



Replicated Ecological Speciation in White Sands Lizards

Introduction

When organisms adapt to a novel environment, a possible consequence is speciation (where one species splits into two or more new species). White Sands (the landscape feature) is an ideal system for studying adaptation and speciation. White Sands formed relatively recently, and the substrate color of the white gypsum habitat contrasts dramatically with that of the surrounding Chihuahuan Desert's dark soil habitat. Three lizard species are found in both White Sands and dark soils habitats; the lesser earless lizard (*Holbrookia maculata*), the eastern fence lizard (*Sceloporus undulatus*), and the little striped whiptail (*Aspidoscelis inornata*). For all three species of lizards, populations in White Sands exhibit blanched body color, while populations in dark soils exhibit a darker brown coloration (Figure 1). The evolution of blanched body color in White Sands is most likely an adaptation to avoid predation by birds. The loggerhead shrike (*Lanius ludovicianus*) and the greater roadrunner (*Geococcyx californianus*) are known to preferentially prey on individuals that are poorly matched to the substrate coloration of their habitat, and both of these species occur in White Sands.

Methods

To measure predation on lizards, we built a number of temporary enclosures within the White Sands environment. One half of each enclosure allowed bird predators to enter freely (the "open" half), and the other half was covered with chicken wire to exclude predators (the "closed" half). We placed *H. maculata* exhibiting White Sands or dark soils body color (manipulated with a non-toxic paint treatment) in the enclosures, and recaptured them after two weeks.

To determine whether White Sands lizards exhibit preference for White Sands mates over dark soils mates, we

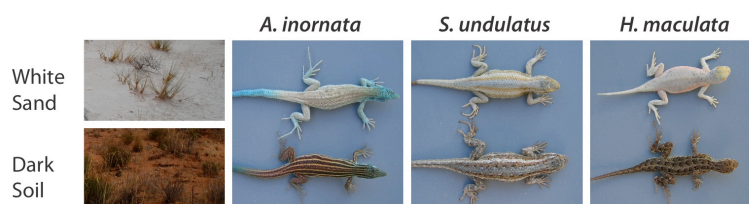


Figure 1. Representative samples of the three lizard species (*A. inornata*, *S. undulatus*, and *H. maculata*) inhabiting White Sands (top row) compared to lizards of the same species in the surrounding dark soils habitat (bottom row). Typical substrate colors are shown on the left (modified from Rosenblum and Harmon 2011).

conducted mate preference trials in the field. We presented White Sands *S. undulatus* males with local (i.e., White Sands) and non-local (i.e., dark soils) females. We quantified how quickly the male began courting each female, as well as how much total time the male spent courting the female.

To quantify differences at the genetic level between White Sands and dark soils lizards, we captured a number of *S. undulatus*, *A. inornata*, and *H. maculata* individuals from White Sands and dark soils populations. We took tissue samples from all individuals and then released lizards at the place they were found. We used genetic techniques to obtain DNA sequence data and compared the degree of DNA sequence similarity between White Sands and dark soils lizards.

Results

We found strong evidence of predation on lizards in White Sands. An average of 56 percent of lizards were recaptured

Research Objectives

In order to understand adaptation and speciation in White Sands lizards we:

- Objective 1 - Measured rates of bird predation on lizards in White Sands.
- Objective 2 - Determined whether White Sands lizards prefer other White Sands lizards as mates.
- Objective 3 - Quantified differences at the genetic level between White Sands and dark soils lizards.

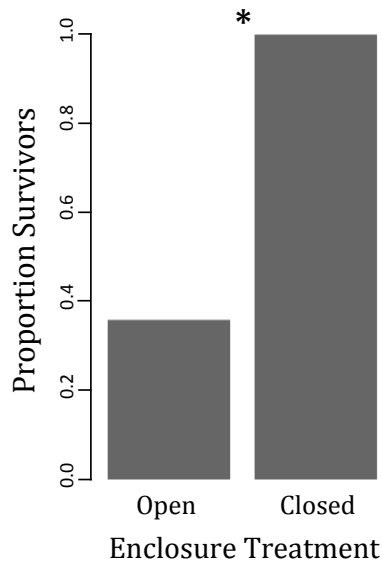


Figure 2. The proportion of surviving lizards in different treatment groups that were recaptured after two weeks in enclosure trials. Lizards in the “closed” treatment (where predators were not allowed to enter enclosures) had a much higher chance of survival than lizards in the “open” treatment (where predators were allowed to enter enclosures).

from open halves of enclosures (Figure 2). In contrast, 100 percent of lizards were recaptured from closed halves of enclosures. In addition, we determined that bird predators were most likely responsible for the observed mortality in open enclosures. Birds most commonly observed in and around enclosures include Loggerhead Shrikes, Greater Roadrunners, Chihuahuan Ravens (*Corvus cryptoleucus*), and Northern Mockingbirds (*Mimus polyglottos*). Although we observed high rates of predation in enclosure trials, body color did not appear to effect lizard survivorship, and we are now refining our experimental design to better test for the affect of camouflage on lizard survival at White Sands.

