3: Relationships between continuous traits and recapture proportions for *Holbrookia maculata* and *Sceloporus cowlesi* as indicated by Z and P-values from Spearman Rank Tests. Lengths, depths, and widths all adjusted for body size (SVL).

Figures

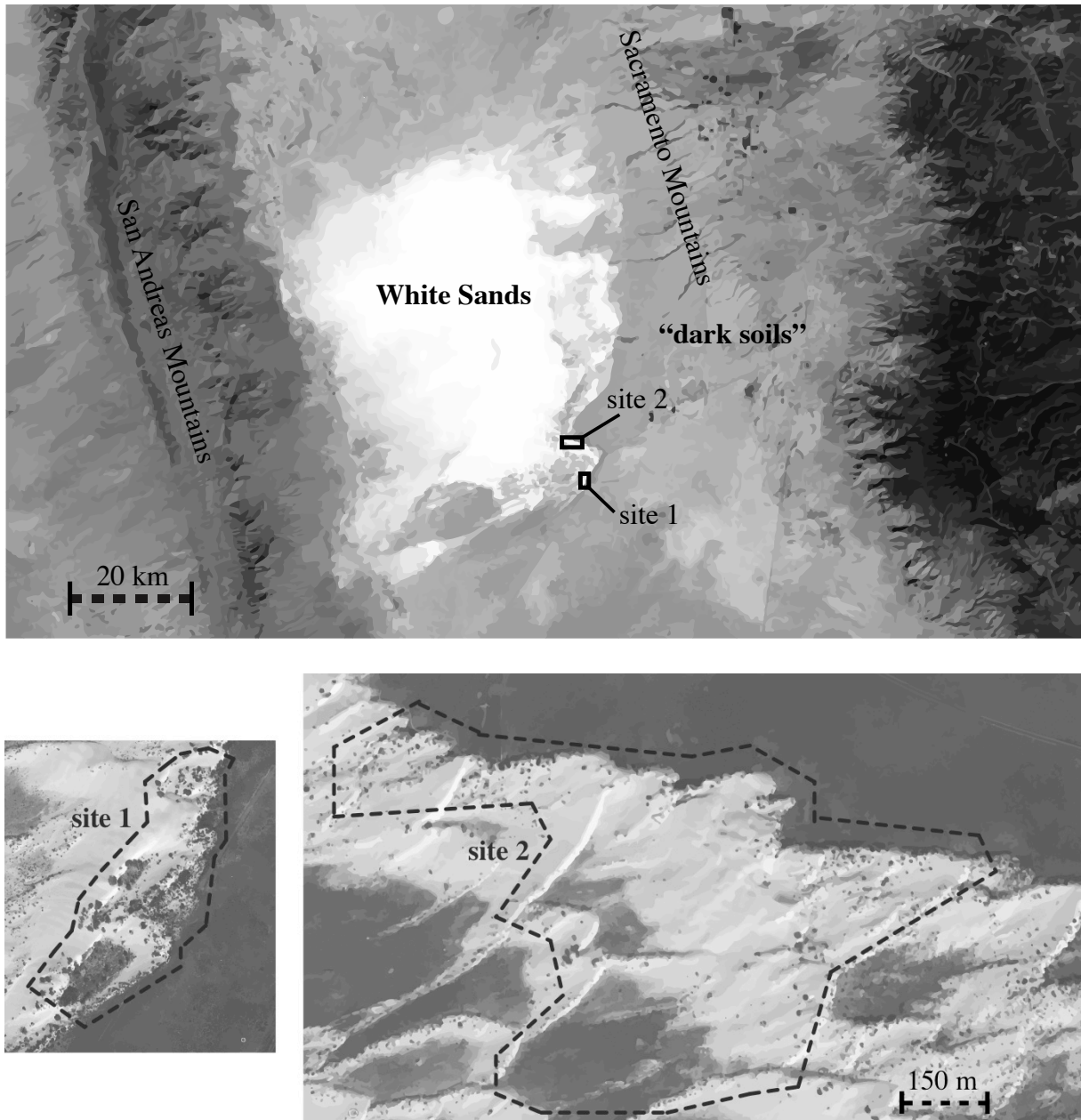


Figure 5.1: Satellite image showing two sampling sites on the ecotone of White Sands (top) and outline of interdunes sampled in Site 1 (bottom left) and Site 2 (bottom right; images adapted from Google Earth).

