



Seasonal Variation in Pelage Coloration of California Ground Squirrels (*Otospermophilus beecheyi*) in Areas of Differing Land Use

David S. JACHOWSKI¹, Jason A. HUBBART^{2*}

¹ Department of Fisheries and Wildlife Sciences, University of Missouri, Columbia, Missouri, USA;

² Departments of Forestry and Soils, Environmental and Atmospheric Sciences, University of Missouri, Columbia, Missouri, USA

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Abstract

The alteration of pelage coloration in small mammals is critical to their ability to thermoregulate and reduce risk of depredation. Physiological condition and seasonal molt cycles both influence pelage coloration, but recent evidence suggests that human land use can influence the morphological characteristics of species. We monitored changes in California ground squirrel (*Otospermophilus beecheyi*) pelage coloration seasonally by measuring pelage luminosity, as well as color tone along two color spectra. We found that an interaction of season and land use type best explained the observed variability in pelage coloration. At sites with native or preserved habitat, *O. beecheyi* maintained lighter pelage coloration into the fall, but darker pelage coloration during the winter compared to sites on agricultural and pasture lands. Our findings suggest that site-specific differences in land use practices could influence the overall coloration of individuals as well as the timing of pelage molts. Our findings also support the concept that *O. beecheyi* is a generalist species with the ability to adapt to human land use changes. More broadly, our findings raise questions regarding the ability of more specialized species to similarly alter pelage coloration as an adaptive strategy to increasingly human-altered landscapes.

Key words: Pelage, California ground squirrel, *Otospermophilus beecheyi*, land use, coloration, molt

*Corresponding Author: J.A.Hubbart, e-mail: hubbartj@missouri.edu, Phone: +15738847732, Fax: +15738821977

INTRODUCTION

There is variability among small mammals in their vulnerability to habitat change. An increasing amount of attention is being placed on the response of small mammals to natural disturbance (Krefting and Ahlgren 1974), human land use (Fitzgibbon 1997) and most recently, climate change (Moritz et al. 2008). Generalist small mammal species, such as *Peromyscus leucopus*, are able to alter their behavior (McCormick and Meiners 2000) and demographic structure (Adler and Wilson 1987) in response to altered habitat conditions. In contrast, highly specialized species tend to exhibit less plasticity, which tends to make them more vulnerable to extirpation (Clavel et al. 2011). However, it is difficult to classify small mammal species as generalists or

specialists given that closely related species can respond differently to changes in habitat conditions (Moritz et al. 2008). To predict the impact of habitat change on small mammals, insight is required regarding the factors that influence particular small mammal species, as well as into the ability of a species to exhibit plasticity in life history traits that allows them to tolerate changes to their surroundings.

Modification of pelage coloration is an important adaptive strategy for many species, particularly small mammals due to their need to thermoregulate and to mitigate high risks of depredation. Solar radiation plays an important role in the management of internal temperature in small mammals, and seasonal alterations in pelage can significantly

influence heat-transfer processes (Walsberg 1990; Walsberg et al. 1997). Adaptive coloration of small mammals, in parallel with background color in their surrounding environments, also is important in minimizing predation risk (Belk and Smith 1996, Caro 2005). Correspondingly, multiple species have adapted seasonal or site-specific pelage coloration patterns that resemble the coloration of the surrounding environment (Severaid 1945; Belk and Smith 1996).

The California ground squirrel, *Otospermophilus beecheyi*, is commonly identified as having a dark brown head, dingy off-white neck and shoulders, and a conspicuous dark triangle on the back between the shoulders (Burt and Grossenheider 1980). Similar to most mammals, *O. beecheyi* has a seasonal molt cycle (Burt and Grossenheider 1976; Hall 1981; Ingles 1965; Tomich 1962). Juvenile *O. beecheyi* emerge from hibernation in May with a sparse, light-colored coat, which is replaced by a more darkly colored coat by late July (Evans and Holdenried 1943). Adults typically begin molting in May; adult males have new pelage by late June and adult females delay the complete growth of new hair until the end of lactation, typically around the end of August (Evans and Holdenried 1943). However, in the last 100 years, field observations have documented a variety of color variations in this species ranging from an overall brown, gray, red or rufous, to blonde or off-white coloration (Grinnell and Dixon 1918; Tomich 1962; Ingles 1965; Burt and Grossenheider 1976; Hall 1981).

