White Sands

National Park Service
Department of the Interior

White Sands National Monument

Evolution in Action: White Animals at White Sands

There has been dramatic convergent evolution of light coloration for many of the animals which inhabit the stark white gypsum dunes of White Sands National Monument. A number of different animal groups (including insects, spiders, toads, lizards, mammals) have blanched coloration on the white dunes and dark coloration in the surrounding dark desert soils (see Table 1). The gypsum sands are geologically recent, formed since the end of the last glaciation. Because of the young age of White Sands, we know that animals with lighter coloration have adapted to their environment quickly, as a result of strong natural selection. White Sands is therefore a dramatic showcase for evolution in action. The rapid, convergent evolution of blanched coloration in many species experiencing the same environment allows us to ask several important questions about the role of natural selection in generating biological diversity.

Why did light coloration evolve?

Animals become better adapted to their environment by a process called natural selection. Traits that increase an individual's reproductive success by improving its fit to the environment tend to spread in a population. Light coloration could evolve through natural selection in dune animals if individuals with light-coloration survived better or reproduced more than individuals with dark coloration. Imagine a population of dark colored lizards moving from the brown desert soil into the white dunes. Assume there is natural variation in color in lizard populations, some individuals being slightly darker and some slightly lighter. Also assume that coloration is heritable, with offspring inheriting their color pattern from their parents. Suppose that the lighter individuals survived better in this new environment and had more offspring than the darker lizards. Because the light-colored individuals were more likely to survive and reproduce, the frequency of light-colored lizards would increase in the next generation. After many generations of selection for lighter individuals, the population could eventually become white. But why would lighter individuals survive and reproduce better on the gypsum dunes? There are two primary hypotheses for why natural selection would favor light individuals: camouflage and thermoregulation. Natural selection for camouflage is the most likely explanation for the light coloration observed at White Sands but the effects of light coloration on thermoregulation require further study.

Natural selection for substrate matching

Particularly for small diurnal animals, we would expect strong selection for substrate matching to avoid being seen by visual predators. Although no studies have directly measured predation intensity on White Sands animals, many researchers have shown that well-camouflaged animals are less likely to be taken by predators (Kiltie, 1992). Avian predators, such as roadrunners and shrikes likely represent a significant threat for small animals at White Sands. Camouflage, or crypsis, is therefore essential for survival. Even nocturnal animals can benefit from matching their habitat, because many nocturnal predators use vision to find prey illuminated Lowe, 1964). Also, predators can benefit from matching their substrate as to avoid detection by prey.

Natural selection for thermoregulation

Another possibility is that lighter coloration has evolved for thermoregulation. Lighter-colored individuals that are active during the day may be better able to regulate body temperature because they reflect more of the intense desert sunlight (Benson, 1933). However, many of the white animals are nocturnal, so regulating absorption of the sun's rays would not be an important selective factor. Additionally, there is no evidence that temperatures at White Sands are any more intense than in the surrounding dark soil habitat. In fact, air and substrate temperatures at White Sands are actually lower than on the dark soils (Hager 2000, Rosenblum unpublished). Hager even suggests that lighter colored lizards are at a disadvantage because they cannot warm as quickly as their dark soil counterparts. Although substrate temperatures are not unusually high at White Sands, it is still possible that large heat loads are imposed on animals because of the reflective properties of gypsum. Further study is necessary, but current evidence is most consistent with light coloration as an adaptation for camouflage not thermoregulation.

Color variation of earless lizard and bleached earless lizard in their environments

What mechanism produces white coloration?

There are three possible mechanisms to explain how light coloration is produced in White Sands animals. First, light coloration may be fixed for each individual from birth. For fixed coloration to evolve, lighter-colored animals must have been more likely to survive, reproduce, and pass their light-color genes on to their offspring.

Second, individuals may be able to change color during their lifetimes to match their current substrate. Changing color in response to the environment is a type of phenotypic plasticity and is known to occur in other animals such as chameleons and anoles. For such a mechanism to evolve, individuals with genes coding for flexible coloration must have been more likely to survive, reproduce, and pass their flexible-color genes on to their offspring.

Third, it is possible that light coloration did not evolve through natural selection but is simply picked up from the environment. Color can be picked up from the environment either from dietary pigments (i.e.: pigments acquired from the food cause an animal to become white) or from direct accumulation (i.e.: gypsum sand on the skin makes an animal appear white). The third possibility, that light color is acquired directly from the environment, is unlikely for most White Sand species. First of all, light coloration is probably not caused by diet. There are pigments which are known to be acquired from the diet in birds and reptiles. However these dietary pigments (called carotenoids) result in yellow and red, not blanched, coloration.

