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SHORT COMMUNICATIONS

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A COMPARISON OF NEST SURVIVAL BETWEEN CLIFF- AND TREE-NESTING GOLDEN EAGLES

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KEY WORDS: *Golden Eagle*; Aquila chrysaetos; *cliff nest*; *daily nest survival*; *nest site substrate*; *tree nest*

Many raptor species build nests on a variety of substrates. For example, Red-tailed Hawks (*Buteo jamaicensis*) build nests on trees, cliffs, and artificial structures (Preston and Beane 2009). An individual or pair's choice of substrate for nesting is based on factors such as the availability of substrates, the minimization of predation risk or disturbance, the influence of intra- and interspecific competition, and the maximization of available prey resources (Newton 1979). These factors may influence reproductive rate, resulting in different reproductive rates at different nesting substrates. For example, Ferruginous Hawks (*Buteo regalis*) nesting on transmission towers in Idaho had higher nest success than those nesting on cliffs (Steenhof et al. 1993). Similarly, nest survival for Aplamado Falcons (*Falco femoralis*) was higher on artificial platforms than natural nest sites (Brown and Collopy 2012).

Golden Eagles (*Aquila chrysaetos*) build nests on a variety of substrates including cliffs (Kochert and Steenhof 2012, McIntyre and Schmidt 2012), trees (Tjernberg 1983, Menkens and Anderson 1987), artificial structures (Kochert and Steenhof 2012), and the ground (Boeker and Ray 1971). However, they often use cliffs exclusively or nearly exclusively where available (Kochert and Steenhof 2012, McIntyre and Schmidt 2012). Substrate selection may be based on availability (Watson 2010), but Haller (1982) suggested that cliffs are preferred over other nesting substrates by Golden Eagles. The high rate of cliff use, and potential preference, may suggest fitness benefits to choosing cliffs, although comparative data on the productivity associated with different nesting substrates are lacking.

We studied a population of Golden Eagles in an area where both cliff- and tree-nesting substrates are widely available. Our objective was to evaluate whether fitness benefits exist based on choice of nest substrate, as reflected in the nest survival of nests on cliffs and trees.

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STUDY AREA

Our 2700-km^2 study area included rural portions of Park County and Sweet Grass County around Livingston, MT U.S.A. (ca. 45°40′N, 110°34′W; Fig. 1). Excluding the cities of Livingston and Big Timber, the approximate density of humans in the study area was 0.89 people/km^2, with tourism and cattle ranching as the primary local economic activities (Park County Planning Department 2013). Golden Eagle nesting territories were located in areas with moderate to low human presence, almost exclusively on private land. Elevations in our study area range from 1225 m to 2600 m, with primary habitat types including subalpine coniferous forests at the upper elevations and forest intermixed with large areas of sagebrush-steppe and grassland at lower elevations; cottonwoods (*Populus* spp.) dominated riparian habitat (Crandall 2013). Forests constituted approximately 20% of the overall area, consisting primarily of Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), and cottonwoods. Suitable trees and cliffs for nesting are widespread throughout the study area. In addition to Golden Eagles, the study area supports breeding populations of Red-tailed Hawks, Swainson's Hawks (*Buteo swainsoni*), Peregrine Falcons (*Falco peregrinus*), Prairie Falcons (*F. mexicanus*), and Bald Eagles (*Haliaeetus leucocephalus*).

METHODS

We primarily followed the terminology of Steenhof and Newton (2007) to describe breeding parameters. We considered a *nesting territory* to be an area that contained, or had contained one or more nests and was within the home range of a mated pair. *Occupancy* indicated the presence of one or more breeding-age Golden Eagles exhibiting territorial behavior such as chasing, undulating, escorting, or nest building (Harmata 1982, Collopy and Edwards 1989). Apparent *nesting attempts* occurred when a breeding-age Golden Eagle appeared to lay eggs and incubate. Other species of eagles sometimes display an incubation posture when they are not actually incubating (Fraser et al. 1983); therefore, we considered all nesting attempts to be apparent and not absolute. *Used nests* were those with an incubating adult, or that contained eggs or young (Kochert and Steenhof 2012). *Nesting success*