While seasonal variations among habitat types, particularly those at differing elevations, are one potential explanation for the observed variation in pelage coloration of this species, human-induced habitat modification also could explain some of the observed variation in pelage coloration (Carraway and Verts 2002, Hale and Lurz 2003). In response to human land use change, small mammals can exhibit flexible demographic, behavioral, or morphological responses (Dickman and Doncaster 1989). The ability of *O. beecheyi* to adapt to and utilize human-modified habitats has enabled it to persist under such conditions, leading Marsh (1998) and Hubbart (2002) to classify it as a generalist species. Beyond demographic evidence, *O. beecheyi* exhibits behavioral plasticity in response to land use changes. For example, Rabin et al. (2006) documented that *O. beecheyi* exhibited elevated vigilance on sites where wind energy development occurred, likely in response to increased noise associated with wind turbines or a more open environment.

In this study we investigated pelage coloration of *O. beecheyi* in habitats representing three land use types to test the hypothesis that modification of habitat by human activity influences the pelage characteristics of this species. We seasonally sampled *O. beecheyi* from native habitat,

agricultural fields, and pasture land to compare seasonal pelage luminosity, as well as color spectra among sites and seasons.

MATERIAL AND METHODS

Study Sites

Research was conducted in Fresno and Madera counties in the south central region of the San Joaquin Valley, California, USA (Fig. 1). Specimens were collected only from the valley floor to avoid confounding the results with elevation-induced ecological and/or environmental effects. All study sites were within approximately 40 km of each other, but were geographically isolated to the extent that movement of individuals between populations was unlikely. Climate attributes were similar for all three study sites. Average annual precipitation ranged from 20-25 cm, average annual temperature was 17°C, and average annual frost-free season ranged from 225-250 days (Hubbart 2002). Prior to human development, study sites were savannah and oak grassland landscapes. They were converted to agriculture in the mid 1900's and then to the land use types present during this work (described below) in the early 1980's.

Study site one was approximately 32 ha, with an elevation of approximately 65 m, near Kerman, California (36°41'37"N, 120°03'17"W). The site was classified as a "preserve" and had not been treated with pesticides or grazed by livestock for more than ten years prior to this study. The vegetation community was classified as "California annual grassland series" and included species of *Bromus*, *Hordeum*, *Vulpia*, and *Erodium* (Sawyer and Keeler-Wolf 1995; Hubbart 2002). Soils were Hesperia sandy loam and were well to moderately well drained, with available water holding capacity ranges from 10-25cm (Huntington 1971).

Study site two was approximately 112 ha, with an elevation of approximately 112 m, near Madera, California (36°57'56"N, 119°49'52"W). The site was classified as "pasture" due to persistent cattle grazing and had no pesticide applications for more than ten years prior to this study. Vegetation was classified as "California annual grassland series" (Sawyer and Keeler-Wolf 1995, Hubbart 2002). Soil types consisted of Atwater loamy sand, Bear Creek loam, and Cometa sandy loam (Ulrich and Stromberg 1962). All soil types were a moderate to well-drained sandy loam (Ulrich and Stromberg 1962).