Second, Benson (1933) argued that it is unlikely for herbivorous animals to turn white from ingesting certain plants. Plants at White Sands are similar to plants present in other areas of the Tularosa Basin and probably take up substances similar to those growing in alkaline soils elsewhere. It is still possible that direct accumulation of gypsum dust or sand on the skin could turn an animal white. The only species for which this appears likely is the white lycosid spider (Table 2), which Bugbee (1942) described as "brown in basic color but its abdomen usually appeared as if covered with hoar-frost." Because "this white color was easily rubbed off when individual specimens were handled," it is possible that the white color is derived from external substances. However, it is also possible that the substance that is easily rubbed off is deposited by the spider and is internally derived. Since light coloration is unlikely to be derived directly from the environment, we must differentiate between the remaining two hypotheses: that individual color is fixed or that individuals are able to change their color to match their current substrate. These predictions have been most thoroughly tested in lizards.

White Sands collared lizard

Coloration in lizards

Many species of lizards are able to quickly change their color in response to external and internal conditions, including temperature, exposure to light, and individual health and excitatory state (Smith, 1946; Norris 1965). Some lizards, like chameleons and anoles, can even change color to more closely match their current substrate. These rapid color changes are termed physiological plasticity and occur as reptiles shift the distribution of pigments between different cell layers. Melanin, the pigment responsible for overall body darkness, is located in melanophore cells. Melanophore cells are distributed several layers below the surface of the skin but also have dendritic processes which reach just below the inner surface of the skin. Reptiles can darken or lighten in color by dispersing or aggregating melanin granules along these dendritic processes (Bagnara and Hadley, 1973).

Scientists have been investigating color change in White Sand lizards for nearly 50 years. Some early results suggested that White Sand lizards could change color, to a limited extent, with environmental stimuli. Bundy (1955) found that bleached earless lizards (Holbrookia maculata ruthveni) held in the laboratory got slightly darker at cold temperatures and slightly lighter at hot temperatures. Similarly, Lowe and Norris (1956) found that Cowles prairie lizards (Sceloporus undulatus cowlesi) darkened slightly when cold. These rapid color changes in response to temperature may help the lizards regulate temperature by increasing heat absorption when the animal is cold and decreasing it when the animal is hot.

Early experiments also suggested that rapid color change could not account for the dramatic blanched coloration observed in White Sands lizards. Bundy (1955) attempted to determine whether color was fixed or flexible in the bleached earless lizard (H. maculata). He collected white lizards from the dunes and non-white individuals from areas near the dunes. He photographed all animals to record their color and then placed them into laboratory cages with either white quartz sand or finely ground black cinders. None of the lizards in Bundy's experiment changed colors to match the ground color in their cages.


Bleached earless lizard

Although the lizards did change color with temperature, as described above, the White Sands lizards never got as dark as the darker lizards. Smith (1943) and Lowe and Norris (1956) also held bleached earless lizards in the laboratory with different-colored sands. The lizards in those experiments also failed to change color to match the color of their current substrate. Similarly, Cowles prairie lizards (S. undulatus) and little striped whiptails (Aspidoscelis inornata, formerly Cnemidophorus inornatus) held in the laboratory for up to two years did not change color (Lowe and Norris, 1956).

These early experiments suggest that the lighter-colored lizards have genes that code for fixed light color and that, unlike chameleons and anoles, they do not change color to match their current background (Table 2). More recently, Rosenblum repeated these experiments in a more controlled fashion (in review). First, she evaluated the ability of lizards to change color rapidly in response to temperature. She collected white and non-white individuals from all three lizard species which inhabit the gypsum dunes (H. maculata, S. undulatus and A. inornata). She exposed the lizards to hot and cold temperatures and used a spectrophotometer to quantify coloration. All three lizard species did become slightly darker with colder temperatures. However, even when cold, white lizards never become as dark as dark lizards. Therefore rapid color change in response to the environment cannot explain observed light coloration (Table 2).