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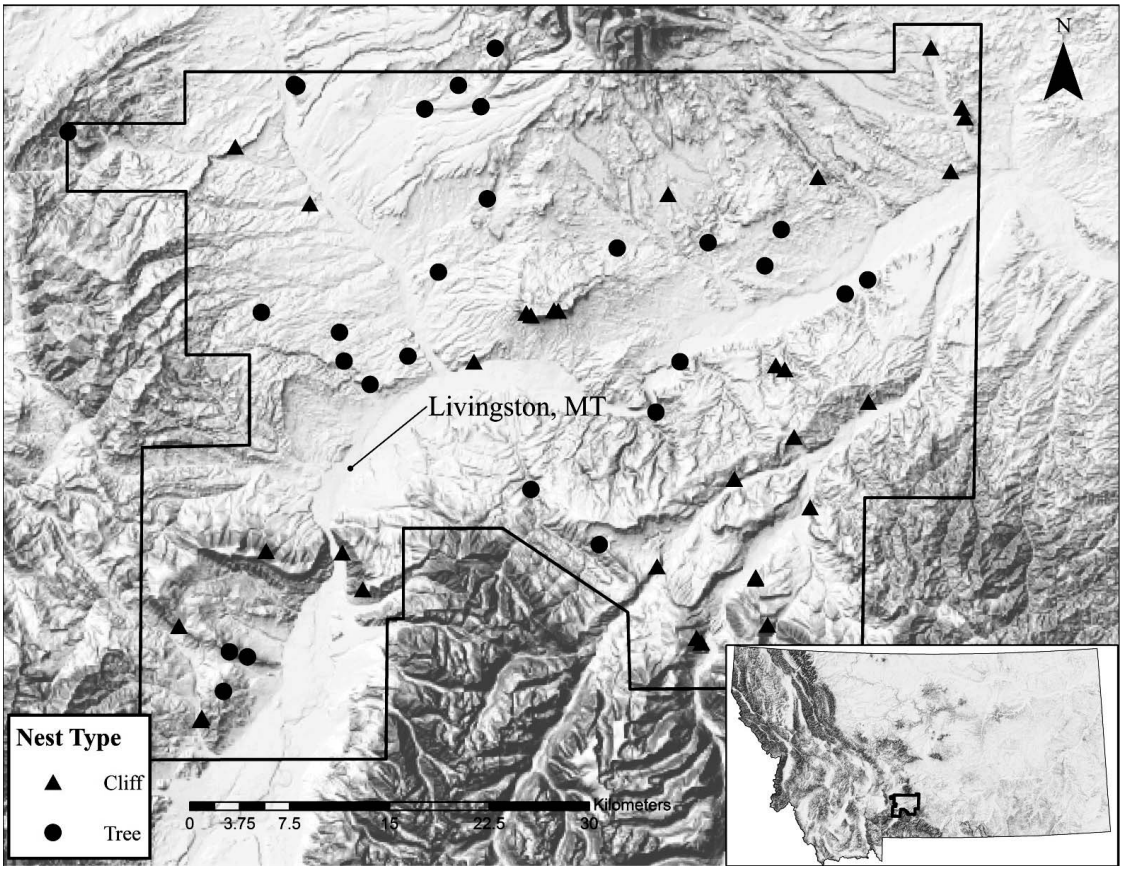


Figure 1. Study area and the distribution of tree and cliff nests used by Golden Eagles from the 2010–2014 nesting seasons. The one tree nest located out of the study area was a used, alternate nest site and was included in the analysis.

reflected pairs that successfully raised one or more eaglets to the minimum acceptable age to fledge in our region, which is 51 d (Brown et al. 2013). Once eagle nestlings reach 51 d (80% of their fledging age), the mortality rate is near 0 and so this age is often used to assess nesting success (Steenhof 1987). We used the term *productivity* to refer to the number of young that reached 80% of their fledging age. Lastly, we used the term *nest survival* to describe estimates based on our daily nest survival analysis.

