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Egg crypsis in a ground-nesting shorebird influences nest survival

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Abstract. Coloration of exposed eggs of ground-nesting birds is thought to reduce predation, with camouflaged eggs that more closely match the area around the nest having greater survival. We tested this hypothesis using digital photographs of 374 Mountain Plover (*Charadrius montanus*) nests and the substrate surrounding each nest to produce covariates in nest survival models. Covariates included values representing the difference between the color of the eggs and that of the substrate, the average egg and substrate colors, and variation in both egg and substrate color. Nest survival decreased as the difference between the color of the eggs and substrate increased (accounted for by two different methods of quantifying color: $\beta_{\Delta E} = -0.021$, SE = 0.024, 95% CI = −0.069, 0.026 and $\beta_{\Delta RGB} = -0.004$, SE = 0.005, 95% CI = −0.013, 0.005) and increased with increasing variability in substrate color ($\beta_{\Delta SDsub} = 2.624$, SE = 2.846, 95% CI = −2.954, 8.202), although after model-averaging these effects were not well-supported. Model-averaged estimates of daily nest survival ranged from 0.90 to 0.98 (unconditional SEs from 0.004 to 0.129). Our results support the egg crypsis hypothesis because eggs that closely match their surroundings have greater survival.

Key words: *Charadrius montanus*; egg crypsis; eggshell color; Mountain Plover; nest survival; Phillips County, Montana, USA.

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INTRODUCTION

For more than a century, scientists have hypothesized that the main adaptive significance of eggshell coloration is camouflage (Wallace 1889), with some evidence for other explanations such as egg recognition and mimicry, eggshell strength, filtering solar radiation (reviewed in detail by Underwood and Sealy 2002), and as an indicator of female quality (Riehl 2011). Anecdotal support for the egg crypsis hypothesis is diverse, with explanations ranging from the suggestions that white eggshells are only possible in concealed nests like those of cavity-nesters (von Haartman 1957), or that birds with pale eggs must keep them permanently covered during incubation (Westmoreland and Best 1976), or be well-suited to defend their nests like swans, herons, or Ostriches (*Struthio camelus*). This hypothesis is appealing because it seems intuitive that selection would act on egg coloration, as more easily detected eggs would be more vulnerable to depredation by visually searching predators.

Many studies have attempted to examine the relationship between egg crypsis and nest survival, although few have found evidence to support this hypothesis (reviewed in Underwood

and Sealy 2002). Some of these studies may have been complicated by study design: in many cases experimenters tested egg camouflage by painting the eggs, as Tinbergen et al. (1962) did in the first study to provide evidence that egg coloration influenced Black-headed Gull (*Larus ridibundus*) nest survival. However, painted eggs could potentially increase nest depredations by providing an olfactory cue for scent predators. Although painted eggs may look camouflaged to the human eye, humans are unlikely to be able to match natural levels of crypsis (Kilner 2006). A further complication of many of these studies is that they were performed using either artificial nests or without any actual nest structure, which are both typically less cryptic than nests constructed by actual birds (Underwood and Sealy 2002) and may have provided biased estimates of nest survival.

Although some studies have looked at the relationship between egg coloration and the habitat surrounding natural nests (Thomas et al. 1989), few have assessed how the two are related to nest survival (Solís and de Lope 1995, Westmoreland and Kiltie 1996, Lloyd et al. 2000, Lee et al. 2010, Colwell et al. 2011) and none have incorporated crypsis into maximum likelihood estimation of daily survival rates (DSR). This method of modeling nest survival allows researchers to generate more biologically meaningful estimates of nest survival and incorporate biological factors of interest into nest survival models (Dinsmore et al. 2002). We tested the egg crypsis hypothesis by modeling DSR of nests of a ground-nesting shorebird and incorporating covariates for nest crypsis in the models. These covariates include values that reflect the degree of difference between egg color and the color of the substrate, as well as values representing the variation in the color of the eggs within a clutch, and the variation of the coloration of the rocks, soil, vegetation, etc. that are found in the area directly surrounding the nest. We predicted that nests with eggs of colors more closely matching the nest substrate would have a greater probability of surviving than nests whose eggs less closely matched the background. We also predicted that nests with eggs that have a high degree of variation in their coloration would have a greater probability of survival than those with lower within-nest variation. Finally, we predicted that birds that nest in substrate that has a high degree of color variation would have greater nest survival than those that nest in areas where the substrate color has a low degree of variation.