Rosenblum then tested whether color is fixed throughout a lizard's lifetime. She collected gravid (pregnant) females from H. maculata and S. undulatus from the gypsum dunes and from nearby dark soil habitats. She raised the eggs and newborn hatchlings from light mothers and from dark mothers in identical conditions. This "common-garden" experiment removes environmental differences as an explanation for color variation. She found that hatchlings had the same coloration as their mothers even when they were raised in the lab on intermediately-colored substrate. This provides strong evidence that light coloration is fixed in these species (Table 2).


Eastern fence lizard at White Sands

Further evidence that color is fixed in White Sands lizards comes from studying a gene called the melanocortin-1 receptor gene (Mc1r). This gene is known to be involved in melanin production in mammals and birds. Rosenblum (2004) studied this gene in White Sands lizards and found variation at the Mc1r gene to be associated with color variation in the little striped whiptail lizard A. inornata. This study not only shows that light coloration has a genetic basis but actually identifies the single gene that is likely responsible for blanched coloration in this species (Table 2).

Striped whiptail lizards display color variation

Coloration in other dune field animals

There have been few attempts to distinguish between the alternative mechanisms for color change in white species other than lizards. However, some observational evidence, and an understanding of the mechanisms of color deposition in different taxa, suggests the likely mechanisms of color change for some other dune-field animals (Table 2). Some amphibians, like reptiles, can quickly change color to match their current substrate (Zim and Smith, 1987). Consistent with this general phenomenon, Stroud and Strohecker (1949) reported that the spadefoot toads they caught on the dunes were "completely white except for black eyes and black marks on the under-side of the hind feet." When they brought these toads into the laboratory, they gradually darkened to "the color typical of the species." Thus, these toads appear to match the color of their current substrate by quickly changing color rather than having fixed white coloration (Table 2).

Spadefoot toad

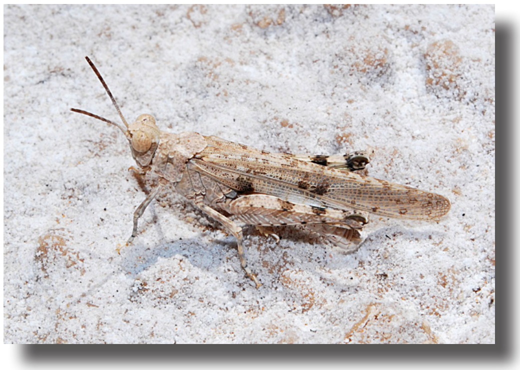
In mammals, fur color is determined by the amount of pigment in the hairs. Once the pigment is deposited in each hair, fur color cannot be changed until the current coat is molted and replaced by another coat. However, even between molts, dune-field mammals may not change color to match their current background. Benson (1933) collected dark-colored pocket mice (Perognathus intermedius rupestris) from the Valley of Fires malpais and held them in the laboratory for several years on differently-colored substrates. Although the mice molted several times in the lab, individual color was fixed. Thus, malpais pocket mice, and possibly white sands pocket mice, seem unable to change color to match their substrate (Table 2).

Apache pocket mouse

In insects, color is usually determined by the amount or type of pigment deposited in the cuticle and epidermis. Like mammals, insects could hypothetically change color between molts by changing the amount or type of pigment. In fact color changes between molts are known to facilitate camouflage in some insects (Chapman, 1969). Other insects can also change their color over the short term (e.g., from day to night) by moving pigment in epidermal cells closer to or further from the exterior (Chapman, 1969).

Mantled toothpick grasshopper

Such short-term color changes typically occur in response to light or temperature. No one has reared white insects from White Sands under controlled conditions with different-colored substrates, so it is too early to conclude whether color is fixed or flexible in these insects. Stroud (1950) did report on color changes in three insects, suggesting that the white insects use two different mechanisms to become white. He reports that the white locust Cibolacris parviceps arida at White Sands is "said to be able to change its color from one instant to the next in accordance with the color of the substrate" (p. 676). This report is consistent with Chapman's general observation that "the colours of grasshoppers and related insects tend to have a general resemblance to the prevailing colour of the environment...and a change in the environment leads to a change in the colour of the insect." In contrast, Stroud (1950) suggests that the color of the two white camel crickets at White Sands is probably fixed as a result of genetic differences between the white and the related brown subspecies. However, Stroud did not cite evidence to back up his reports, so it is not clear how he justifies these conclusions.



Hebard's desert grasshopper

From the available evidence, white animals in the dunes appear to use all three mechanisms of color change (Table 2). The white spiders may derive their light color from the substrate itself. The toad, and possibly some insects, may change color to match their current environment. The lizards and mammals seem to have individually fixed color that likely evolved in response to selection pressure for substrate-matching. Controlled experiments with more dune-field animals are necessary to test whether individuals held in the laboratory change color to match their substrate and to determine whether white individuals bred in the laboratory have white offspring.

