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Review paper

Conservation significance of alternative nests of golden eagles

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ABSTRACT

Golden eagles (*Aquila chrysaetos*) are long-lived raptors that maintain nesting territories that may be occupied for a century or longer. Within occupied nesting territories there is one nest in which eagles lay their eggs in a given year (i.e., the used nest), but there are usually other nests (i.e., alternative nests). Conservation plans often protect used nests, but not alternative nests or nesting territories that appear vacant. Our objective is to review literature on golden eagle use of alternative nests and occupancy of nesting territories to determine if alternative nests are biologically significant and warrant greater conservation consideration. Our review shows that: (1) alternative nests or their associated habitat are most often in core areas of golden eagle nesting territories; (2) alternative nests likely will become used in the future; (3) probability of an alternative nest becoming used is greatest where prey availability is high and alternative nest sites are limited; (4) likelihood of annual occupancy or reoccupancy of golden eagle nesting territories is high; and (5) prey availability is the most important determinant of nesting territory occupancy and breeding activity. We recommend alternative nests be treated with the same deference as used nests in land use planning.

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1. Introduction

In the United States, the US Fish and Wildlife Service (Service) and state fish and wildlife agencies (States) have responsibility for protecting and managing golden eagles under a variety of laws, most notably the Bald and Golden Eagle Protection Act (16 United States Code 668–668d; hereafter Act). The Act delegates to the Service the ability to permit take (defined by regulations to include disturbance, injury or death of eagles or destruction of nests and eggs) as "necessary for the protection of other interests in any particular locality" after determining the take is "compatible with the preservation of the bald eagle (*Haliaeetus leucocephalus*) or golden eagle (*Aquila chrysaetos*)" (scientific names added). Take by disturbance results when disruptive activities cause a decrease in eagle productivity by interfering with normal breeding, feeding, or sheltering behavior, or cause nest abandonment. Under these regulations, the Service can permit take of eagles and eagle nests under certain circumstances, but it must first assess the likely extent of take and determine that the take is compatible with the preservation of eagles. The Service defines "compatible with the preservation of eagles" as maintaining stable numbers of breeding pairs (US Fish and Wildlife Service, 2009).

The Service provides guidance on how to avoid non-lethal take of bald eagles from disturbance (US Fish and Wildlife Service, 2007) and how to assess potential lethal take of either eagle species at wind energy facilities (US Fish and Wildlife Service, 2013). Both documents acknowledge that alternative nests should be considered when assessing and predicting effects of take on eagles, but neither bases this on scientific information. Take is possible at alternative nests if potentially lethal or disturbing structures are constructed nearby and eagles subsequently re-use the alternative nest or spend time in the area. Thus, the likelihood of take associated with alternative nests depends on the probability they will be used for nesting or as activity centers in the future. Currently, wildlife managers do not know how to objectively and consistently assess the value of alternative nests to golden eagles when assessing actions that might take eagles.

Golden eagles are long-lived raptors that, in the absence of persecution and with adequate prey, generally exhibit a high degree of population stability (Kochert et al., 2002; Palmer, 1988). Under these conditions golden eagles maintain long-enduring nesting territories, some of which have been occupied at least intermittently for a century or longer (Palmer, 1988). This persistence extends long past life spans of individual eagles, such that long-term occupancy reflects serial reoccupation of nesting territories by successive individuals. Persistent occupancy of nesting territories is likely a function of: (1) long ($>$20 yr) reproductive careers of individual golden eagles (Kochert et al., 2002; Watson, 2010); (2) limited suitable nesting sites and territoriality, which constrain, in some landscapes, the number of golden eagle pairs that can breed in a given area (Hunt, 1998; Kochert et al., 2002; Palmer, 1988); and (3) long-term pair bonds (Collopy and Edwards, 1989; Harmata, 1982; Watson, 2010).