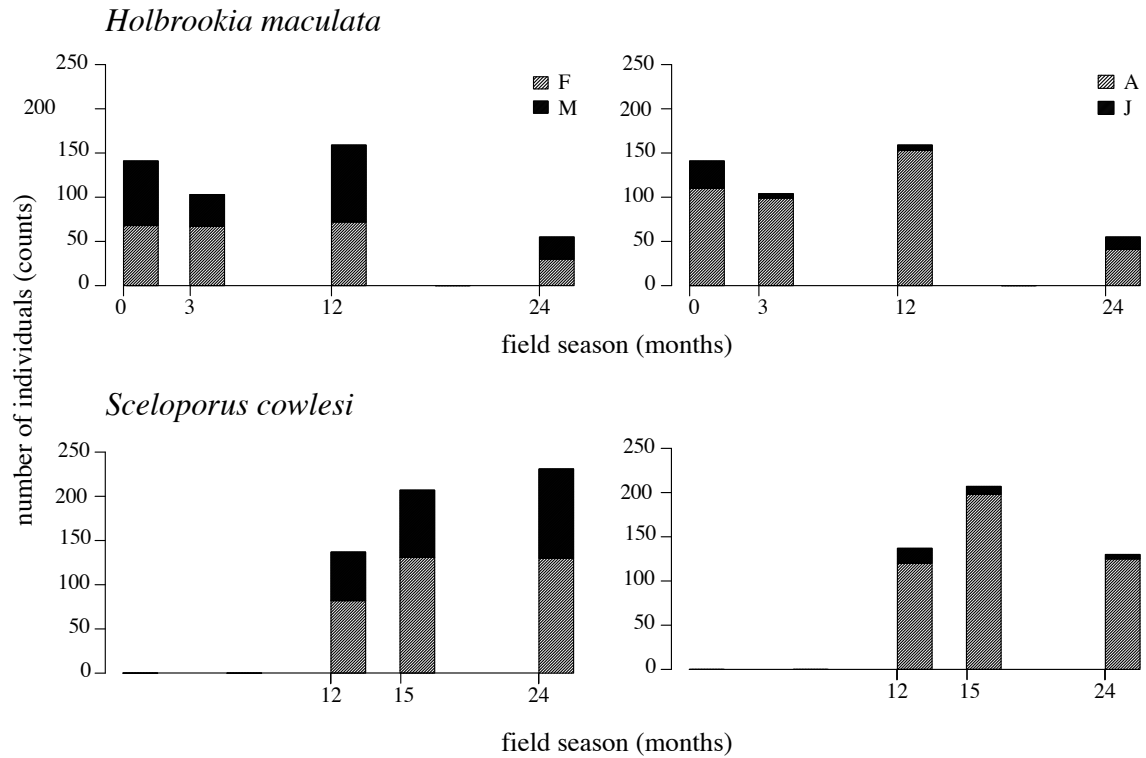


Figure 5.2: Sex ratio (top) and age class ratio (bottom) for *Holbrookia maculata* (left) and *Sceloporus cowlesi* (right) combined for two sites (since no significant differences were observed between them) over five sampling periods. Number of individuals captured at the 24-month mark for *H. maculata* is lower because only Site 1 was sampled