Why are some dune field animals *not* white?

Although some populations of dune-field animals display lighter coloration than their dark soil neighbors, many animals that live in the dunes are not unusually colored. Among insects, for example, Stroud (1950) noted that "the absence of adaptation to the soil color is more striking than its presence". He collected 343 insect species at eight different collecting sites within the dunes, and only four of those species were lighter colored than expected (Table 1). Similarly, Blair (1943) trapped twenty-three different species of mammals in the dunes, and only three were lighter colored than expected (Table 1). The absence of light coloration in these species raises the question of why light coloration has not evolved more often. There are three primary hypotheses to explain the lack of light coloration in many animals on the dunes: insufficient genetic variation, different experience of selection pressures, and constraining effects of gene flow. More research is necessary to determine the relative importance of different explanations of why light coloration is relatively rare in animals inhabiting the dunes.

Kangaroo rat

Lack of genetic variation

In species without light coloration, it is possible that there was simply no genetic variation for color upon which natural selection could act. Natural selection can only produce a better fit between an organism and its environment if the trait is genetically transmitted to offspring and if there is variation for the trait. Take the example of if light coloration caused by gypsum sand grains adhering to an animal's fur. In this case there is no genetic basis for the light coloration, and offspring of lighter-colored individuals would not also be lighter-colored. Take another example of a population colonizing the gypsum dunes all being exactly identical in color. In this case, natural selection would have no variation on which to act. In White Sand lizards we know that color traits have a genetic basis (see above), however in many other groups more study is necessary before rejecting the insufficient genetic variation hypothesis.

Different selection pressures

It is possible that different species experience different selection pressures at White Sands. This hypothesis could apply in a number of different contexts: some species may experience weaker or stronger selection for substrate matching, some species may experience trade-offs between selection for crypsis and thermoregulation, and some species may have defenses other than light color against predation.

First, lighter coloration could be slower to evolve in species where the benefit of being lighter is lower (i.e., less intensity of selection). For example, large nocturnal predators like kit fox may benefit less from being camouflaged to the white sands than would a small mouse or lizard, because the larger predators have few visually-hunting predators of their own. Note, though, that it is possible that predators would be better able to sneak up on unwary prey if they, too, blended in with the habitat.

Kit fox

Also, lighter color may be slower to evolve in species that spend less time moving around on the open sands and therefore benefit less from being camouflaged to the sands. For example, the bleached earless lizard (H. maculata) forages in the open on the sand, while the Cowles prairie lizard (S. undulatus) forages primarily in darker vegetation (Hager 2001). Because of these differences in foraging ecology, the Cowles prairie lizard probably benefits less from being camouflaged to the white sands of the open dunes. This may help explain why the bleached earless lizard is much lighter-colored than is the Cowles prairie lizard (Dixon, 1967).

Cowles prairie lizard

Second, lighter color may be slower to evolve in species in which light coloration yields some benefits and dark coloration yields others (i.e., opposing selective pressures or trade-offs). Especially for ectothermic (cold-blooded) organisms like lizards and insects, darker animals can absorb heat more quickly than lighter-colored animals and therefore reach their optimal activity temperature more quickly. For example, we know that White Sands lizards can never get as dark in color as their counterparts that live on dark soil. Local adaptation to White Sands may therefore reduce temperature-regulation benefits from darker coloration. If it takes lighter lizards longer to warm up in the morning or if they must maintain lower activity temperatures, it may compromise their ability to forage for food or escape from predators. Thus, camouflage coloration may not have evolved in some ectothermic animals if the benefits of dark coloration for facilitating temperature regulation outweigh the benefits of camouflage.

Third, light coloration may not have evolved in some species because they have other means of defending against predators and do not need camouflage. For example, the black darkling beetle makes itself obvious as it marches across the white sands in the middle of the day, so it seems surprising that it has not adopted white camouflage coloration. However, its common name, the stinkbug, hints at why it does not need to be camouflaged. If they are threatened, these beetles stand on their heads and, if the threat continues, spray chemicals that make them an unappealing meal for predators. Some other species that do not have camouflage coloration may also have other kinds of defenses that protect them against predators and make camouflage unnecessary.