Within a typical golden eagle nesting territory in a given year there are multiple alternative nests, but eggs are laid in only one (the used nest); in rare cases, re-nesting may occur in a different nest, in which case there may be two used nests. Nests per nesting territory averaged $<$2.0 on 36 territories in Montana (McGahan, 1968), 2.4 on 49 territories in Sweden (Tjenberg, 1983), 3.4 on 411 territories in Britain (Watson, 2010; Watson and Brockie, 1997), 4.5 on 20 territories in Scotland (Watson, 2010), and 6.9 on 66 territories in Idaho (Kochert and Steenhof, 2012). Given the near universal presence of alternative nests in golden eagle territories across the species' range, it seems they serve an important function. An obvious question, then, is of what conservation significance are these alternative nests? More specifically, in situations where wildlife managers must protect golden eagles, do presence and location of alternative nests predict relatively high levels of current or future use of an area by golden eagles? Or, do they solely reflect past use?

In this paper we review scientific literature and identify knowledge gaps on use of alternative nests by golden eagles. We distinguish between two types of alternative nests: (1) currently un-used nests in occupied nesting territories, where there is also a used nest, and (2) un-used nests in nesting territories that are currently vacant, where there is no used nest. Our intent in conducting the review was to compile and summarize the available literature on the biological and management importance of alternative (or inactive) nests of golden eagles to better understand the importance of these structures and their surrounding habitat. This is a question of increasing management importance as our agencies and others seek to balance resource development in eagle habitat with legal mandates and eagle population objectives. We organized our review around two broad questions, with a subset of more specific questions under each. We use this query structure as the framework for this paper:

(3.1.) What is the biological and conservation significance of alternative nests in nesting territories occupied by golden eagles? (see 2.1 for definitions):

(3.1.1) How much do alternative nests and attributes of habitat associated with such nests serve as attractants that indirectly will place a territory's occupants at risk of mortality or disturbance if threatening activities (e.g., wind energy facility) are constructed nearby?
(3.1.2) What is the probability that a given alternative nest will be used for nesting in future years?
(3.1.3) Does the probability that alternative nests will be re-used for nesting in future years vary spatially or by nest type?
(3.2.) What is the conservation significance of nests in vacant nesting territories of golden eagles?
(3.2.1) How often are vacant territories occupied in subsequent years and what makes territories desirable for reoccupancy?
(3.2.2) How accurate are assessments that nesting territories are vacant?
(3.2.3) Do nests, or the associated habitat features (cliff, perches, surrounding foraging habitat) that initially facilitated or prompted nest-building, serve as attractants for non-breeding eagles?
(3.2.4) Do patterns in territory occupancy vary predictably geographically or with habitat?

2. Methods

2.1. Definitions

Postupalsky (1974) and Steenhof and Newton (2007) make a compelling case for consistent use of clearly defined terms when discussing raptor reproductive success, and we largely follow their terminology. We define a *nest* as a structure built or used by eagles for the purpose of breeding regardless of whether eggs are laid in the nest in a given year or in any year. We use the term *nesting site* to describe the specific location of the nest on the landscape. We define a *nesting territory* as a defended area containing one or more nests within the range of a mated pair of eagles. Regardless of whether such nests were built by the current resident pair, they typically are situated more closely together than they are from nests of conspecific breeding pairs (Postupalsky, 1974). A *used nest* (equivalent to occupied nest in Postupalsky, 1974) is a nest in which, in a given year, either: (1) young were raised; (2) eggs were laid; (3) one adult was observed in incubation position; (4) two adults were observed on or near the nest and no other used nests were present within the nesting territory that year; (5) one adult and one eagle in subadult plumage were observed in or near the nest and mating behavior also was observed, and no other used nests were present within the nesting territory that year; or (6) the nest was repaired and fresh sticks and golden eagle feathers molted that year were present, and no other used nests were present within the nesting territory that year. Criteria (4)–(6) do not constitute proof a nest was used, but are suggestive of such. An *occupied nesting territory* is a nesting territory with a used nest, or with a pair of presumably mated eagles in residence. A *potentially occupied nesting territory* is a nesting territory where occupancy is unconfirmed but where there is limited evidence suggesting occupancy (e.g., observation of a lone adult). A *vacant nesting territory* is either (1) a territory documented as occupied or potentially occupied in at least one other year but not meeting the criteria of an occupied territory in the current year; or (2) what likely is a territory owing to presence of an alternative nest or group of alternative nests observed in the current breeding season, but not meeting the criteria of an occupied territory. The phrase *breeding activity* refers to times or places where a nest within a nesting territory is used. An *alternative nest* is one of potentially several nests within a nesting territory that is not a used nest in the current year (or at the current time, allowing for the rare instance of re-nesting, when eggs might be laid in two nests in a year). In a year when a nesting territory is occupied by a pair but eggs are not laid (i.e., there is no used nest), all nests in that territory are considered alternative nests. Postupalsky (1974) distinguished between an inactive nest, which has a known history of being a used nest, and an alternative nest, for which there is no known history of breeding activity. In practice it is usually impossible to distinguish between these two types of nests, so we combine both categories under the term alternative nests. A *successful nest* is a nest used during a breeding attempt in which at least one young fledged in a given year. An *unsuccessful nest* is a nest used during a breeding attempt in which no young fledged in a given year because either (1) no eggs were laid, (2) eggs failed to hatch, or (3) eggs hatched but young died before fledging.