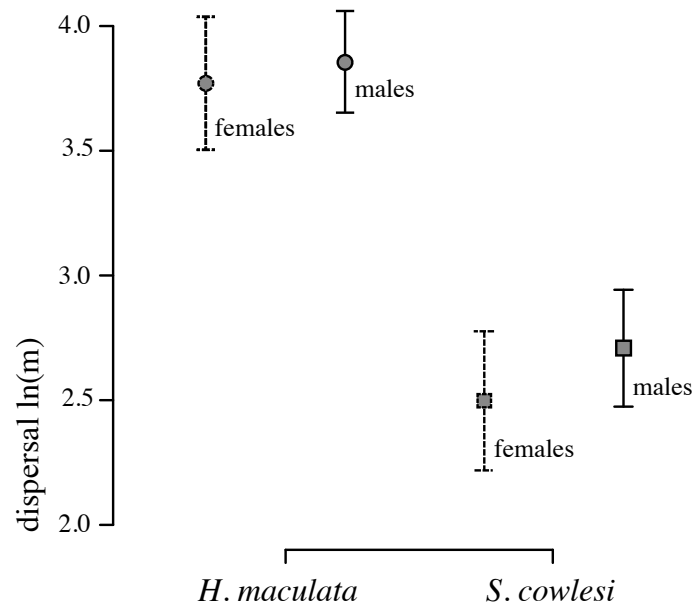


Figure 5.3: Differences in mean movement over one year for both sexes of *Holbrookia maculata* and *Sceloporus cowlesi*. Error bars represent standard errors of the mean.