We observed a preference for local mates in the White Sands system, where White Sands males preferentially courted local females (i.e., began courting White Sands females more quickly than dark soils females, and spent a longer total amount of time courting White Sands females than dark soils females; Figure 3). In contrast, males from dark soils populations did not exhibit a preference for local mates (i.e., they courted White Sands and dark soils females similarly). We also found that aspects of female behavior and female body color influenced male courtship.

We observed genetic differentiation between White Sands and dark soils populations that varied from species to species. *A. inornata* exhibited little to no genetic differentiation between White Sands and dark soil

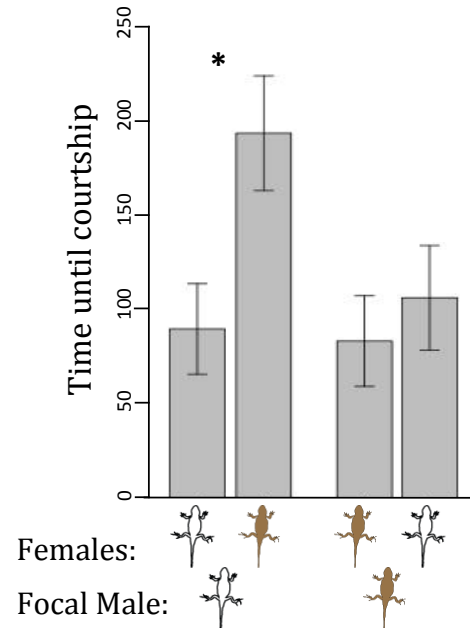


Figure 3. During mate preference trials, the amount of time (in seconds) that passed before males began courting females from White Sands and dark soils. White Sands males courted White Sands females more quickly than dark soils females, while dark soils males did not exhibit a difference in time until courtship for White Sands and dark soils females (modified from Hardwick et al. 2012).

habitats. *S. undulatus* showed intermediate levels, and *H. maculata* had a high degree of genetic differentiation by habitat. These results could be explained by patterns of geographic structure among species; *H. maculata* is a habitat specialist with small isolated populations, *S. undulatus* is distributed more continuously than *H. maculata*, but has limited dispersal across populations, and *A. inornata* is continuously distributed with high dispersal rates. We also found a specific genetic mutation responsible for blanched color in two of the three White Sands species. Mutations in the melanocortin-1 receptor gene (*Mcl1r*) appear to cause light coloration in *S. undulatus* and *A. inornata* (Figure 4).

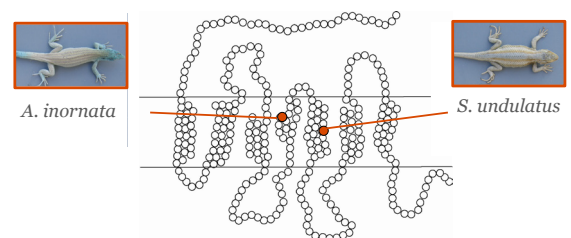


Figure 4. Schematic of the *Mcl1r* gene with the position of the mutations that cause light coloration in *A. inornata* and *S. undulatus* marked (modified from Rosenblum et al. 2009).

Discussion

Research to date indicates that White Sands and dark soils lizards are in the process of adapting to distinct environments, and that *S. undulatus*, *A. inornata*, and *H. maculata* exhibit varying degrees of progress towards speciation. Specifically, we have learned that:

1. Lizards in White Sands experience high rates of predation from local birds. This suggests that characteristics that help lizards avoid predation, such as camouflage, likely play an important role in survival in White Sands.
2. White Sands lizards prefer other White Sands individuals as mates. This indicates that some degree of reproductive isolation exists in the White Sands system, where White Sands and dark soils lizards do not frequently interbreed.
3. Though all three species of lizards exhibit similar locally adaptive traits (i.e., blanched color in White Sands), they also exhibit varying degrees of genetic differentiation between White Sands and dark soils populations. This suggests that species-specific traits, such as dispersal rate, can play an important role in determining the degree of progress towards speciation. It is also remarkable that two of the three White Sands lizards have mutations in the exact same gene responsible for light coloration.

White Sands lizards provide us with a unique opportunity to gain insight into the process of adaptation and speciation. In the future we will:

1. Conduct more extensive enclosure studies to further investigate the role of color on survivorship, as well as seasonal and geographic variation in predation rates;
2. Perform additional experiments to determine which characteristics (e.g., visual cues such as body color and mating display behavior, chemical cues such as pheromones) are used to inform mate preference; and
3. Identify additional traits important for adaptation to the White Sands environment, and determine the genetic basis of those traits (i.e., locate the genes and the mutations within those genes responsible for adaptive characteristics).

Overall White Sands represents one of the most promising systems in the world to understand how quickly animals can adapt to new environments and how the process of speciation unfolds in nature.

White Sands Science Symposium

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References

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