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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

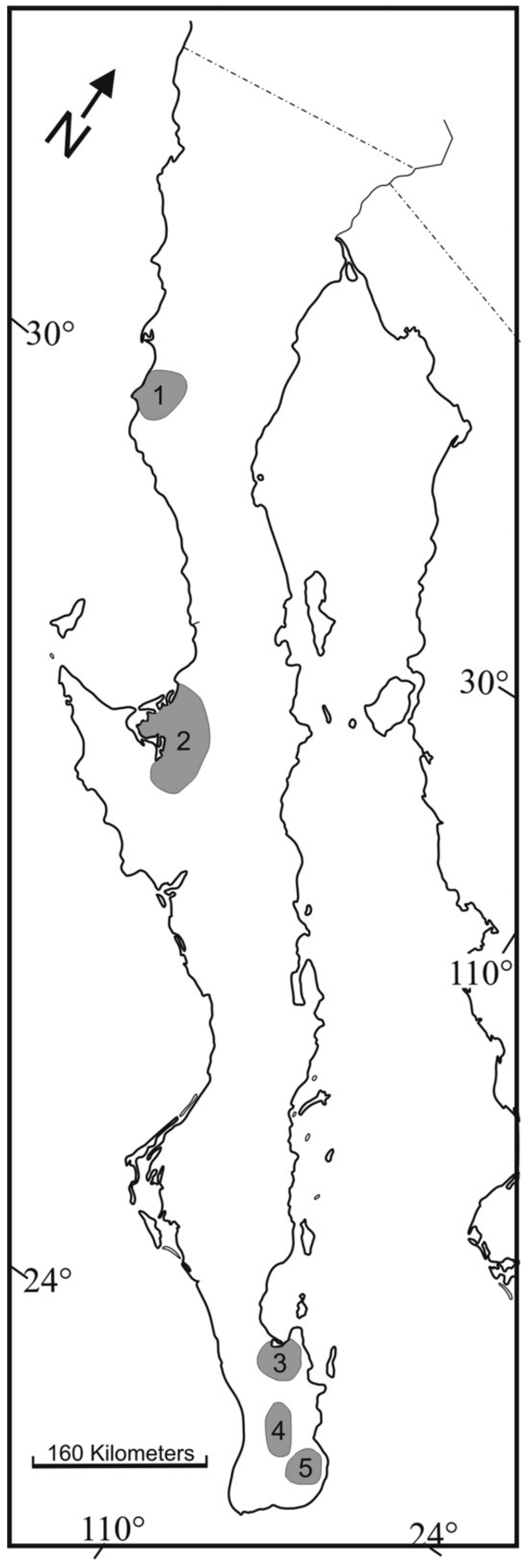

Fig. 1. Map showing sampling locations. Each locality is numbered as in the Materials and Methods section: (1) El Rosario, coastal Mediterranean scrub; (2) the Vizcaino Desert, sandy desert; (3) La Paz, urban desert scrub; (4) Valle de La Laguna, temperate forest; (5) Santa Anita, tropical desert scrub.

with a slightly prominent saggital crest; a sub-adult scored 3–4.5 when both sutures were not completely closed (skin of this age showed adult pelage); and a juvenile or young scored 4 or less (skin with juvenile pelage). Chronological age in juveniles is less than six months old (silky-gray pelage); young adults' or subadults' age is between 9 to 15 months old (dark reddish brown adult pelage); and adults are older than 18 months old (always with adult pelage; Daly and Patton 1986).