Methods

Study species

To examine the relationship between egg crypsis and nest survival we used the Mountain Plover (*Charadrius montanus*) as a model species. Mountain Plovers are ground-nesting shorebirds of conservation concern (Knopf and Wunder 2006) that have a high degree of variability in egg coloration, with basal colors ranging from dark olive, to tan, to light pinkish or cinnamon, all with irregular darker markings (maculation) that are more prevalent on the larger end of the egg (Fig. 1; Knopf and Wunder 2006). Male Mountain Plovers display and dig scrapes throughout their territory to attract females, and, while it is uncertain which sex ultimately selects the nest location (Graul 1973, Knopf and Wunder 2006), it is likely that the female makes the final decision on where to place the eggs. After the pair bond is formed the female Mountain Plover lays sets of three blunt pyriform eggs, generally in two nest cups, with the first nest tended by the male and the second by the female (Graul 1973). These eggs are cryptically colored to match the heterogeneous substrate around the nest (Graul 1973), which suggests that nest predation occurs by visual predators (Merilaita et al. 1999).

Field data collection

During the summers of 2006–2010 we studied Mountain Plovers breeding in an approximately 3,000-km^2 area in southern Phillips County in north-central Montana (47°40′–47°55′ N, 107°35′–108°30′ W), described in detail by Dinsmore et al. (2002). Field work began in mid-May and continued until the end of the birds' breeding season, usually late July or early August. Nest searching and monitoring and the capture, handling, and banding techniques were similar across years and followed those described by Dinsmore et al. (2002). We individually color-banded birds and because Mountain Plovers are sexually monomorphic (Iko et al. 2004) we

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Fig. 1. Representative colors of Mountain Plover (*Charadrius montanus*) eggs photographed in Phillips County, Montana, USA from 2006 to 2010.

determined sex from feather or blood samples (Avian Biotech International, Tallahassee, Florida) using techniques outlined in Dinsmore et al. (2002). We photographed Mountain Plover clutches using a handheld 5 megapixel digital camera with 2,592 × 1,944 pixels of resolution at a height of ~1.5 m to include the substrate immediately around the nest in the photograph. This work was conducted under Iowa State University's Institutional Animal Care and Use Committee protocol number 5-06-6129-Q.

Color analysis

From the photographs, we determined the red, green, and blue (RGB) color values of 1000 pixels randomly selected from the ~0.65 m^2 rectangular area centered on the nest, not including the nest cup and eggs, and 1000 randomly selected pixels of the eggshells alone from a cropped portion of the original image. These primary colors correspond to three different types of cones in the human eye (Coelho et al. 2006). To sample the RGB values we used the "ReadImages" package (Loecher 2012) in the statistical program R version 2.14.0 (R Development Core Team 2011). We calculated the mean and pooled standard deviation of the RGB values for both the eggs and substrate to give a single covariate value for each of mean nest substrate, mean egg color, variation in substrate color, and variation in egg color to include in a nest survival model. We used two different numerical values as covariates to represent the degree of difference between the nest substrate and egg color. The first, ΔRGB, was the Euclidean distance between the three-dimensional mean RGB values of the egg color and substrate color. The second, Δ*E*, was produced using methods outlined in Nguyen et al. (2007), described below.

As an alternative to the RGB color space, the *L*a*b** color space of the Commission Internationale de l'Eclairage (CIE) is recommended by Kim et al. (2000) and Coelho et al. (2006) as it more closely approximates and linearly correlates with the human eye. In this color space, *L** indicates luminosity ranging between 0 (black) and 100 (white), *a** indicates the red–green axis ranging between −60 (green) and 60 (red), and *b** indicates the yellow–blue axis ranging between −60 (blue) and 60 (yellow; Nguyen et al. 2007). After converting the RGB values to the *L*a*b** color space using tools from www.brucelindbloom.com (Nguyen et al. 2007) we then calculated Δ*E*, the linear distance between

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Table 1. Table of main effects models of color covariates used in maximum likelihood modeling of Mountain Plover (*Charadrius montanus*) daily nest survival in Phillips County, Montana, USA from 2006 to 2010. Models are ranked by ascending ΔAIC_c values with the number of parameters (K), model deviance, and Akaike weights.