Study site three was approximately 16 ha, with an elevation of approximately 114 m, near Sanger, California (36°46'02"N, 119°35'36"W). The site was classified as "agriculture" and was regularly treated with pesticides, insecticides, and/or herbicides over the past ten years while

under almond grove production (Hubbart 2002). Sawyer and Keeler-Wolf (1995) classified the habitat type as ruderal (plant species that are first to colonize disturbed lands). Due to frequent use of herbicides, this site had relatively low abundance and diversity in vegetation. Dominant vegetation included species of puncture vine (*Tribulus terrestris*), *Echinochloa* spp., *Salsola tragus*, *Conyza bonariensis*, and *Amaranthus* spp. (Hubbart 2002). Site three consisted of well-drained Atwater sandy loam soils (Ulrich and Stromberg 1962).

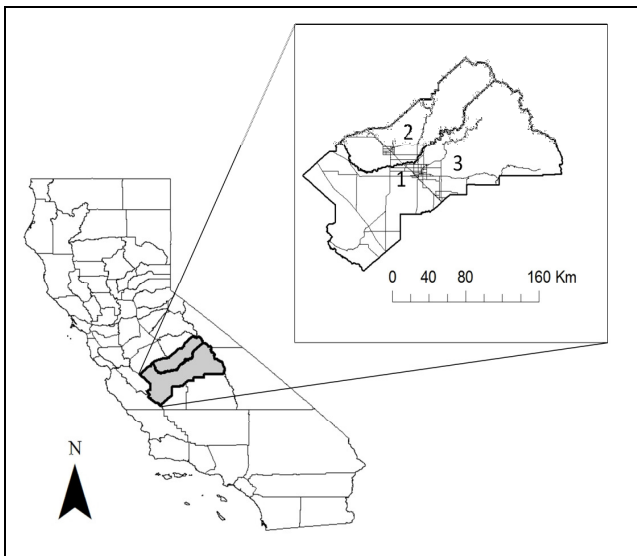


Figure 1 Location of study area in Fresno and Madera counties in the south-central region of the San Joaquin Valley, California (USA). California ground squirrels (*Otospermophilus beecheyi*) were sampled from three study sites (inset map) highlighted 1 (preserve), 2 (pasture), and 3 (agriculture)

Field Sampling

We examined preserved laboratory specimens of *O. beecheyi* collected during the course of previous research projects (see Anderson 2000 and Hubbart 2002) during each of four annual seasons (i.e. spring, summer, fall and winter) in each of the study sites. Specimens were collected during spring (March-May), summer (June-August), fall (September-November), and winter (December-February) between April 2001 and January 2002. During each season, researchers visited sites and secured the first 15 individuals encountered in an attempt to avoid bias towards certain age, sex, and/or size classes (see Hubbart 2002). Upon collection in the field, *O. beecheyi* were immediately placed in a sterile sealable bag and placed in a 20° C freezer (Hubbart et al. 2011). Specimens remained in the 20° C freezer until pelage was sampled in the laboratory.

Laboratory Analysis

We photographed each specimen of *O. beecheyi* using an Olympus C-3000 Zoom Digital Camera with a resolution of 2048/1536 pixels per image mounted 0.5 m above the specimen. For each specimen, we photographed 6 locations along the dorsal side (Fig. 2). Location A was at the top of the head centered between the ears. Locations B, C, E, and F were lateral to the midline (two on each side) of the animal within a rectangular pattern measuring 3 cm by 4 cm below mid-torso to above the tail. Location B was on the left side at mid-torso. Location C was approximately 2-3 cm posterior to spot B. Location D was 1 cm forward of the base of the tail, location E was chiral (opposite the midline) to spot C and location F was chiral to location B.

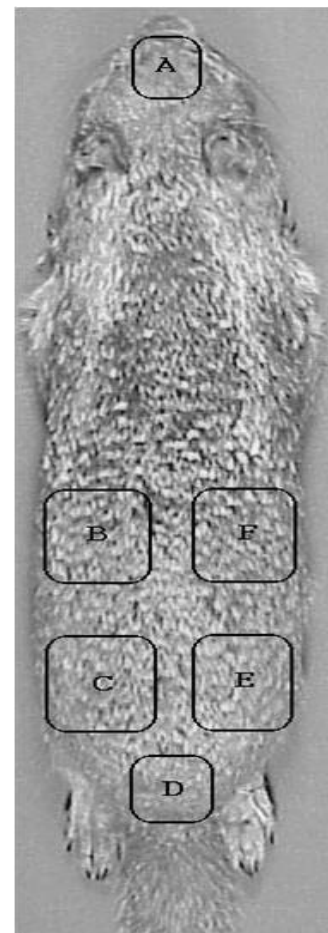


Figure 2 Six locations of photographic analyses of pelage coloration on California ground squirrels (*Otospermophilus beecheyi*).