Darkling beetle

Gene flow constraining adaptation

Finally, if there is dispersal between populations in different habitats, gene flow may constrain local adaptation. When there is gene flow between populations under different selective pressures, genes favored in one habitat (e.g.: dark coloration genes in the desert surrounding the dunes) can inundate another habitat. Such gene flow can reduce the chance that individuals on the gypsum dunes become adapted to their local environment, even for species where light coloration is beneficial. The extent of gene flow between dunes and non-dunes populations does seem to predict the extent of camouflage coloration in some lizards, mammals, and insects.

In lizards, both classic and recent work suggests that gene flow may hinder local adaptation of dunes populations. Dixon (1967) documented that dunes populations of the bleached earless lizard (H. maculata) were isolated from the nearest dark soil population (located 29 km southeast), whereas there were populations of Cowles prairie lizard (S. undulatus) immediately outside of the dune field. He hypothesized that gene flow could explain why the bleached earless lizard is lighter colored than the Cowles prairie lizard. Rosenblum (in review) has tested this hypothesis with modern methods for all three White Sand lizards. She measured lizard color with a spectrophotometer and levels of gene flow using molecular markers. She found that the bleached earless lizard is lighter in color and better substrate-matched than either the Cowles prairie lizard or the little striped whiptail. Furthermore, this corresponds exactly to observed levels of gene flow; there is more gene flow between dark soil and white sand populations for the Cowles prairie lizard and the little striped whiptail than for the bleached earless lizard. This suggests that the degree of genetic isolation of dune populations may be very important in determining the outcome of natural selection.

Differences in the extent of gene flow between populations may also explain coloration patterns in dune-field mammals. Both Benson (1933) and Blair (1943) noted that species that were isolated on the white sands were more likely to have evolved camouflage coloration than species that had populations in the surrounding area. The same is true of dark-colored animals living on the black lava at the Valley of Fires malpais. Of the nine small mammals trapped by Blair (1943) within the dune field, five species are probably not reproductively isolated from non-dunes populations, because there are animals living in the quartz sands surrounding the dunes.

Spotted ground squirrel

Of these five species, only one (20%), the spotted ground squirrel (Spermophilus spilosoma), has evolved lighter color. In contrast, of the four species that are isolated from non-dunes populations, two species (50%) have evolved white or lighter color, the Apache pocket mouse (Perognathus flavescens apachii) and the southern plains woodrat (Neotoma micropus leucophaea). Although sample sizes are quite small and modern methods were not used to measure gene flow, these data do at least suggest that mammals that are isolated in the dunes are more likely to develop camouflage coloration.

White Sands camel cricket

Finally, the two camouflaged camel crickets in the dunes apparently differ in both the extent of gene flow between dunes and non-dunes populations and in the extent to which most animals within the dunes have colors that match the white sands. Ammobaenites were not collected at the eleven collecting localities immediately outside of the dunes, but Daihinoides were collected at sites outside of the dunes. As expected if these differences in gene flow affect the ability of the dunes populations to evolve camouflage coloration, all of the collected Ammobaenites were white, while the collected Daihinoides "vary in coloration from brown individuals to individuals which show considerable pigment reduction" (Stroud and Strohecker, 1949, p. 126).

Can natural selection at White Sands lead to speciation?

The dune field can be considered a sand island in a sea of desert. Just as oceanic islands often have unusual species that are not found elsewhere, islands of habitat like the White Sands dune field can also have species not found elsewhere. Species that are restricted geographically to one or a few localities are called endemic species. Endemic forms can evolve fairly quickly if they are geographically or genetically isolated and if they are exposed to unique selection pressures. But can selection for local adaptation actually lead to speciation? Again, we have preliminary data on this question for White Sands lizards, but more research is necessary for other taxa.

White moth found at White Sands

Mate choice and reproductive isolation

One mechanism by which natural selection can lead to reproductive isolation is when traits important in local adaptation are also important for mate choice. For example, if lighter lizards prefer to mate with other light lizards, there may be an interaction between natural and sexual selection. But do lizards really choose mates based on their color? Dorsal coloration is not known to be important for mate choice, but lizards have other color patches which are used for communication and mate choice. These signaling colors are usually bright yellow, red or blue and actually can be affected by changes in melanin production. Since White Sands lizards produce less melanin, there may be a connection between natural selection and sexual selection for lizards at White Sands.