We conducted nest searches and monitoring during five breeding seasons (2010–2014), focusing initially on areas with known Golden Eagle nests (McGahan 1968, D. Craighead unpubl. data). In addition to checking locations with known nests, we also searched for new nests by viewing large areas from strategic vantage points and scanning likely habitat with binoculars and spotting scopes. We also located new nesting territories opportunistically while traveling within the study area. We primarily searched for nests using 4-wheel-drive vehicles and on foot. We began searching for nests during the egg-laying and early incubation periods to reduce the probability of missing early failures. When we located territorial birds, we attempted to confirm whether the pair had initiated a nesting attempt. Once we confirmed a bird displaying incubation posture in a nest, we revisited the nest at least one more time during the nestling period. If nestlings were present, they were aged using a photographic guide (Driscoll 2010) that enables age estimation to within 5 d. We revisited nests with young at least one additional time to determine nesting success.

We assessed the influence of nest substrate on daily nest survival rate (DSR) using a DSR analysis in a Bayesian framework (Schmidt et al. 2010). This builds upon a previous analysis of nest survival in our study area using data collected from 2010 through 2013 (Crandall et al. 2015). The DSR analysis treats each day of the nesting season as an independent series of Bernoulli trials where 1 represents a nest with a bird incubating or young present and 0 represents a failed nesting attempt. For the analysis, we built our capture history for the DSR analysis based on

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Table 1. Number of occupied nesting territories with known tree- or cliff-nesting Golden Eagles, and estimates for apparent nesting attempts, nest success, and the total number of young produced by tree- and cliff-nesting Golden Eagles in south-central Montana.

	Tree-nesting Eagles				Cliff-nesting Eagles			
Year	Occupied	Nesting Attempts	Successful Nests	Total Young	Occupied	Nesting Attempts	Successful Nests	Total Young
2010	13	13	10	10	18	18	10	11
2011	19	13	8	10	23	16	9	12
2012	19	11	6	8	22	16	9	13
2013	19	15	9	11	22	14	11	16
2014	19	12	7	11	22	17	11	15

(1) the day the nest was first seen with an adult incubating, (2) the last day the nest was seen with either an adult incubating or young, and (3) the last day the nest was checked. We assessed only two models, which focused on the importance of nesting substrate to explain DSR. We first tested a full model, which included a binary variable representing nesting substrate (0 for a used cliff or 1 for a used tree nest) and a habitat variable representing terrain ruggedness (TRI) measured at the core-area scale. We included TRI based on previous analyses that identified TRI, measured within 1000 m of a used nest, as the only significant habitat variable explaining DSR (Crandall et al. 2015). Terrain ruggedness provides an estimate of the change in topography between neighboring raster cells. A value close to 0 represents little change in topography or a flat landscape, whereas higher values (the highest value in our study area was 115) represent a large change in topography between neighboring cells or a very rugged area. We used TRI in our previous analysis to account for orographic uplift, which is selected by Golden Eagles, yet was inversely related to DSR (Crandall et al. 2015).

After testing the full model, we examined a reduced model which included only the habitat variable reflecting terrain ruggedness. We used Deviance Information Criteria (DIC) to evaluate the contribution of nest type to DSR by comparing the full model with the reduced model. We used 95% credible intervals (CRI) to evaluate the strength and relationship of our tested variables with respect to DSR. We included a random effect of nest ID in both models to account for multiple observed nesting attempts at individual nests. For both models, we used uninformative priors with uniform distributions in the interval of −10 to 10 for the intercept and coefficient estimates, and we used a minimum of 100,000 iterations with a burn-in period of ≥20,000. We used the package R2WinBUGS to access WinBUGS using R (Version 3.1.1) for our analysis (Spiegelhalter et al. 2004, Sturtz et al. 2005, R Development Core Team 2014). We used the Gelman-Rubin diagnostic and visual inspection of the chains to assess convergence of the Markov chain Monte Carlo runs using the coda package in R (Gelman and Rubin 1992, Plummer et al. 2006). We estimated the total nesting season survival rate from our best model using a 101-d nesting period for Golden Eagles (Brown et al. 2013).