We measured the color of each digital photograph in Adobe Photoshop© analysis software (Adobe Systems Inc.,

San Jose, California), using the techniques outlined in Anderson (2000). We used a Gaussian blur filter with a 13-pixel radius to average the colors of the pelage to allow for a better representation, thus moderating color extremes (Anderson 2000). Each image was analyzed using the *L-A-B* color setting to allow for truer color representation (International Commission on Illumination 1971), where *L* represents luminance, which ranges from white (100) to black (0), *A* represents the green (-120) to magenta (120) color spectrum, and *B* represents the blue (-120) to yellow (120) color spectrum.

Data Analysis

For each specimen, we used multivariate analyses to evaluate the influence of habitat type, season, and squirrel age and sex on *L*, *A*, and *B* coloration. We averaged color values at 6 locations on each squirrel for each color spectrum independently and treated this mean value as the dependent variables in an analysis of variance. We identified independent variables for inclusion in our model based on an *a priori* literature review, where we found support to include independent variables for sex, age class, and season. We included habitat type as an independent variable, and given that habitat conditions are likely to vary seasonally among the sites of different land use types, we included a habitat*season interaction. We set $\alpha= 0.05$ for evaluating statistical significance. When interactive effects were supported, we selected and interpreted interactions in favor of main effects models.

RESULTS

We analyzed the coloration of 181 specimens of *O. beecheyi* collected seasonally across each of our three study sites. Generally, the morphological characteristics of specimens were found to be within normal parameters of *O. beecheyi* as reported by Anderson (2000) and others (Grinnell and Dixon 1918; Tomich 1962; Ingles 1965; Burt and Grossenheider 1976; Hall 1981). However, we observed a relatively high degree of variation in our three measures of pelage coloration that were most consistently explained by a significant interactive effect of season and habitat type (Table 1).

Luminance (*L*) of *O. beecheyi* pelage exhibited a trend of being lowest in the spring, summer and fall, being 3-23% higher during the winter at the agriculture and pasture sites (Fig. 3, inset A). In contrast, at the preserve site, luminance was 29% and 42% lower during the winter compared to the pasture and agriculture sites respectively, and 43% lower

during winter than when the same preserve site was sampled during the fall (Fig. 3, inset A).

We observed that differences in coloration on the green to magenta color spectrum (*A*) were greatest in the fall (Fig. 3, inset B). We observed similar *A* spectrum coloration patterns among sites during spring, summer, and winter (Fig. 3, inset B). During the fall, *A* spectrum coloration was 21% and 28% higher, and closer toward red or magenta coloration, at the preserve site compared to the pasture and agriculture sites respectively.

Table 1 Results of analysis of variance procedure used to evaluate support for factors hypothesized to influence California ground squirrel pelage luminance measured in the white to black color spectrum (*L*), green to magenta color spectrum (*A*) and blue to yellow color spectrum (*B*).