Covariate	K	ΔAIC_c†	Deviance	w_i
Pooled standard deviation of substrate RGB color values (SDsub)	2	0.00	891.37	0.39
Difference between egg color and substrate color in $L^*a^*b^*$ color space (ΔE)	2	0.66	892.03	0.28
Difference between egg color and substrate color from RGB color values (ΔRGB)	2	1.01	892.38	0.24
Pooled standard deviation of egg RGB color values (SDRGB)	2	4.53	895.90	0.04
Mean RGB value for substrate color	2	5.32	896.70	0.03
Mean RGB value for egg color	2	6.03	897.40	0.02

† The AIC_c value of the best model was 895.38.

two colors in $L^*a^*b^*$, with the formula (Kim et al. 2000, Coelho et al. 2006):

$$\Delta E = \sqrt{\Delta L^{*2} + \Delta a^{*2} + \Delta b^{*2}}.$$

We used the MIXED procedure in SAS version 9.3 (SAS Institute 2011) to model each of the six color covariates (ΔE, ΔRGB, mean RGB eggs, mean RGB substrate, SD RGB eggs, and SD RGB substrate) in relation to the sex of the incubating adult, while accounting for multiple nests tended by the same individuals. We constructed a single mixed model for each covariate and examined the fixed effect of sex with individual birds as a random effect. Effects were then examined using F tests. This model assumes normality so the values for the Δ covariates had to be ln-transformed. We used $\alpha = 0.05$ as the level of statistical significance for all hypothesis tests.

Nest survival

We modeled daily nest survival rates using the nest survival model (Dinsmore et al. 2002) in Program MARK (White and Burnham 1999). First we built a set of candidate models using the six nest-specific covariates related to color (Table 1), one per model, to determine which covariates were most important. The three competitive models (<2.0 ΔAIC_c from the top model) were then added singly and additively in a hierarchical approach to reference models containing the factors that Dinsmore et al. (2002) found important in a previous analysis of this species' nest survival. The initial covariates included sex of the incubating adult, nest age, a quadratic time trend based on the Julian day of the nesting season, and daily precipitation determined from a NOAA weather station in the study area, with the added effects of clutch size and a quadratic effect of nest age. We evaluated models using Akaike's information criterion corrected for small sample sizes (AIC_c; Akaike 1973, Burnham and Anderson 2002). We did not adjust for overdispersion because Program MARK does not include a goodness-of-fit bootstrap simulation for the nest survival model. We anticipated multiple competitive models from the second modeling stage because we included metrics for the degree of difference between nest substrate and egg color. We therefore model-averaged nest survival estimates across the complete set of models, as this method incorporates model selection uncertainty and strength of support for each model (Burnham and Anderson 2002).

Results

We photographed 374 Mountain Plover nests and monitored them for a total of 4273 exposure days during the five years of this study. Of these, 166 nests were tended by 119 females, 167 were tended by 120 males, and 41 were tended by 39 birds of unknown sex. Thirty females were found incubating more than one set of eggs. Ten female plovers and eight male plovers re-nested within the same breeding season after their initial nest was unsuccessful. Both within and between breeding seasons females tended to lay eggs with similar background color across nests (Fig. 2) and there was weak evidence that egg color tended to more closely match substrate color of later nests, as both ΔRGB and ΔE tended to decrease within individuals through time. None of the six color covariate values differed between male-tended, female-tended, and nests tended by plovers of unknown sex (Type III tests for fixed effects [MIXED]: df = 2 and 276, all $P > 0.05$).