Results

We located 47 nesting territories and documented 145 nesting attempts at 60 different nests. Occupancy rates were very high in our study area so nearly all of the 47 nesting territories were occupied each year (Table 1). Of the 60 nests used by eagles during the study, 28 (46.7%) were in trees and 32 (53.3%) were on cliffs (Fig. 1). Of the 28 tree nests, 10 were used once, six were used twice, seven were used three times, and five were used four times; none were used all 5 yr. Golden Eagles in six nesting territories used two different tree nests during the 2010–2014 nesting seasons. Of the 32 cliff nests, nine were used once, nine were used twice, five were used three times, three were used four times, and six were used all 5 yr. Golden Eagles in six territories used two cliff nests and eagles in one territory used three cliff nests during our study period. Tree species with nests included 21 in Douglas-firs (75%) and seven in cottonwoods (25%). All cottonwood nests were in live trees but two nests in Douglas-firs were in snags. Either trees or cliffs were used exclusively for nesting in our monitored nesting territories. The average proportion of pairs that made a nesting attempt in territories with tree nests was 0.74 (95% Confidence Interval (CI) = 0.41, 1.00) and for cliff nests was 0.77 (95% CI = 0.50, 1.00, Table 1). Apparent nest success rates for tree-nesting Golden Eagles was 0.62 (95% CI = 0.44, 0.80) and 0.62 (95% CI = 0.42, 0.82; Table 1) for those nesting on cliffs. The proportion of pairs that made a nesting attempt for all nesting territories combined was 0.76 (95% CI = 0.49, 1.00) across the 5-yr study, and the apparent nest success rate for all eagles was 0.62 (95% CI = 0.54, 0.70; Table 1).

The full model was ranked below the reduced model in capacity to explain DSR, thus our results showed no support for inclusion of the nest substrate variable (Table 2). In addition, the 95% CRI for the nest type variable in the full model overlapped 0 ($\beta_{\text{nest type}} = -0.18$, 95% CRI = −0.93, 0.56). As in our previous analysis (Crandall et al. 2015), our results for the entire 5-yr study showed support for a negative effect of terrain ruggedness on DSR ($\beta_{\text{TRI}} = -0.23$, 95% CRI

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Table 2. Model selection results describing the influence of tree or cliff nest on daily nest survival from 142 Golden Eagle nests and factors influencing the use of either a tree or cliff nest at 47 breeding-season home ranges from 2010–2014 ranked using Deviance Information Criterion (DIC) also showing the change in DIC (ΔDIC) and the number of parameters in each model (*K*). TRI is terrain ruggedness index.

DAILY NEST SURVIVAL	*K*	DIC	ΔDIC
TRI	2	194.3	0.0
TRI + Nest Type (cliff/tree)	3	195.3	1.0

= –0.39, –0.10). The estimated DSR from the reduced model was 0.995 (95% CRI = 0.978, 0.999) and the estimated annual nest survival was 0.62 (95% CRI = 0.11, 0.92).

DISCUSSION

We found no difference in daily survival at Golden Eagle nests based on whether they nested on trees or cliffs. Comparisons of nest success for other raptors that use multiple nest substrates are rare, and those published often contrast artificial platforms and natural nest sites (Steenhof et al. 1993, Fargallo et al. 2001, Brown and Collopy 2012). Comparing our results with those from studies using artificial nesting platforms or nest boxes may be inappropriate because of the human element involved in choosing the locations for platforms. Transmission line towers may provide an adequate comparison, because raptors may have the opportunity to choose sites among towers. In one such study, Golden Eagle nest success did not differ between nests on transmission line towers and those on cliffs, although there were many more nesting attempts made in cliff nests ($n = 199$) than tower nests ($n = 23$; Steenhof et al. 1993). In Wyoming, 56% of tree-nesting Golden Eagles were successful, compared to 43% on rock outcrops and peaks, 52% on human-made structures, and 44% on creek banks (Phillips and Beske 1990). In the Wyoming-based study, there were almost five times more nesting attempts made in tree nests monitored ($n = 498$) than the other three non-tree categories ($n = 108$; Phillips and Beske 1990). To our knowledge, these are the only two studies that compared nest success for Golden Eagles by nesting substrate. For other raptors, Ferruginous Hawks had higher nest success on towers compared to natural substrates, whereas Red-tailed Hawk nest success did not vary with nesting substrate (Steenhof et al. 1993). Elsewhere, Black Kites (*Milvus migrans*) nesting in both trees and on cliffs did not differ in mean clutch size or mean number of young fledged, although the comparison was only made in nesting territories where kites used both (Sergio et al. 2003). Based on these limited comparisons, it is unclear whether a broad trend in breeding success exists for members of the same species using different nesting substrates.