Color spectrum	Effect	<i>F</i>	<i>DF</i>	<i>P</i>
L	Sex	1.64	1	0.2081
	Age	13.99	1	0.0003
	Season	1.24	3	0.2977
	Habitat	1.58	2	0.2091
	Season*Habitat	10.81	6	<0.0001
A	Sex	1.24	1	0.2666
	Age	0.34	1	0.5592
	Season	3.55	3	0.0160
	Habitat	1.45	2	0.2367
	Season*Habitat	5.73	6	<0.0001
B	Sex	0.05	1	0.8287
	Age	7.81	1	0.0058
	Season	5.27	3	0.0017
	Habitat	2.01	2	0.1377
	Season*Habitat	11.79	6	<0.0001

Similar to luminance, we observed that differences in the blue to yellow color spectrum (*B*) were greatest among sites during the fall and winter (Fig. 3, inset C). Coloration among sites was similar during spring and summer seasons. During the fall, *B* spectrum coloration values were 20-24% higher on the preserve site compared to the pasture and agriculture sites, indicating a more yellowish tone. We observed that spectrum *B* coloration values were 27-30% lower during the winter on the preserve site compared to the pasture and agriculture sites respectively, and 43% lower during the winter than when the same preserve site was sampled during the fall (Fig. 3, inset C).

The age class of the specimen also significantly influenced pelage luminosity and spectrum *B* coloration

(Table 1). Adult individuals had 24% lighter pelage than juveniles at the agriculture site (Fig. 4, inset A). Similarly, we observed pelage to have increased yellow tint in adults on the agriculture site compared to juveniles based on a 10% difference in spectrum B values (Fig. 4, inset C). In other comparisons among sites based on age class, juveniles and adults appeared to have similar coloration patterns.

(inset A), spectrum A which represents the green to magenta color spectrum (inset B), and spectrum B which represents the blue to yellow color spectrum (inset C). Mean values were calculated based on averaging results taken from 6 locations on each individual squirrel (Fig. 2).

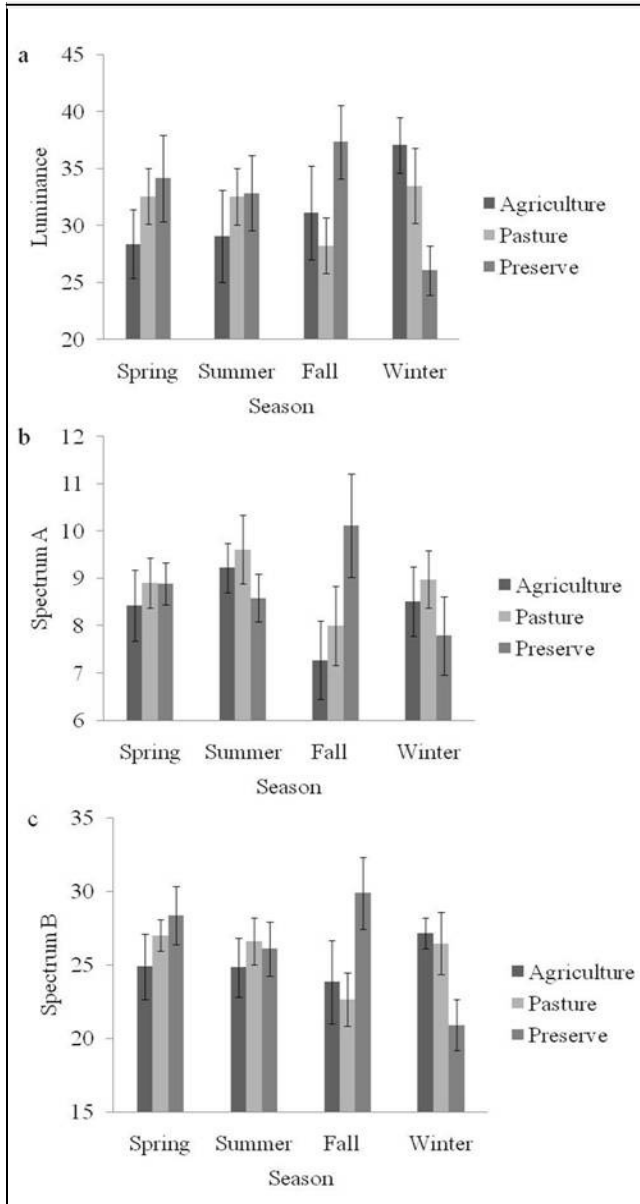


Figure 3 Mean (with 95% confidence interval) coloration of pelage on California ground squirrels (*Otospermophilus beecheyi*) in relation to habitat type and season for luminance, L, which ranges from white (100) to black (0)