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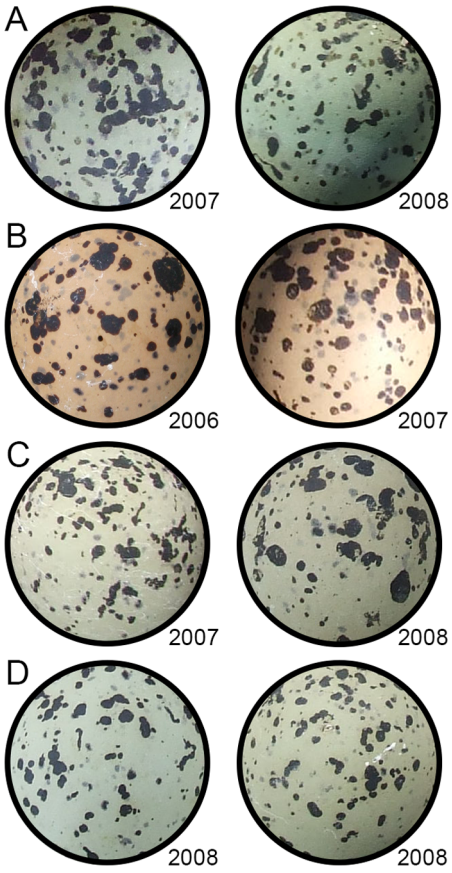

Fig. 2. Sample eggshell colors of female-incubated Mountain Plover (*Charadrius montanus*) eggs photographed in Phillips County, Montana, USA from 2006 to 2008. Samples are from four different individuals from nests found in consecutive breeding seasons (A–C) and one from two different nests within the same breeding season (D).

The initial model selection of color covariates found that neither mean egg color, mean substrate color, nor variation in egg color were correlated with daily nest survival ($\Delta AIC_c > 2.00$ from the top model). However, the degree of difference between egg color and substrate color (both ΔRGB and ΔE) was important as well as the variation in substrate color (SDsub; Table 1). After adding the color covariates to the baseline nest survival model there were eight competitive models ($\Delta AIC_c < 2.00$; Table 2) with similar AIC_c weights ranging from 0.18 to 0.07. All of the competitive models contained one of the two covariates for degree of difference between egg and substrate color and five also had the additive effect of variation in substrate color. Both covariates for the degree of difference between egg color and substrate color had negative effects on DSR ($\beta_{\Delta E} = -0.021$, SE = 0.024, 95% CI = −0.069, 0.026, and $\beta_{\Delta RGB} = -0.004$, SE = 0.005, 95% CI = −0.013, 0.005) while the variation in color around the nest had a positive effect on nest survival ($\beta_{\Delta SDsub} = 2.624$, SE = 2.846, 95% CI = −2.954, 8.202). The model-averaged estimates of these effects were not well-supported because the 95% CIs included zero. Model-averaged estimates of daily nest survival ranged from 0.90 to 0.98 with unconditional SEs ranging from 0.004 to 0.129. Sex of the incubating adult and nest age had strong effects on nest survival, with males tending to have lower rates of nest survival than females and DSR increasing as the eggs got closer to hatch (Fig. 3).

Discussion

Past attempts to show that egg coloration is an adaptation for camouflage to reduce nest depredation have produced inconclusive results (Underwood and Sealy 2002). Here we show that nest survival increases as the contrast in color decreases between eggs and the substrate surrounding the Mountain Plover nest. Although the model-averaged results were not well-supported (βs overlapping zero), this is a result of model-averaging this particular model set and within each individual model the color differences (Δs) were all strong (95% CIs did not include zero). This provides support for the egg crypsis hypothesis, and eggs that more closely match the substrate surrounding the nest (and so are more highly camouflaged) have a greater probability of surviving to hatch. Visual predators that would have difficulty detecting cryptically colored eggs likely depend on detecting the movements of the incubating adult as it leaves the nest (Colwell et al. 2011). Mountain Plovers have uniparental incubation and time their off-bouts from the nest to avoid detection by visual predators while still attending to their own needs (Skrade and Dinsmore 2012). As a result, they leave the nest to forage and interact with other plovers frequently and for long periods at night (Skrade and Dinsmore 2012).

There is substantial variation in basal or

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Table 2. Summary of competing models evaluating relationships between Mountain Plover (*Charadrius montanus*) daily nest survival and egg and substrate coloration in Phillips County, Montana, USA from 2006 to 2010. All models contain the effect of the sex of the incubating adult, a quadratic time trend across the breeding season (TT), clutch size, and daily precipitation. Age and Age^2 refer to the linear and quadratic effect of daily nest age. ΔE is the difference between egg color and substrate color in $L^*a^*b^*$ color space while ΔRGB is the difference between egg color and substrate color from RGB color values. Models are ranked by ascending ΔAIC_c values with the number of parameters (K), model deviance, and Akaike weights.