Coloration analysis

The pelage color of 222 specimens was determined with an X-Rite Digital Swatchbook® spectrophotometer (X-Rite, Inc., Grandville, MI, USA) and was compared to the CIE (Commission Internationale d'Eclairage, or International Commission on Illumination) Standard Illuminant F7 for fluorescent illumination, which represents a broad-band daylight fluorescent lamp (6500 K). We chose this standard as all the measurements were taken indoors under fluorescent ambient lighting. The instrument provides the reflectance spectrum (390–700 nm) of the object being measured, as well as tri-stimuli color scores (CIE X, Y, and Z). Color was measured on each individual specimen using a 3 mm-diameter port placed on the mid-dorsal surface on the nape behind the ears. Because of the small area actually measured, three separate measurements were taken and averaged. Only adult and subadult specimens of both sexes were analysed ($n = 222$); moulting individuals were excluded. Old adults and juvenile pocket gophers were also excluded because the sample size per locality was small or null (0–5 individuals), and they were not represented in all the study localities. In case of juveniles, all specimens were moulting; in this situation gray pelage coloration still prevails and is noticeably very different to the soil coloration of their habitat.

Soil color under dry and moist conditions was also recorded for all localities. Soil coloration was not measured in situ because ambient daylight varied in each habitat, which affects the reflectance spectrum of soil particles being measured by the spectrophotometer. Instead soil coloration was measured as pelage coloration was taken. On the other hand, we did not measure the terrestrial layer because our spectrophotometer only takes measurements of 3 mm in diameter on an object; therefore, measuring it would result in an impossible task. In the laboratory, we deposited each soil sample in a plastic container and measured its color under dry condition with the spectrophotometer taking three separate measurements that were then averaged. Subsequently, we sprinkled each sample with a constant volume of clean water sprayed from a constant distance (20 cm) and recorded its color under moist (not wet) conditions.

The variation in pelage and soil brightness was evaluated by adding the three color scores (CIE X, Y, and Z). When brightness is represented by the sum of the three variables, it is possible that pelages with very different colors (hue) have the same brightness. However, in our samples all populations are chromatically similar on the nape so that the brightness indices are meaningfully comparable (Álvarez Castañeda et al. 2009). A dispersion analysis (considering range between minimum–maximum values) was done to obtain variation in coloration brightness for samples from each habitat, sex and age group. A Kruskal–Wallis analysis (multiple comparisons with Dunn's method) was used to test for differences in pelage brightness between ages, sexes, and soil coloration (dry and moist) at each locality and also between different localities for individuals of the same age and same sex. The analyses were carried out with Statistica^{TM} ver. 5.0 (StatSoft, Inc., Tulsa, OK, USA) and SigmaStat ver. 3.10 (Systat Sofware, Inc., Point Richmond, CA, USA).

Results

Dispersion analysis indicated that subadult males showed a wider variation in color than adult males in two out of five studied populations (tropical desert scrub and sandy desert; Fig. 2, see horizontally). In temperate forest, female subadults had an ampler range than female adults. In urban desert scrub and coastal