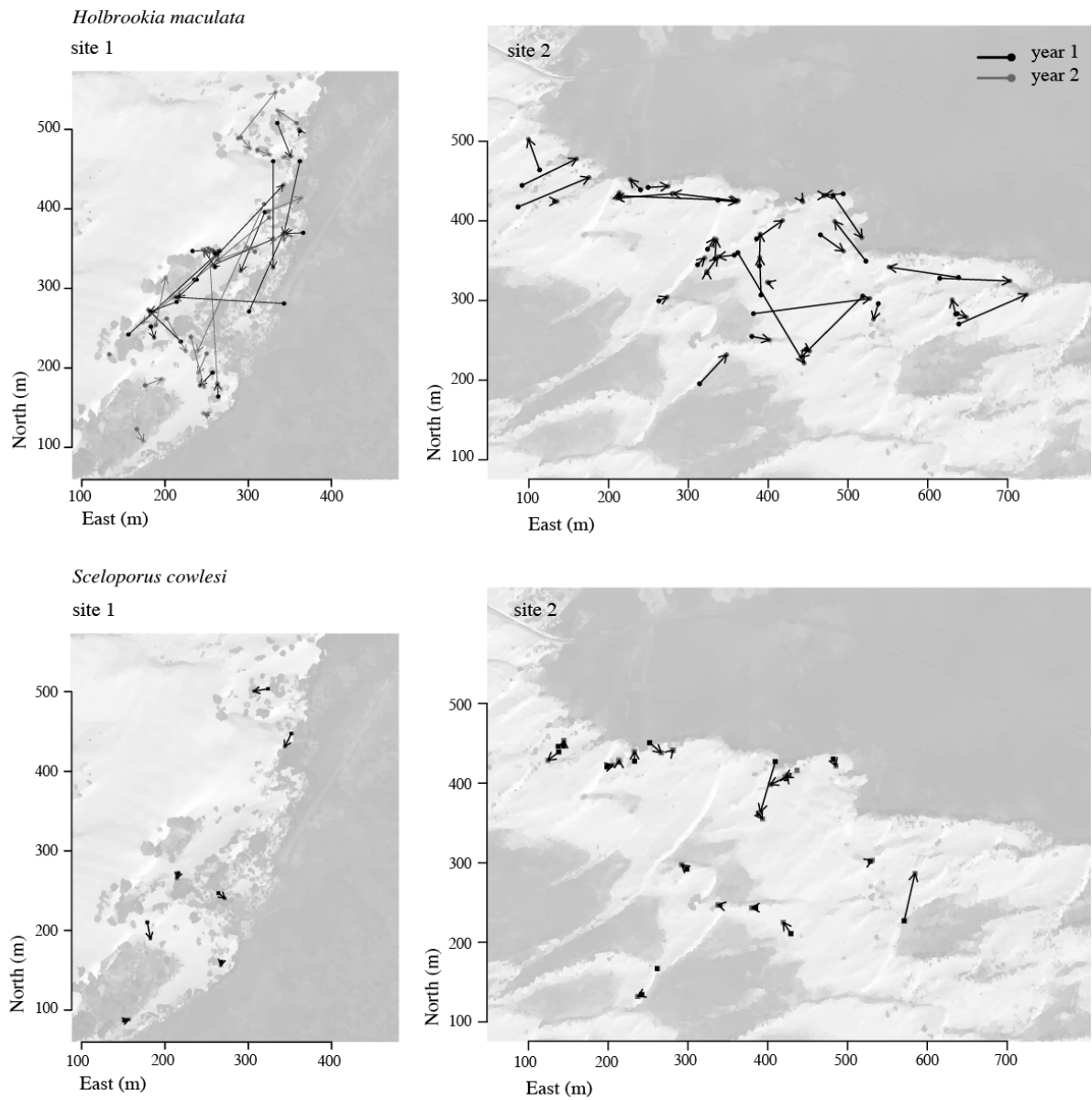


Figure 5.4: Yearly movement of recaptured *Holbrookia maculata* and *Sceloporus cowlesi* at Site 1 and Site 2.