Greater earless lizard

Several studies have now shown that lizards on and off the dunes show differences in signaling colors. Both Hager (2001) and Rosenblum (in prep) have documented differences in signaling colors between White Sands and dark soil populations of the bleached earless lizard (H. maculata). Female lizards of this species have bright yellow, orange and red markings on their throats and sides which are used to communicate during the breeding season. Rosenblum also found differences in signaling colors for the other two White Sand lizard species. For the Cowles prairie lizard (S. undulatus), males have bright blue colors on their bellies which are different in dune and non-dune populations. For the little striped whiptail (A. inornata), head color is important for communication, and again there are differences between White Sands and dark soil individuals. Differences in signaling coloration and mating preference between dune and non-dune populations do not necessarily mean that dune populations are reproductively isolated. However, it means that the raw material is available for sexual selection.

Ideally, we would like to test mate choice directly. Rosenblum (in prep) was able to do this with the bleached earless lizard (H. maculata), the lizard that is most highly-adapted to the gypsum environment. She conducted a number of different mate-choice experiments to see if White Sands females preferred to mate with light males or dark males. In fact, light females did have a preference for light males. Furthermore, she found morphological differences between White Sand and dark soil populations of H. maculata. In addition to their blanched coloration, White Sand populations are unique in the shape of their bodies, their heads and their feet. These morphological differences could be further specializations to the sandy environment. Again, these results do not necessarily mean that White Sands bleached earless lizards should be considered a new species, but the extensive differences between dune and non-dune populations suggest that natural selection at White Sands could lead to reproductive isolation.

Defining species at White Sands

At this time, none of the White Sands animals are considered new species. However, six subspecies (Table 1) are restricted to the dune field and therefore could be considered endemic. The number of endemic subspecies or species depends on how species and subspecies are defined, an area of great debate in evolutionary biology. Most of the taxonomic work on dune-field animals was done many years ago, and application of modern taxonomic techniques could help to clarify the status of endemic forms at White Sands.

One area of increasing interest for evolutionary biologists is how to define units for conservation. Although forms at White Sands may not be unique species, some might be considered Evolutionary Significant Units or Management Units (ESUs or MUs, sensu Moritz 1994). These designations help scientists and managers consider what unique evolutionary processes have occurred over a given landscape. Recent studies have shown that landscapes like White Sands in which there is a dramatic change in the environment (termed ecotones) are especially important in generating biological diversity. Conserving ecotones may allow us to protect species that already exist while allowing new species to evolve. Ultimately, White Sands can be a classroom for the study of evolution in action and a natural laboratory for conserving our biological resources.


Ecotone

Table 1: Description of the species reported to have light-colored populations on the gypsum dune fields of White Sands National Monument.

Species	*Description of coloration*	*Source*
Reptiles Bleached earless lizard (*Holbrookia maculata* subspecies *ruthveni*)1	"The dorsal color...is a light, grayish cream, more yellowish on the sides....Under the microscope no pigment granules are discernible except on the sides of the belly, where on each side two small, black spots are formed by a concentration of dark pigment granules" (p. 343, Smith, 1943).	Bundy, 1955 Dixon, 1967 Lewis, 1949 Smith, 1943
Cowles prairie lizard (*Sceloporus undulatus* subspecies *cowlesi*)2	"On the middorsal surface of the body there is a broad light blue stripe" from the head to the base of the tail. "This wide light blue stripe is bordered on either side by complete light tan...stripes" alternating with white stripes. The top of the tail is bluish towards the base and grades into pale gray towards the tip. The underside of the tail "is pure white." (p. 127, Lowe and Norris, 1956)	Dixon, 1967 Lowe & Norris, 1956
Little striped Whiptail (*Aspidoscelis inornata*, formerly *Cnemidophorus inornatus*)	Color "is strikingly different from typical normal colored samples from southern New Mexico." In Las Cruces, the ground color is "dark brown to chocolate brown with the 7 white lines greatly contrasting against the dark ground color." (p. 17). In dunes populations, "the ground color is pale yellowish-gray to pale bluish-gray with the 6 to 7 light stripes present but somewhat obscure. The limbs are pale blue without a suffusion of grayish bars on the dorsal surfaces in most specimens. The head is light brown to gray-blue in females, bright sky-blue to blue in males" (pp. 16-17, Lowe and Norris, 1956).	Dixon, 1967
Amphibians Spadefoot toad (*Scaphiopus couchii*)	"completely white except for black eyes and black marks on the underside of the hind feet." (p. 232)	Stroud, 1949
Mammals Apache pocket mouse (*Perognathus flavescens* subspecies *apachii*)1, 3	Fur color ranges "from white almost to the yellow color normally found in apache pocket mice. The majority are nearly white and match the color of the background very well." (p. 27, Benson, 1933)	Benson, 1933