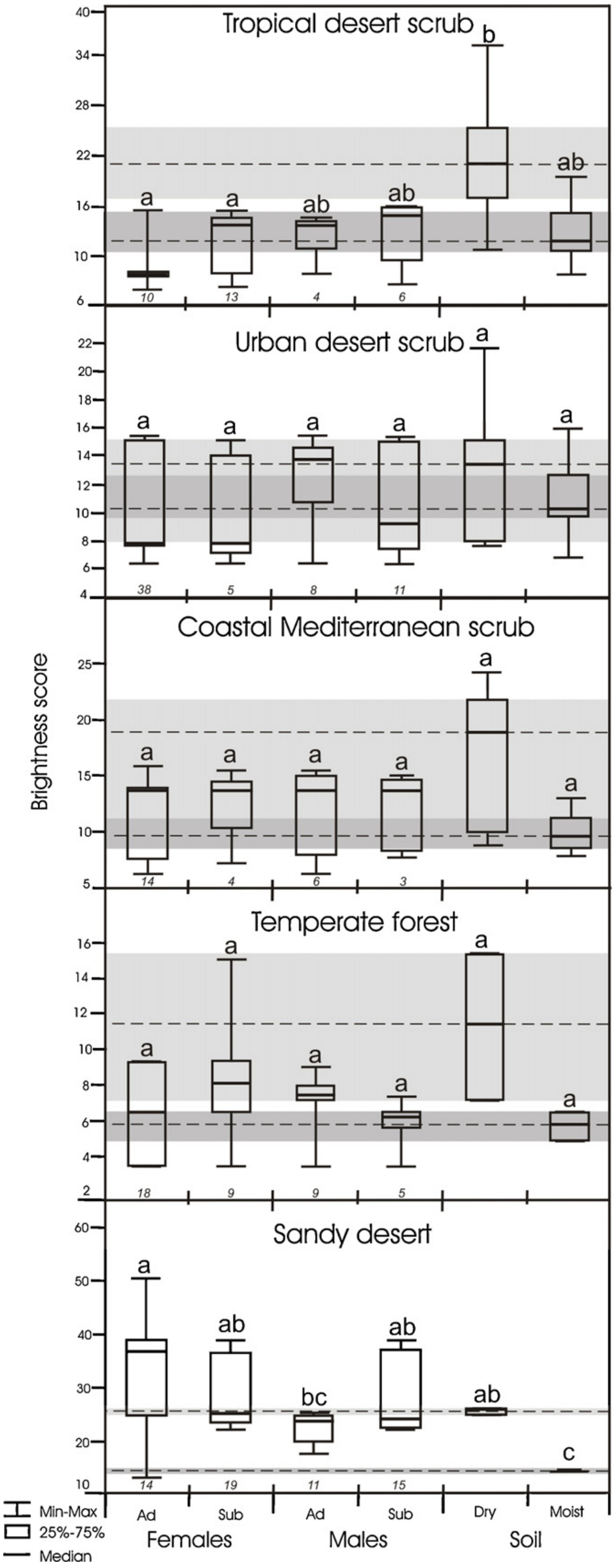

Fig. 2. Median, percentiles (25–75%), and minimum–maximum values of pelage brightness for each sex, age class, and habitat soil samples, respectively. Habitats are arranged along a gradient of high vegetation cover to open conditions. Shades represent percentile areas of soil brightness: light gray = dry soil; dark gray = moist soil. Different groups as result of post hoc pairwise multiple comparisons (Dunn's method) are indicated with different letter combinations (a, b, c, ab, bc). The Q values are provided in the text. The italic numbers under the bars indicate the sample size for each category of individuals.

Mediterranean scrub adult specimens were more or equally variable than subadults.

In all habitats, adult females were more variable in pelage brightness than adult males, except in urban desert scrub where both were equally variable. Also subadult females were more variable than subadult males in three habitats, urban desert scrub, coastal Mediterranean scrub, and temperate forest. In sandy desert, subadult males were as variable as subadult females. Only in the most open habitat, sandy desert, adult females differed from adult males in median coloration (Kruskal–Wallis test, $H = 35.15$, $df = 5$, 79, $P < 0.01$; post hoc pairwise comparisons, $Q = 3.17$, $\alpha = 0.05$).

The average variation coefficient indicated that pocket gopher specimens from urban desert scrub (locality 3 in Fig. 1) had a more variable coloration followed by those from tropical desert scrub (locality 5, habitat with more vegetation) and those from the coastal Mediterranean scrub (locality 1). Specimens with the lowest variation coefficient were those from sandy desert (locality 2); which is the habitat with less vegetation cover.

The Kruskal–Wallis analysis followed by Dunn's multiple comparisons test ($\alpha = 0.05$) showed that specimens of both sexes and age classes were not significantly different from dry soil color in all the localities except for tropical desert scrub where dry soil color was significantly lighter (more brightness) than that of females, both adults and subadults (Kruskal–Wallis, $H = 20.12$, $df = 5$, 55, $P < 0.01$; post hoc pairwise comparisons, $Q = 4.29$, and $Q = 3.19$, respectively). On the other hand, in the sandy desert moist soil was significantly darker (lower brightness) in color than that of adult ($Q = 5.37$) and subadult ($Q = 4.25$) females, subadult males ($Q = 3.85$), and dry soil ($Q = 4.15$).