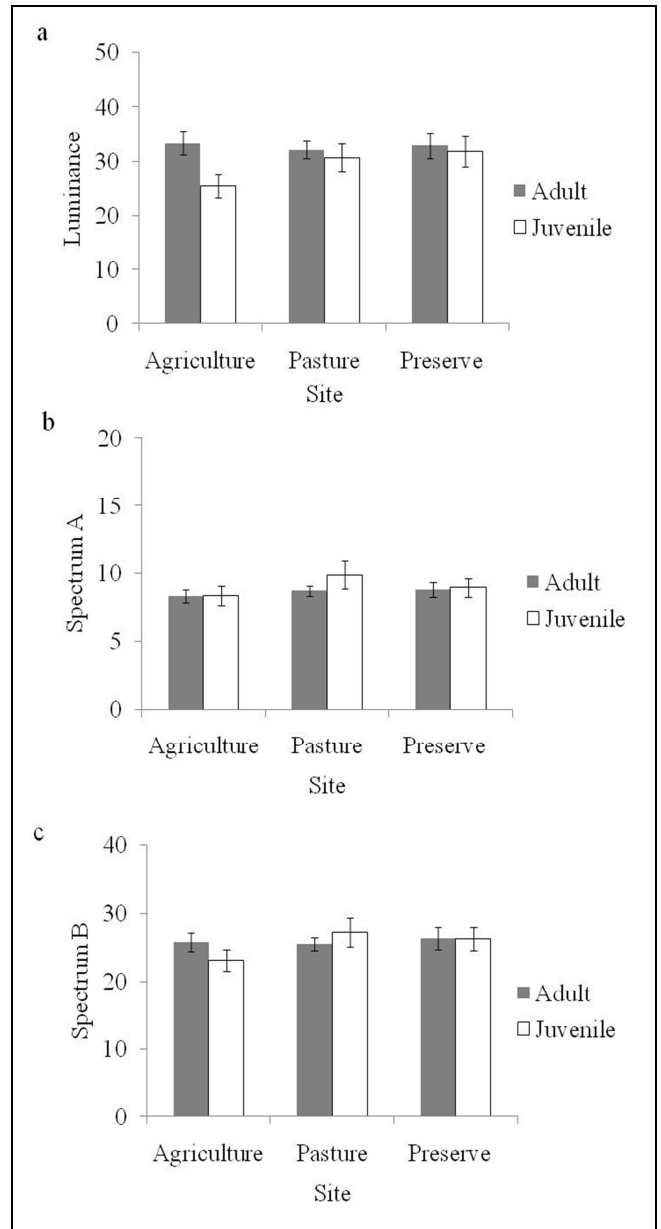


Figure 4 Mean (with 95% confidence interval) coloration of pelage on California ground squirrels (*Otospermophilus beecheyi*) in relation to age class for luminance L which which ranges from white (100) to black (0) (inset A), spectrum A which represents the green to magenta color spectrum (inset B), and spectrum B which represents the blue to yellow color spectrum (inset C). Mean values were calculated based on averaging results taken from 6 locations on each individual squirrel (Fig. 2).

DISCUSSION

The differences we observed among habitat types suggest that *O. beecheyi* exhibits site-specific variation in seasonal coloration patterns. Photoperiod, previously hypothesized to be the primary factor influencing seasonal molt and variations in coloration patterns (Bissonnette and Wilson 1939; Joy and Mrosovsky 1982), was consistent across our study sites, which occupied a relatively small geographic area. Rather than seasonal fluctuations alone, our results support findings from other taxa, which suggest that habitat is a key component of variation in pelage coloration (Rounds 1987).