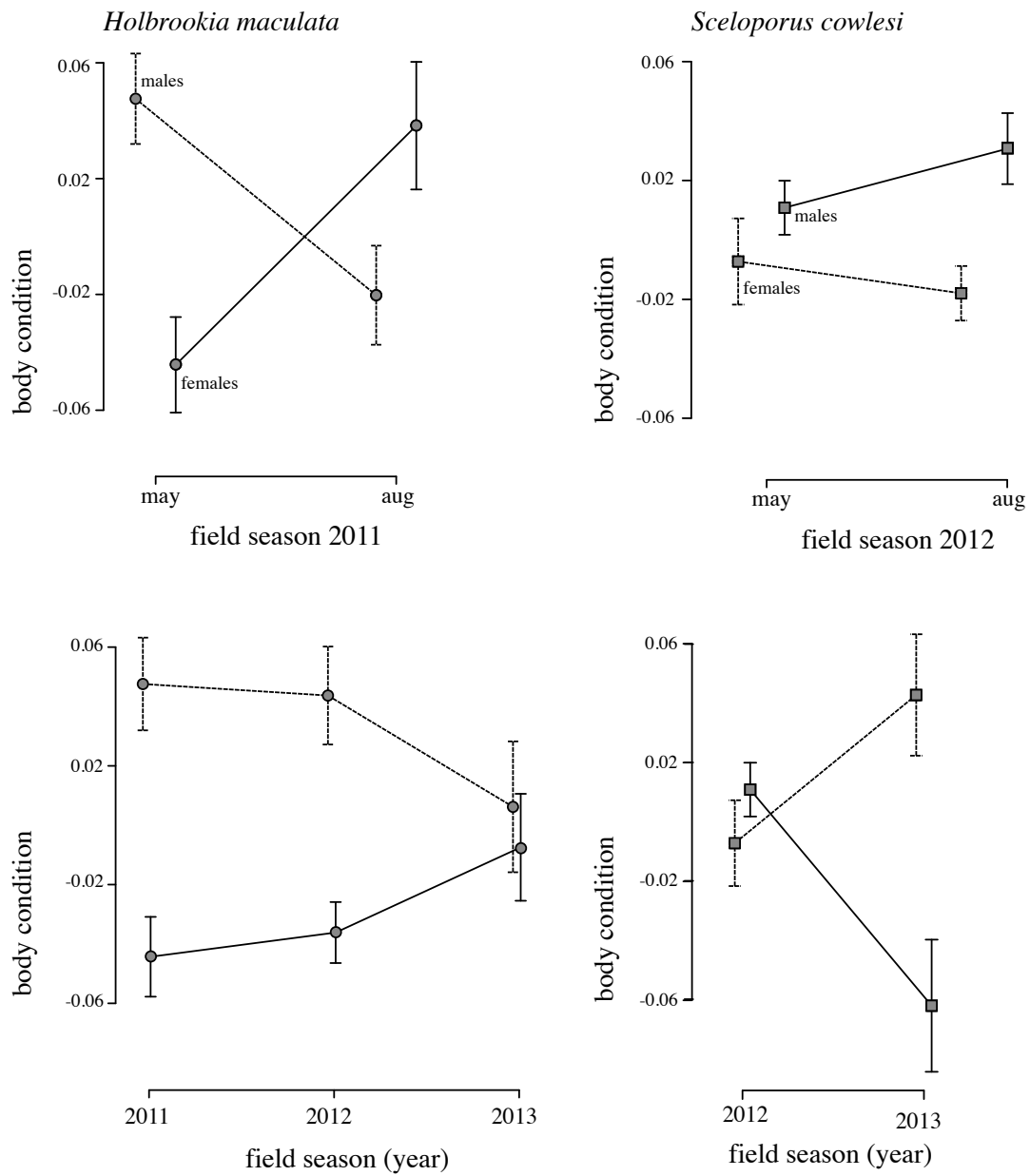


Figure 5.5: Variation in condition across years and the activity season for both males and females of *Holbrookia maculata* and *Sceloporus cowlesi*. Error bars represent standard errors of the mean.

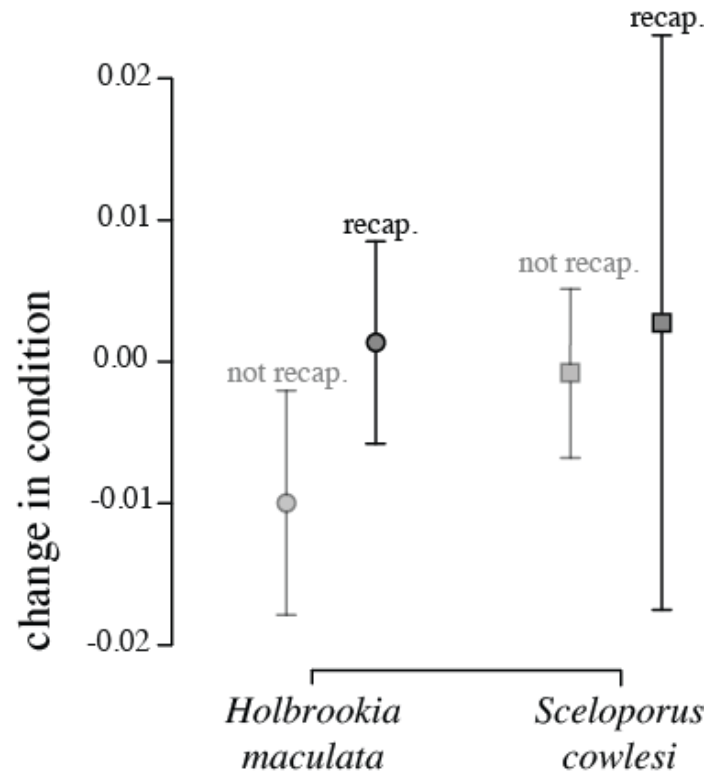


Figure 5.6: Recapture status in subsequent years based on change in condition over the activity season for *Holbrookia maculata* (left) and *Sceloporus cowlesi* (right). Error bars represent standard errors of the mean. Note that condition is shown as the response variable for clarity; however, we performed statistical analysis with recapture status as the dependent variable.