Specimens from the sandy desert were significantly lighter in color than those from the other habitats. Adult females from this population were significantly lighter than those from all other habitats (Kruskal–Wallis, $H = 43.15$, $df = 4$, 94, $P < 0.01$); subadult females were more lightly colored than those from other habitats (Kruskal–Wallis, $H = 36.47$, $df = 4$, 50, $P < 0.01$), except for those from the coastal Mediterranean scrub; adult males were more lightly colored than those from the coastal Mediterranean scrub and the temperate forest (Kruskal–Wallis, $H = 27.91$, $df = 4$, 38, $P < 0.01$); and subadult males were more lightly colored (Kruskal–Wallis, $H = 31.51$, $df = 4$, 40, $P < 0.01$) than those from the urban desert scrub and the temperate forest (Fig. 2, see vertically).

Discussion

This study shows a number of associations between pelage variation in color brightness of pocket gophers and biological and ecological variables. In general, the results confirm the hypotheses but show additionally that habitat characteristics have to be considered because they determine the level of natural selection pressures.

As predicted, we found less variation in coloration patterns in adults than in subadult individuals, indicating that young individuals with extreme colors are lost in the population due to natural selection. However, in two habitats (coastal Mediterranean scrub and desert urban scrub) the pelage color variation was not wider for subadults; therefore, the data showed that selection acts differentially on pelage coloration on the evaluated habitats.

In all cases, adult males' pelage coloration was more uniform than that of adult females, except in urban desert scrub where both female and male are equally variable. This result indicates stronger negative selection on males because they spend more time on the surface searching for territories, and extreme colors result more vulnerable to predation. Daly and Patton (1990) reported philopatry in pocket gopher females because they found the ratio female/male of 1:1.2 of individuals seen within 40 m of their original place; 1:1.75 had moved between 40–100 m, and 1:4 moved between 100–200 m. Adult female dispersal is not common; they establish a territory and breed at younger ages than males (about one year old in females and after 15 months old in males; Daly and Patton 1990). Therefore, males are more vulnerable to above ground predation, which is further revealed by a female-biased adult sex ratio (2.6:1). A sex ratio skewed towards females is a common characteristic of pocket gophers. Daly and Patton (1990) found in *T. bottae* populations from California that a three-year sex ratio always favoured females, which rose partly because adult females lived longer than males; sex ratio was 1.7:l in one-year old individuals compared to 3.7:1 in older animals.

We found an association between having a less variable color and living in open habitats where visibility might be high, and individuals with conspicuous pelage coloration were more vulnerable to predation. Pocket gopher specimens from sandy desert, which is the habitat with less vegetation cover, showed less brightness variation. On the contrary, specimens from urban desert scrub showed a more variable coloration followed by those from tropical desert scrub, where both habitats have more vegetation cover. Several experiments have demonstrated selection of rodents with a conspicuous pelage by owls and serpents, in both light-colored and dark soils (Smith and Watson 1972; Kaufman 1974, 1975; Clarke 1983; Brown et al. 1988), which implies that a conspicuous pelage is more easily predated, particularly when vegetation cover is sparse. Vegetation cover in the tropical desert scrub is very dense, which probably could affect raptors' effectiveness. In the urban desert scrub gophers were collected within urban areas, where a reduced activity of raptors could be expected. An analysis of pellets of the owl *Tyto alba* in La Paz area indicated low predation on pocket gophers (Álvarez-Castañeda et al. 2004). Habitats with intermediate vegetation cover also showed intermediate variation in color pelage (e.g., Mediterranean scrub). Thus, in open habitats coloration pattern of all pocket gopher categories was less variable than that of individuals from habitats with more vegetation cover.