Model	K	ΔAIC_c†	Deviance	w_i
Age + ΔE + Pooled SD of substrate RGB color values	9	0.00	859.95	0.18
Age + ΔRGB + Pooled SD of substrate RGB color values	9	0.11	860.06	0.17
Age + ΔE	8	0.63	862.59	0.13
Age^2 + ΔE + Pooled SD of substrate RGB color values	10	0.95	858.89	0.11
Age + ΔRGB	8	1.03	862.99	0.11
Age^2 + ΔRGB + Pooled SD of substrate RGB color values	10	1.04	858.99	0.10
Age^2 + ΔE	9	1.59	861.54	0.08
Age^2 + ΔRGB	9	1.97	861.92	0.07
Age + Pooled SD of substrate RGB color values	8	3.37	865.33	0.03
Age^2 + Pooled SD of substrate RGB color values	9	4.09	864.05	0.02

† The AIC_c value of the best model was 877.99.

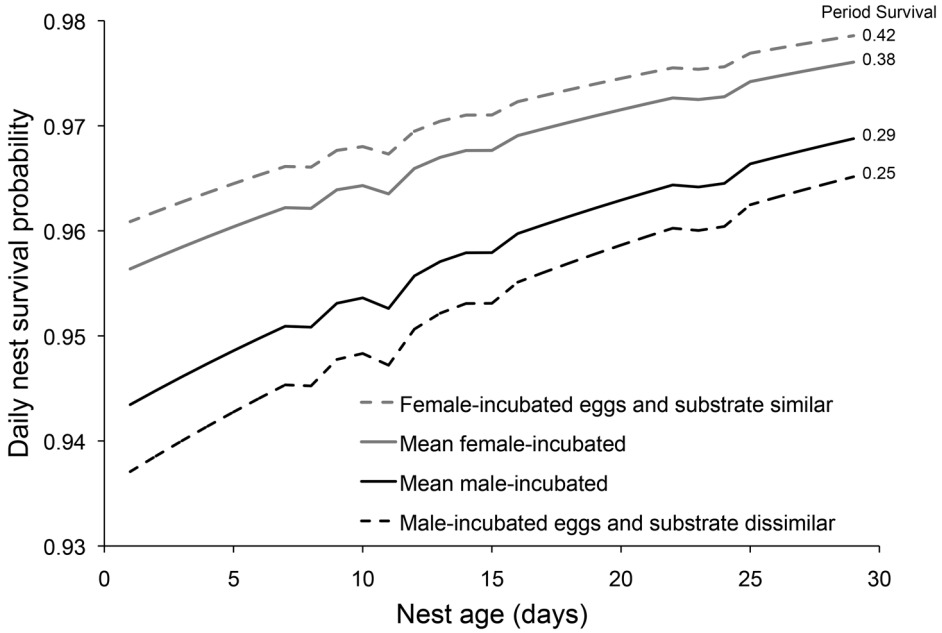

Fig. 3. Predicted daily survival rates from the model-averaged results of a nest survival analysis of Mountain Plovers (*Charadrius montanus*) in Phillips County, Montana, USA, from 2006 to 2010. Estimates were produced for the 29-day incubation period of male- and female-incubated eggs for nests initiated on the mean date of nest initiation (1 June) in 2006. Real precipitation values for that range of dates were used. To demonstrate the effect of egg crypsis on nest survival examples of female-incubated eggs that are similarly colored to the nesting substrate (−1 SD from mean value of ΔE, the linear difference between the color of the eggs and the substrate surrounding the nest in $L^*a^*b^*$ color space) and male-incubated eggs that are dissimilarly colored (+1 SD from mean value of ΔE) to the nesting substrate are included.