Species	*Description of coloration*	*Source*
White sands wood rat (*Neotoma micropus* subspecies *leucophaea*)1, 4	"Upper parts pale ashy gray or near pale smoke gray, purest on cheeks, shoulders, and sides, the top of head and back thinly mixed with black producing a finely lined effect; under parts white." (p. 472, Goldman, 1933	Goldman, 1933
Spotted ground squirrel (*Spermophilus spilosoma*)	"somewhat paler than the Alamogordo specimens." (p. 220, Blair, 1941).	Blair, 1941 ***Source***
Insects		
Camel cricket (*Ammobaenites phrixocnemoides* subspecies *arenicolus*)1	"Wholly colorless,...a translucent white..., the eyes are black and the spurs and spines are reddish but unpigmented." (p. 242).	Stroud, 1950
Camel cricket (*Daihinoides hastiferum* subspecies *larvale*)1	"Entirely white and the light color must be due to a lack of any pigment as one can see through the epidermis and observe internal organs" (Bugbee, 1942).	Bugbee, 1942 Stroud, 1950 Stroud & Strohecker, 1949
Locustid (*Cibolacris parviceps arida*)	"Reddish brown specimens were taken on red soil near La Luz, but those from the White Sands dunes area were very light in color" (p. 676).	Stroud, 1950
Tiger beetle (*Cicindela praetextata*)	Some beetles "were very near the typical form but others have very broad white margins covering more than half the elytra" (p. 676).	Stroud, 1950
Arachnids		
Lycosid spider	"brown in basic color but its abdomen usually appeared as if covered with hoar-frost. This white color was easily rubbed off when individual specimens were handled."	Bugbee, 1942
Scorpion (*Vejovis boreus*)	"light-colored"	Bugbee, 1942
Solpugid (*Eremobates affinis*)	"white in color"	Bugbee, 1942

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1 Endemic subspecies (i.e., subspecies is found only in the White Sands dune field).

2 A different subspecies (S. u. tristichus) is dark at the Valley of Fires (Lewis, 1949).

3 A related species (P. intermedius ater) is dark at the Valley of Fires (Dice, 1929).

4 A related species (N. albigula melas) is dark at the Valley of Fires (Dice, 1929)

Table 2: Probable mechanisms of color change for light-colored species at White Sands National Monument.

Mechanism of color change	*Species*	*Basis for conclusion*	*Source*
Color fixed in individuals	Bleached earless lizard *(Holbrookia maculata* subspecies *ruthveni)*	- Individuals held in lab on different-colored substrates do not change color. - Offspring from White Sands mothers are light in color when raised in the lab.	Bundy, 1955 Lowe & Norris, 1956 Rosenblum, in review
	Cowles prairie lizard *(Sceloporus undulatus* subspecies *cowlesi)*	- Individuals held in lab with different-colored substrates do not change color. - Offspring from White Sands mothers are light in color when raised in the lab.	Lowe & Norris, 1956 Rosenblum, in review
	Little striped Whiptail (*Aspidoscelis inornata* formerly *Cnemidophorus inornatus*)	- Individuals held in lab with different-colored substrates do not change color. - A single gene (the Mc1r gene) is highly associated with light coloration.	Lowe & Norris, 1956 Rosenblum 2004
	Apache pocket mouse *(Perognathus flavescens* subspecies *apachii)*	- Dark individuals of the related P. intermedius ater from Valley of Fires held in lab with different-colored substrates do not change color.	Benson, 1933
	Camel cricket *(Ammobaenites phrixocnemoides* subspecies *arenicolus)*	- Assertion by author.	Stroud, 1950
	Camel cricket (*Daihinoides hastiferum* subspecies *larvale*)	- Assertion by author.	Stroud, 1950
Color changes rapidly to match substrate	Spadefoot toad (Scaphiopus couchii)	- Individuals in lab do change color.	Stroud, 1949
Color changes at molt to match substrate	Locustid (Cibolacris parviceps subspecies arida)	- Assertion by author.	Stroud, 1950
Color derived from environment	Lycosid spider	- White color rubs off easily to reveal brown underneath; color may still be internally derived.	Bugbee, 1942

Literature Cited:

Bagnara, J.T., and M.E. Hadley. 1973. Chromatophores and color change: the comparative physiology of animal pigmentation. Prentice Hall, Inc., NJ.