Pelage coloration of analysed individuals matched soil coloration; nevertheless, they matched better to dry soil coloration rather than to that one in moist conditions; contrary to what Krupa and Geluso (2000) suggested. Thus we found that in the Baja California peninsula, where there are mainly desert habitats with scarce humidity, soil coloration is pale and pelage coloration of pocket gophers matches that of the soil on which individuals are active. However, each habitat type showed minor differences. Urban and tropical desert scrubs showed a great variation in soil color over very short distances. Under those conditions, the pocket gopher coloration showed a wider variation. On the other hand, the temperate forest dry soils showed a wide coloration range around light coloration (high brightness), while the individuals showed the smallest variation range of pelage color in this study; they tended towards dark colorations, such as that of moist soil. In this locality we found more humidity and organic matter in the soil than in the other habitats.

In conclusion, the hypotheses were confirmed with our results; however, selection does not impose an equal pressure on pelage coloration on the habitats evaluated; other factors such as population density and presence of predators need to be assessed. The strongest effects are found in the most open habitats and there is less strong support for the predictions in habitats where predator assemblage is diminished. Our analysis provides important data about associations between pelage variation in color brightness of pocket gophers and biological and ecological variables. It is necessary to conduct detailed studies of the effect of predation selection on *T. anitae* in different habitats, on predators occurring at specific localities, their density, and the possibilities of consuming other preys available. On the other hand, studies about the dispersal pattern of Mexican pocket gophers, and particularly *T. anitae*, are a priority to know if these movements aboveground are similar to those reported for other fossorial rodents from other latitudes.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.mambio.2011.12.003.

References

Allen, J.A., 1898. Description of new mammals from western Mexico and Lower California. Bull. Amer. Mus. Nat. Hist. 10, 143–158.

Álvarez-Castañeda, S.T., 2010. Phylogenetic structure of the *Thomomys bottae–umbrinus* complex in North America. Mol. Phylogenet. Evol. 54, 671–679.

Álvarez-Castañeda, S.T., Cárdenas, N., Méndez, L., 2004. Analysis of mammal remains from owl pellets (*Tyto alba*), in a suburban area in Baja California. J. Arid Environ. 59, 59–69.

Álvarez Castañeda, S.T., Lidicker Jr., W.Z., Rios, E., 2009. Revision of the *Dipodomys merriami* complex in the Baja California Peninsula, Mexico. J. Mammal. 90, 992–1008.

Andersen, D.C., 1982. Belowground herbivory: the adaptive geometry of Geomyid burrows. Am. Nat. 119, 18–28.

Brown, J.S., Kotler, B.P., Smith, R.J., Wirtz II, W.O., 1988. The effects of owl predation on the foraging behavior of heteromyid rodents. Oecologia 76, 408–415.

Burtt Jr., E.H., 1981. The adaptiveness of animal colors. Bioscience 31, 723–729.

Caro, T., 2005. The adaptative significance of coloration in mammals. Bioscience 55, 125–136.

Caro, T., Stankowich, T., 2010. The function of contrasting pelage markings in artiodactyls. Behav. Ecol. 21, 78–84.

Clarke, J.A., 1983. Moonlight's influence on predator/prey interaction between short-eared owls (*Asio flammeus*) and deermice (*Peromyscus maniculatus*). Behav. Ecol. Sociobiol. 13, 205–209.

Cott, H.B., 1940. Adaptive Colouration in Mammals. Methuen, London.

Daly, J.C., Patton, J.L., 1986. Growth, reproduction, and sexual dimorphism in *Thomomys bottae* pocket gophers. J. Mammal. 67, 256–265.

Daly, J.C., Patton, J.L., 1990. Dispersal, gene flow, and allelic diversity between local populations of *Thomomys bottae* pocket gophers in the coastal ranges of California. Evolution 44, 1283–1294.

Davis, A.K., Castleberry, S.B., 2010. Pelage color of red bats *Lasiurus borealis* varies with body size: An image analysis of museum specimens. Curr. Zool. 56, 401–405.

Dice, L.R., 1947. Effectiveness of selection by owls of deer-mice (*Peromyscus maniculatus*) which contrast in color with their background. Contr. Lab. Vert. Biol., Univ. Mich. 34, 1–20.

