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Original Investigation

# Pelage color variation in pocket gophers (Rodentia: Geomyidae) in relation to sex, age and differences in habitat

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ABSTRACT

Pelage coloration is a phenotypic characteristic in mammals that could be associated with an individual's survival and fitness; thus coloration gains adaptive importance. In geomyids, pelage coloration shows a relationship with the color of soils on which they live, mainly freshly dug soil of their burrows. This characteristic could be due to a camouflage adaptation to avoid predators. Pocket gophers disperse aboveground to establish a territory before they reach reproductive condition, and males disperse longer distances than females. The aim of this study was to evaluate pelage color variation in pocket gophers (*Thomomys anitae*) in relation to habitat differences, sex, and age, and determine its association to the color of the soil on which they live. Brightness of *T. anitae*'s dorsal pelage coloration and that of soil samples from five different habitats in the Baja California peninsula, Mexico were measured to test four hypotheses: (1) Subadults show a wide coloration range, but extreme colors are lost in adulthood due to natural selection. (2) Males are more vulnerable to depredation than females; therefore, males' coloration is more homogenous as a protective camouflage. (3) In open habitats pocket gophers are more exposed to being detected by predators, therefore their pelage coloration pattern is less variable than that of individuals from habitats with more vegetation cover. (4) Pelage coloration better matches soil coloration in moist conditions similar to that of freshly dug soil of their burrows. The results confirmed our predictions; however, selection does not impose an equal pressure on pelage coloration on the five habitats evaluated; other factors such as population density and predator presence need to be assessed. The strongest effects are found in the most open habitat, and there is less strong support for predictions in habitats where predator assemblage is diminished.

## Introduction

Pelage coloration in mammals is an important phenotypic characteristic that permits an individual to interact with other animals and with its environment (Lai et al. 2008). Pelage color usually varies to some degree across individuals in many species (Davis and Castleberry 2010); consequently, coloration could be associated with survival as a component of an individual's fitness (Lai et al. 2008). Based on the hypothesis that different parts of the body in different mammal species are subject to several selective pressures, pelage coloration has a great adaptive importance (Caro 2005). The three most important adaptive functions of pelage are concealment, communication, and thermoregulation (Cott 1940; Caro 2005; Lai et al. 2008). In general, prey animals have evolved a variety of visual characteristics in order to minimize detection by predators (Rowland 2009); therefore, color patterns should be inconspicuous or cryptic against visual background (Endler 1990). Similarly, pelage color patterns provide crypsis for predators while hunting (Ortolani 1999). Contrary to crypsis or camouflage, for efficient intraspecific communication (e.g., courtship, territoriality, or alarm signals) and in interspecific signals (aposematic coloration), color patterns in mammals should be as conspicuous as possible (Endler 1990; Caro 2005). Additionally, coloration in mammals might affect temperature exchange with their environment and thus their thermoregulatory properties. The relationship between pelage coloration and solar heating varies significantly, e.g., darker colors either may increase or decrease heat gain (Burtt 1981; Walsberg 1983).

Albeit mammalian coloration could be diverse, many species have pelage that appears drab in color, and may range only in shades of brown to black (Davis and Castleberry 2010). Generally, uniform body coloration in rodents provides protective camouflage, which is believed to be driven by the need to avoid detection by avian and mammalian predators with the whole pelage matching the background where animals are active (Sumner 1921; Dice 1947; Lawlor 1976; Krupa and Geluso 2000; Caro and

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Stankowich 2010). In rodents such as pocket gophers (Geomyidae), pelage coloration is uniform, but it displays a wide intraspecific variability (Ingles 1950; Hafner et al. 2009). This characteristic has been related to different habitats occupied by different species or populations throughout their distribution, from desert to alpine environments (Patton and Brylsky 1987). Several studies have shown a relationship between pocket gophers' pelage color and that of soils on which they live (Ingles 1950; Kennerly 1954; Hendrickson 1972; Patton 1973; Krupa and Geluso 2000). Getz (1957) examined the association between pelage and soil coloration along altitudinal gradients. He observed that pocket gophers tend to be darker in highlands where soil is also darker, and lighter in lowlands where it is paler (Getz 1957). Similar results were obtained for populations from the Baja California peninsula, in Mexico, where pocket gophers inhabiting temperate forests in high elevations are darker than those living in desert habitats in the lowlands (Rios and Álvarez-Castañeda 2007).