Site-specific differences are likely due, in part, to variations in timing of the molting processes (Grinnell and Dixon 1918). *O. beecheyi* pelage typically gets lighter in late summer as a result of molting (Burt and Grossenheider 1976) and prolonged exposure to sunlight, which is known to cause chemical reactions that result in color loss (Grinnell and Dixon 1918; Foss et al. 1995; Medvedev 1999). We similarly observed this general trend toward lighter coloration through the summer at all three study sites. However, in the fall, individuals at the preserve site were lighter, and had higher *A* (i.e., red) and *B* (i.e., yellow) color spectrum scores compared to the other two sites. Interestingly, this was followed by individuals from the preserve site becoming darker during the winter season compared to the other two sites. This dramatic shift suggests that individuals at the preserve site likely molt and transition to a darker pelage color earlier (i.e., during the winter) relative to individuals at the agriculture and pasture sites.

The decreased values for luminance, red and yellow pelage coloration that we observed during winter at the preserve site could be due to an increase in the need for thermoregulation or for avoidance of predation. Decreased luminance during winter has been observed in eastern gray squirrels (*Sciurus carolinensis*) to avoid heat loss (Innes and Lavigne 1979). Luminance values were lowest at the preserve site during the winter, indicative of darker coloration, suggesting that winter severity might be more pronounced at the preserve site compared to the agriculture and pasture sites. Variation in pelage coloration among sites also could be due to the need for concealing coloration patterns to reduce predation risk (Benson 1933; Dice and Blossom 1937; Simpson 1994). Luminance values might be higher in agriculture and pasture sites due to increased predation risk associated with limited concealing ground cover or differing soil color conditions (Belk and Smith 1996).

In comparing pelage coloration differences among land use types, it is also important to consider the potential direct effects of human disturbance on coloration patterns due to the

physiological condition of individuals at each site. Molting is known to be influenced by the overall condition of the individual, and is generally associated with a high energetic cost (Neuhaus 2000). Assuming the preserve site used in this study mimics natural conditions, the human disturbance associated with agriculture and pasture settings might lead to increased environmental stress and thus delay pelage coloration changes during the fall and winter relative to the pasture site. Beyond molting itself, physiological condition of animals could likely influence the coloration of the pelage. For example, in the red fox (*Vulpes vulpes*), increased redness in coat coloration was found to be correlated with increased size and weight of the adrenal gland (Keeler et al. 1970). Future research that directly assesses physiological condition of individuals could provide further insight into the role of physiology in pelage coloration of *O. beecheyi*.

It is unclear why we failed to detect significant differences among sites following the spring/summer molt. In contrast to the relatively high amount of among-site variation we observed during the fall and winter seasons, we observed a more consistent coat coloration across all sites during the spring and summer seasons. The failure to detect differences among sites during the spring and summer seasons relative to the fall and winter seasons suggests that seasonal variability in molt cues varies greatly among sites during the shift to colder winter weather, but is consistent among sites during the spring and summer months. Future work that includes measurement of local climate conditions and soil color is needed to test the finer-scale influences of site-specific conditions that could more fully explain the observed significant differences in coloration patterns among sites.

Overall, our findings support the opinion that *O. beecheyi* is a generalist species with high adaptability to novel manmade habitats (Marsh 1998). The plasticity in pelage coloration suggests that site-specific habitat conditions influence seasonal changes in pelage coloration. This type of morphological plasticity, along with the well-documented behavioral (Rabin et al. 2006) and demographic (Fitch 1948) plasticity of this species likely helps it to exploit man-made habitats and tolerate human disturbance. These types of plasticity are unlikely to be observed in highly specialized species, which tend to be more vulnerable to human disturbances and climate change (Clavel et al. 2011). Future comparative studies that assess morphological plasticity, in addition to behavioral and demographic plasticity, of species of conservation concern could provide insight into the ability of species to withstand subtle but potentially significant changes in life history strategies.

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