Benson, S.B. 1933. Concealing coloration among some desert rodents of the southwestern United States. Univ. Calif. Pub. Zool. 40:1-70.

Blair, W.F. 1941. Annotated list of mammals of the Tularosa Basin, New Mexico. Am. Midl. Nat. 26:218-229.

Blair, W.F. 1943. Ecological distribution of mammals in the Tularosa Basin. Contrib. Lab. Vert. Biol., U. Mich. 20:1-24.

Bugbee, R.E. 1942. Notes on animal occurrence and activity in the White Sands National Monument, New Mexico. Trans. Kans. Acad. Sci. 45:315-321.

Bundy, R.E. 1955. Color Variation in Two Species of Lizards (Phrynosoma modestum and Holbrookia maculata subspecies) (Ph.D.): University of Wisconsin.

Chapman, R.F. 1969. The Insects: Structure and Function. American Elsevier Publishing Co., Inc, NY.

Dice, L.R. 1929. Description of two new pocket mice and a new woodrat from New Mexico. Occas. Papers Mus. Zool., U. Mich. 203:1-4.

Dixon, J.R. 1967. Aspects of the biology of the lizards of the White Sands, New Mexico. Contrib. Sci 129:1-22.

Goldman, E.A. 1933. New mammals from Arizona, New Mexico, and Colorado. J. Wash. Acad. Sci. 23:463-473.

Hager, S. B. 2000. Variation in body temperature and thermoregulatory behavior between two popultions of the lesser earless lizard, Holbrookia maculata. Contemp. Herp. 2000:online.

Hager, S. B. 2001. Microhabitat use and activity patterns of Holbrookia maculata and Sceloporus undulatus at White Sands National Monument, New Mexico. J. Herp. 35:326-330.

Hager, S. B. 2001. Quantification of body coloration for the lesser earless lizard, Holbrookia maculata: Evidence for interpopulational differences. Southwest. Nat. 47:229-307.

Kiltie, R. A. 1992. Tests of hypotheses on predation as a factor maintaining polymorphic melanism in coastal-plain fox squirrels Sciurus niger L. Biol. J. Linn. Soc. 451:17-38.

Lewis, T.H. 1949. Dark coloration in the reptiles of the Tularosa malpais, New Mexico. Copeia 3:181-184.

Lowe, C.H., and K. S. Norris. 1956. A subspecies of the lizard Sceloporus undulatus from the White Sands of New Mexico. Herpetologica 12:125-127.

Moritz, C.,1999. Conservation units and translocations: Strategies for conserving evolutionary processes. Hereditas 130:217-228.

Norris, K.S., and C.H. Lowe. 1964. An analysis of background color-matching in amphibians and reptiles. Ecology 45:565-580.

Norris, K. S. 1965. Color adaptation in desert reptiles and its thermal relationships. Lizard Ecology: A Symposium. ed W.W. Milstead. University of Missouri Press, MI.

Rosenblum, E.B. in review. The role of phenotypic plasticity in color variation of Tularosa Basin lizards.

Rosenblum, E.B. in review. Convergent evolution and divergent selection: lizards at the White Sands ecotone

Rosenblum, E.B. in prep. Ecological divergence and mating preference in the Lesser Earless Lizard.

Rosenblum, E.B., H.E. Hoekstra, and M.W. Nachman. 2004. Adaptive reptile color variation and the evolution of the Mc1r gene. Evolution 58:1794-1808.

Smith, H.M. 1943. The White Sands earless lizard. Zool. Ser. Field Mus. Nat. Hist. 24:339-344.

Smith, H.M. 1946. Handbook of Lizards: Lizards of the United States and of Canada. Comstock Publishing Co., Ithaca, NY.

Stroud, C.P. 1949. A white spadefoot toad from the New Mexico White Sands. Copeia 1949:232.

Stroud, C.P. 1950. A survey of the insects of White Sands National Monument, Tularosa Basin, New Mexico. Am. Midl. Nat. 44:659-677.

Stroud, C.P., and H.F. Strohecker. 1949. Notes on White Sands Gryllacrididae (Orthoptera). Proc. Ent. Soc. Wash. 51:125-126.

Zim, H.S., and H.M. Smith. 1987. Reptiles and Amphibians. Golden Press, NY.

White Sands weevil