The foundation for our comparison of nest survival between cliff- and tree-nesting eagles was the possibility that reduced limitation in nest-site selection could enhance or reduce pressures that ultimately influence nest survival. For example, Martínez-Abraín et al. (2010) found large tree-nesting raptors place their nests further from roads than similar cliff-nesting species, likely to avoid human disturbance, thus potentially increasing the probability of producing young. Alternatively, flexibility in nest-site selection may increase the availability of suitable nest sites, thus allowing raptors to nest closer to potential competitors, intensifying the influence of intra- and interspecific competition (Newton 1979). Whether the influence of competition differs between cliff- and tree-nesting Golden Eagles is unknown, but we surmise differences could exist based on the availability and distribution of the substrates. Regardless of potential causes, our results suggest that nesting substrate alone does not influence breeding success of Golden Eagles in our study area.

There have been contradictory estimates of population trends for, and consequently concern over future threats to, Golden Eagle populations in the Rocky Mountain Region (Kochert and Steenhof 2002, Hoffman and Smith 2003, Millsap et al. 2013). This has spawned increased interest and monitoring activities by state and federal agencies, with the goal of adequately assessing the current status of the population, documenting nests, and recording productivity (U.S.F.W.S. 2013). Our study was not designed to estimate detection probabilities of Golden Eagle nests based on substrates, but accounting for differences in the ability to detect tree and cliff nests should be considered when conducting such searches. In Alaska, the probability of detecting Golden Eagle cliff nests from fixed-wing aircraft and helicopters was approximately 0.70 (Booms et al. 2010). Olson et al. (2015) estimated detection probably of Golden Eagle nests on cliffs, man-made structures, rocks and rims and cottonwood trees in Wyoming as 0.60 (SE = 0.061) from a fixed-wing aircraft and 0.67 (SE = 0.062) from helicopters. We are unaware of any published estimates of detection probabilities of Golden Eagle nests in coniferous trees. Nests in coniferous trees in our study area were generally less visible than nests on other substrates (R. Crandall unpubl. data). Thus, we surmise detection probability for nests in coniferous trees is lower than published estimates of nests on other substrates. Our results emphasize the potential importance of tree-nesting Golden Eagles to density and productivity estimates in areas similar to ours, and underscore the importance of incorporating protocols that enable the reasonable detection rates for potential nesting substrates.

COMPARACIÓN DE LA SUPERVIVENCIA DEL NIDO ENTRE INDIVIDUOS DE *AQUILA CHRYSAETOS* QUE NIDIFICAN EN ROQUEDOS O EN ÁRBOLES

RESUMEN.—*Aquila chrysaetos* elige numerosos sustratos diferentes sobre los que construir sus nidos, incluyendo roquedos, árboles, estructuras artificiales y el suelo. Sin

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embargo, *A. chrysaetos* aparece asociada a menudo con nidos en roquedos debido a un sesgo hacia el uso de este tipo de nidos en numerosas áreas. Se ha sugerido que *A. chrysaetos* prefiere los roquedos para nidificar en áreas con múltiples sustratos disponibles, implicando beneficios en la eficacia biológica de los nidos ubicados en roquedos. Estudiamos una población de *A. chrysaetos* que utilizó un número casi equivalente de nidos en roquedos y en árboles en un área donde ambos sustratos de nidificación estaban ampliamente disponibles. En nuestra población de *A. chrysaetos* encontramos que el sustrato del nido no influye en la supervivencia del nido. Nuestros resultados sugieren que no hubo beneficios en la eficacia biológica asociados con el sustrato del nido.

[Traducción del equipo editorial]

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