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background color in the eggs of Mountain Plovers (Fig. 1) in addition to variation in the amount of maculation or degree of spotting on the eggs. In our study females tended to lay eggs with a similar basal color (Fig. 2) and the variability in egg coloration within a clutch did not have a significant effect on nest survival. This result is inconsistent with the prediction that intraclutch variability in color would enhance crypticity. However, variation in egg coloration within a clutch may not play as great a role in egg camouflage as the arrangement of the spots on the surface of the eggshells and how closely that patterning matches the area around the nest (Westmoreland and Kiltie 1996, Colwell et al. 2011) which we did not examine. The amount and arrangement of maculation on the shells may be important to nest survival, as two similarly colored eggs in a clutch with little maculation could create a larger "object" that would be more easily detected by predators (Hockey 1982). This is supported by a study of egg coloration of Namaqua Sandgrouse (*Pterocles namaqua*), another ground-nesting bird, in which clutches exhibiting diversity in background color, pigment pattern or pigment intensity between eggs survived better than clutches in which eggs were uniformly colored (Lloyd et al. 2000).

There have been some criticisms of the use of digital photography in analyses of wildlife coloration (Stevens 2011). Most cameras have a non-linear response in the recorded image to changes in light intensity, natural biases occur in cameras towards certain wavelengths of light, and variations in ambient light conditions require corrections (Stevens et al. 2007). However, in this study we used data from the same photographs to compare differences in egg and substrate color, so light conditions were the same for both the eggs and substrate (Lee et al. 2010) and we found the same pattern of nest survival when we examined the relationship between color differences in the RGB and in the *L*a*b** color space after corrections.

Corvids such as the Black-billed Magpie (*Pica hudsonia*) and Common Raven (*Corvus corax*) are known visual nest predators of the Mountain Plover (Knopf and Wunder 2006; *personal observations*). Avian vision differs from human vision in multiple aspects (Endler and Mielke 2005), such as their ability to see in the ultraviolet (Kevan et al. 2001). However, this ultraviolet sensitivity appears to be more prevalent in passerines than in shorebirds (Ödeen and Håstad 2003, Ödeen et al. 2010), suggesting that the avian visual nest predators of Mountain Plovers may view eggs and nests slightly differently than the plovers themselves. In general, the eggs of ground-nesting birds absorb, rather than reflect, ultraviolet light (Bakken et al. 1978, Avilés et al. 2006) as does the vegetation of the region (Ruhland et al. 2013), and most substrate materials (Chávez et al. 2003), so eggs and nest substrate will tend to be similar. Although our method of examining egg and substrate coloration does not take into account ultraviolet color, the trend we found of decreasing nest survival as the contrast between eggs and substrate increased would likely hold true even in the ultraviolet spectrum (Cherry and Gosler 2010). An analysis that included ultraviolet reflectance would likely show that eggs in nests where the surrounding nesting substrate is very uniform, with either predominant vegetation or rocks, would have lower survival than areas with variation in the nesting substrate as the eggs would tend to stand out (Spottiswoode and Stevens 2010), similar to our finding that nest survival increased with substrate color diversity. We did not convert the images to grayscale as in another study of egg coloration and nest survival (Lee et al. 2010). Nest depredation of Mountain Plovers by predators such as canids, which view the world dichromatically (Jacobs et al. 1993), have been observed primarily at night and the animals appeared to find the nest by scent rather than sight (*personal observations*).

Even a small degree of camouflage confers a survival advantage to prey (Krebs and Davies 2003) and this is supported by the pattern that we found of greater nest survival of clutches more closely matching the surrounding substrate. A recent study of another ground-nesting bird with cryptically colored eggs (Japanese Quail, *Coturnix japonica*) found that females, if provided with a choice, will consistently select nest locations that most closely resemble the coloration of their eggs (Lovell et al. 2013). This suggests that female birds have some prior knowledge of their own egg coloration. Mountain Plovers as a species have a high degree of variability in egg color, which is likely an adaptation to the highly

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variable nest substrates across their breeding range (Knopf and Wunder 2006). However, the cryptic coloration of Mountain Plover eggs to avoid visual nest predators is only one aspect of the evolutionary arms race that is occurring in this system. Like those of other ground-nesting birds, Mountain Plover nests are vulnerable to olfactory predators. This limitation may be offset by a behavioral adaptation of this species because many of the items that they incorporate into their nest contents (e.g., prairie dog dung, sage, club mosses) may function as olfactory camouflage (*personal observations*); further research should be conducted to determine what role, if any, aromatic Mountain Plover nesting material plays in minimizing nest depredation.

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