The pocket gopher lives in a closed burrow most of its life adapted to an herbivorous fossorial habit (Patton 1972). However, young individuals are expelled from the mother's burrow when they are about 35 days old (Patton 1999). During dispersal pocket gophers need to move on the surface to a suitable unoccupied habitat, establishing a territory and building its own burrow system (Williams and Baker 1976; Jones and Baxter 2004). Dispersal occurs largely above ground during night time (Patton 1999). Daly and Patton (1990) observed that most aboveground movements that occurred for the gophers *Thomomys bottae* were before they reached reproductive condition. The authors found that males disperse longer distances than females with a maximum distance of 200 m of their natal range. Consequently, males are expected to face a higher predation risk than females. In particular, individuals having a coloration that contrasts with soil color could be more easily detected by predators. Adult dispersal is considered uncommon although Daly and Patton (1990) reported that some reproductive adults can disperse during the breeding season. Williams and Baker (1976) found that vagility in *T. bottae* is relatively low as compared to that of other pocket gopher species (e.g., *Pappogeomys castanops*). Nevertheless, it is possible that pocket gopher populations from the Baja California peninsula follow similar dispersal pattern like *T. bottae*, where males spend more time on the surface looking for territories than females do. In the past, populations from the Baja California peninsula were considered as *T. bottae* (Jones and Baxter 2004); however, such populations have been recently recognised as *T. anitae* (Allen 1898; Álvarez-Castañeda 2010). *Thomomys anitae* occurs throughout the Baja California peninsula in very diverse habitat conditions, including sand and desert lowlands to tropical deciduous forest and temperate forest in highlands (Patton 1999). In addition to dispersal, another potentially risky activity undertaken by geomyids occurs when individuals are shoving excavated soil out onto the ground surface (Andersen 1982), especially when their background is composed of a mound of recently excavated soil. Krupa and Geluso (2000) found that pelage coloration of one pocket gopher species (*Geomys bursarius*) matches the color of the freshly dug soil of their burrows, suggesting it is due to a camouflage adaptation to avoid predators.

The purpose of this paper is to evaluate pelage color variation in pocket gophers in relation to habitat differences, sex, and age, and determine if their coloration is related to the color of the soil on which they live. We focussed on more specific questions on adaptive coloration functions in a species for which data on aboveground dispersal and activities are scarce. We evaluated *T. anitae*'s dorsal pelage coloration from five different populations in the Baja California peninsula, comparing between sexes, adults, and subadults, and its relationship to soil coloration as possible protective camouflage. We tested four specific hypotheses that derived from previous studies: (1) Subadults show a wide coloration range, but extreme colors are lost in adulthood due to natural selection. Therefore, we expect higher variation in coloration patterns in subadults than in adults. (2) Males spend more time on the surface searching for territories, thus they are more exposed to predation, and consequently surviving males' coloration better matches soil color than that of females as a protective camouflage. Therefore, males' coloration will be more homogenous than that of females. (3) In open habitats pocket gophers are more exposed to be detected by predators. Based on a vegetation cover gradient, in open areas we would expect to find pocket gophers with a coloration pattern that matches soil color and less variable than that of individuals from closed habitats, because individuals with conspicuous coloration in poor vegetation cover are more easily predated. (4) All individuals' pelage coloration better matches soil coloration in moist conditions, which is similar to the color of the mound built with excavated soil and deposited aboveground, where pocket gophers are more frequently exposed while shoving it out onto the ground surface.

## Material and methods

### *Sampling strategy*

We analysed skin samples of pocket gopher specimens (*Thomomys anitae*) from five localities collected from 1993 to 2007 (Fig. 1, Appendix A, Supplementary information). To avoid seasonal effects on coloration changes, we only used specimens collected at each locality in autumn or winter. These localities encompass a range of habitat types at different latitudes and vegetation cover: (1) El Rosario, a coastal Mediterranean scrub with an open area mainly farmed with alfalfa and barley fields and surrounded by natural vegetation with agaves; (2) the Vizcaino Desert, an open area of sandy desert with crop fields; (3) La Paz, an urban area with desert scrub patches and grassland with some scattered fruit trees; (4) Valle de La Laguna, an open valley with grasslands bordered by pine–oak woods and a temperate forest on the upper part of a mountain; and (5) Santa Anita, a desert scrub area with tropical climate, many crop fields, and fruit trees, which is the habitat with more vegetation cover. The specimens are housed in the Mammal Collection of the Centro de Investigaciones Biológicas del Noroeste (CIB; see online Appendix A, Supplementary information) for detailed information of samples) and kept under dark conditions. Skins of most specimens had not been treated with preservatives or exposed to chemicals and were kept for four years. Thus, we considered that skin coloration had not been affected.

In addition, ten soil samples were taken at each locality and analysed for coloration, except those from the temperate forest ($n = 2$), because the specimens collected were restricted to a very small and homogeneous habitat and soil coloration was very similar. Each soil sample was taken by digging the ground to a depth of 10–15 cm in the same area where the individuals were collected; samples were kept in paper bags.

### *Age determination*

Age class for each specimen was determined using the numerical scores defined by Daly and Patton (1986) based on the grade of closure of the supraoccipital–exoccipital and basioccipital–basiesphenoid sutures: sutures open (score 1), partly closed (score 2), or fused (score 3). An overall score from 2 to 6 was determined by summing the scores for each suture; midpoints between classes were distinguished. Each specimen was assigned to one of four age categories: an old adult scored 6 when cranial sutures were completely closed and the skull was very robust with a very prominent saggital crest; adult age scored 5 when only one suture was completely closed and