2.2. Approach

We conducted a literature search to identify published papers on topics associated with the keywords "inactive nest", "active nest", "occupied territory", "vacant territory", "occupied nest", and "nest success". We searched literature specific to golden eagles, as well as for other species of Accipitriformes, Falconiformes, and Strigiformes, though we draw on the latter two sparingly. We used the following search engines and sources: Biological Abstracts, Cambridge Journal Online, JSTOR Biological Sciences Collection, Oxford Journals, ProQuest Environmental Science Journals, Royal Society Publications, SAGE Journals Online, SciELO Complete, SORA, SpringerLink contemporary, Taylor and Francis, Web of Science, Wildlife and Ecology Studies Worldwide, Wiley-Blackwell Full Collection, and Zoological Record. Our search produced 102 potentially applicable references, of which 27 were actually relevant to our questions. These 27 papers are cited and discussed in Section 3, and comprise the majority of the citations in bibliography. A few relevant papers not captured in our search were brought to our attention by reviewers, and we included these as well.

We supplemented our literature review with an analysis of data collected from adult golden eagles equipped with Platform Transmitter Terminals (PTTs) by JW in Washington and Oregon ($n = 14$ golden eagles on 14 nesting territories) and

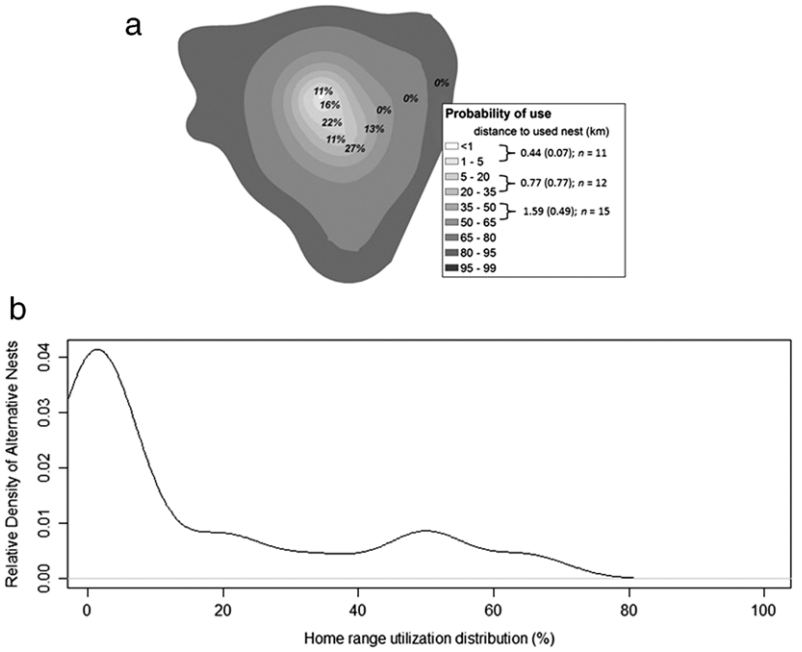

Fig. 1. Alternative nests of golden eagles are typically located in intensively used parts of the home range. Panel (a) shows the hypothetical annual home range of a golden eagle displaying summary statistics for the distribution of alternative nests ($n = 38$) on 14 eagle home ranges in the Pacific Northwest (adapted from Watson et al., 2014b). Shaded contours depict variable probability of eagle use throughout ranges, derived from Brownian Bridge range analysis of GPS-monitored eagles (Watson et al., 2014a). The percentage of alternative nests in each contour reflects their abundance within areas of varied intensity of eagle use, and distances (mean, SD) indicate their proximities to the used nest. Panel (b) is a density plot of the same data in panel (a), with the addition of one golden eagle territory and two alternative nests from New Mexico (see Section 2.2).

RM in New Mexico ($n = 1$ golden eagle on a single nesting territory). PTT data from Washington were analyzed as described by Watson et al. (2014a,b). The utilization distribution for the New Mexico individual was based on kernel-density analysis of 5730 fixes over a two year period using the kde and isopleth methods in Geospatial Modeling Environment (Beyer, 2012).

3. Results and discussion

3.1. What is the biological and conservation significance of alternative nests in occupied golden eagle nesting territories?

3.1.1. Do alternative nests and surrounding habitat features serve as attractants for golden eagles?