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Supplementary Material

Sampling effort

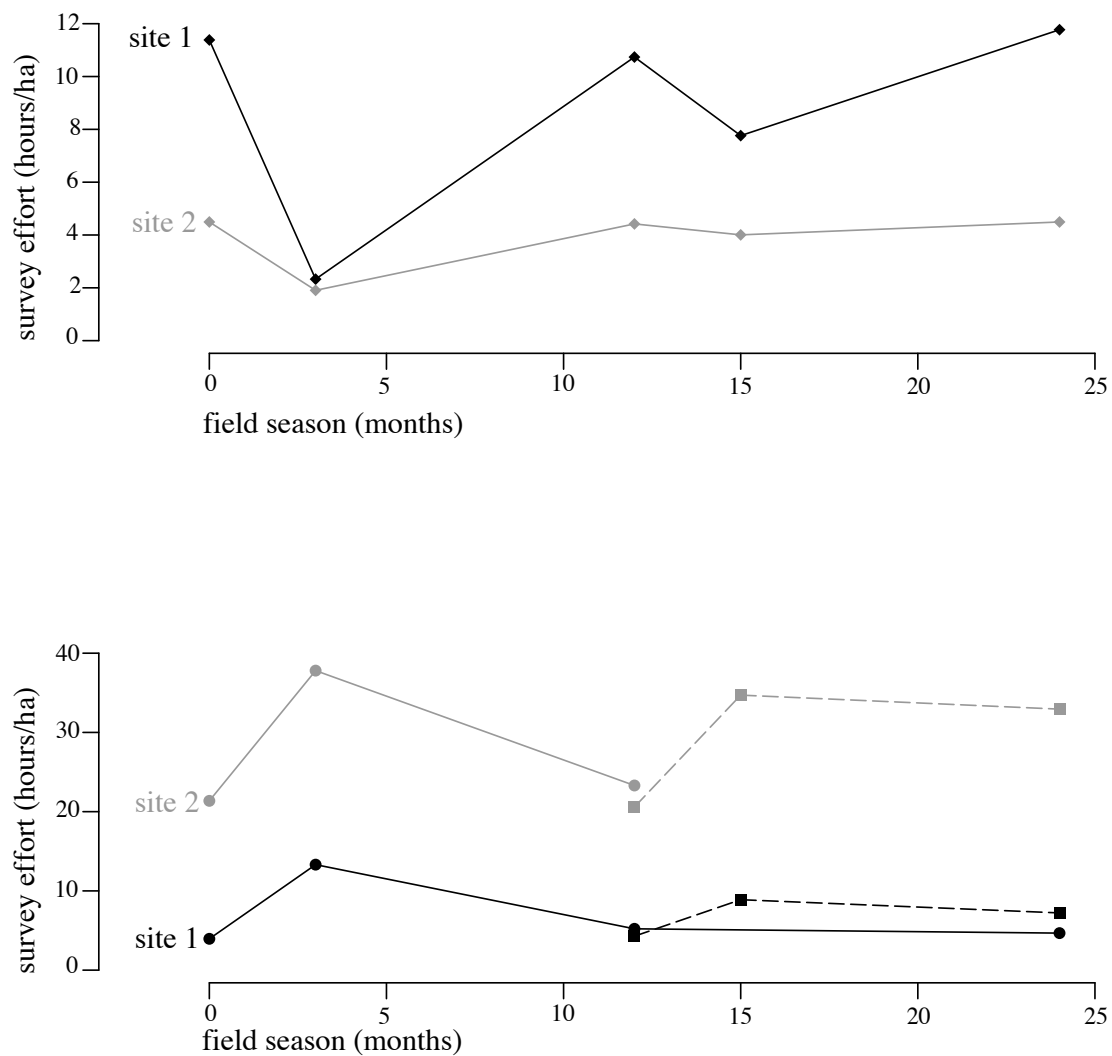


Figure S5.1: Surveying effort in combined total hours (of one to four surveyors) per hectare of each study site for five sampling occasions over three years (top). Number of lizards captured for each study site for *Holbrookia maculata* (circles, solid lines), and *Sceloporus cowlesi* (squares, dashed lines) for five sampling occasions over three years.