Endler, J.A., 1990. On the measurement and classification of color in studies of animal color patterns. Biol. J. Linn. Soc. 41, 315–352.

Getz, L.L., 1957. Color variation in pocket gophers. Thomomys. J. Mammal. 38, 523–526.

Hafner, M.S., Hafner, D.J., Demastes, J.W., Hasty, G.L., Light, J.E., Spradling, T.A., 2009. Evolutionary relationships of pocket gophers of the genus *Pappogeomys* (Rodentia: Geomyidae). J. Mammal. 90, 47–56.

Hendrickson, L., 1972. Variation in the plains pocket gopher (*Geomys bursarius*) along a transect across Kansas and eastern Colorado. Trans. Kans. Acad. Sci. 75, 322–368.

Ingles, L.G., 1950. Pigmental variations in populations of pocket gophers. Evolution 4, 353–357.

Jones, C.A., Baxter, C.N., 2004. Thomomys bottae. Mammal. Species 742, 1–14.

Kaufman, D.W., 1974. Differential predation on active and inactive prey by owls. Auk 91, 172–173.

Kaufman, D.W., 1975. Concealing coloration: how is effectiveness of selection related to conspicuousness? Am. Midl. Nat. 93, 245–247.

Kennerly Jr., E., 1954. Local differentiation in the pocket gopher (*Geomys personatus*) in southern Texas. Texas J. Sci. 6, 297–329.

Krupa, J.J., Geluso, K.N., 2000. Matching the color of excavated soil: cryptic coloration in the plains pocket gopher (*Geomys bursarius*). J. Mammal. 81, 86–96.

Lai, Y.C., Shiroishi, T., Moriwaki, K., Motokawa, M., Yu, H.T., 2008. Variation of coat color in house mice throughout Asia. J. Zool. 274, 270–276.

Lawlor, T.E., 1976. Coat color adaptations of rodents occurring on lava beds: reanalysis of an exceptional case. J. Mammal. 57, 391–397.

Ortolani, A., 1999. Spots, stripes, tail tips and dark eyes: predicting the function of carnivore colour patterns using the comparative method. Biol. J. Linn. Soc. Lond. 67, 433–476.

Patton, J.L., 1972. Patterns of geographic variation in karyotype in the pocket gopher, *Thomomys bottae* (Eydoux and Gervais). Evolution 26, 574–586.

Patton, J.L., 1973. An analysis of natural hybridization between the pocket gophers, *Thomomys bottae* and *Thomomys umbrinus* in Arizona. J. Mammal. 54, 561–584.

Patton, J.L., 1999. Family geomyidae. In: Álvarez-Castañeda, S.T., Patton, J.L. (Eds.), Mamíferos del Noroeste de México. La Paz, BCS, México. Centro de Investigaciones Biológicas del Noroeste, pp. 321–350.

Patton, J.L., Brylsky, P.V., 1987. Pocket gophers in alfalfa fields: causes and consequences of habitat-related body size variation. Am. Nat. 130, 493–506.

Rios, E., Álvarez-Castañeda, S.T., 2007. Environmental responses to altitudinal gradients and subspecific validity in pocket gophers (*Thomomys bottae*). J. Mammal. 88, 926–934.

Rowland, H.M., 2009. From Abbott Thayer to the present day: what have we learned about the function of countershading? Philos. T. R. Soc. – B. 364, 59–527.

Smith, G.C., Watson, D., 1972. Selection patterns of corn snakes, *Elaphe guttata*, of different phenotypes of the house mouse, *Mus musculus*. Copeia 1972, 529–532.

Sumner, F.B., 1921. Desert and lava-dwelling mice, and the problem of protective coloration in mammals. J. Mammal. 2, 75–86.

Walsberg, G.E., 1983. Coat colour and solar heat gain in animals. Bioscience 33, 88–91.

Williams, L., Baker, R.J., 1976. Vagility and local movements of pocket gophers (Geomyidae: Rodentia). Am. Midl. Nat. 96, 303–316.