Our review revealed substantial evidence that alternative nests are attractive features for breeding pairs of golden eagles, either as serviceable nesting structures or because they are situated in habitats otherwise suited for territory occupants. Boeker and Ray (1971) noted that, in the southwestern United States, placement of alternative nests of golden eagles were related to attractive terrain features (e.g., cliffs overlooking grasslands with abundant prey) and to proximity of conspecific breeding pairs. McGahan (1968) noted that alternative nests in Montana "…tend to be revisited by territory occupants each year". Camenzind (1969) found that 3 of 11 pairs of golden eagles in central Utah visited multiple nests in a single breeding season. Kochert and Steenhof (2012) stated that "…Golden eagles occasionally add new material to alternative nests they do not use during a nesting season; this could increase longevity of existing nests and reduce the need for new construction. Some pairs we studied built new nests in years when they did not lay eggs. Pairs that do not lay eggs also commonly add new material to existing alternative nests…". Alternative nests may be visited throughout the year (Newton, 1979). Data from golden eagles monitored via PTTs in Washington, Oregon, and New Mexico revealed that alternative nests were most often within the most intensively used parts of the home range (Fig. 1). In New Mexico, high use of the area encompassing alternative nests was observed even though no nest was used in the territory during either year the territorial adult male was tracked.

The propensity for golden eagles to visit and maintain alternative nests within their nesting territory not only suggests these structures serve as an attractant, but that their maintenance and defense serve important biological functions. Watson (2010) noted that alternative nests of golden eagles in the British Isles often were at opposite ends of hunting ranges and, as such, might reinforce ownership of the territory. In some cases, alternative nests may be built in "frustration" due to failure to attract a mate, or to advertise territory occupancy (Newton, 1979; Postupalsky, 1974).

We found no specific references to possible attractiveness of alternative nests to golden eagles other than the territory holders. For some other species of raptors, however, non-breeders can be attracted to the area around occupied nesting

territories. For example, where peregrine falcon (*Falco peregrinus*) populations were extirpated due to effects of DDT, White et al. (as quoted in Hunt, 1998) stated that "…floaters appear to accumulate around local, reintroduced populations rather than colonize vacant habitat, a condition so scarce in earlier times that natural selection may have failed to maintain adaptations relating to its recognition and exploitation". Dispersing juvenile spotted owls (*Strix occidentalis*) tended to hone in on activity centers of existing breeding pairs and often settled on adjacent vacant territories (Lahaye et al., 2001). We suggest that golden eagles may also engage in this activity and suggest it be evaluated in future studies.

3.1.2. What is the probability that a given alternative nest will be used for nesting in future years?

Our review of the literature suggests high likelihood that golden eagles will use alternative nests for future nesting (i.e., they will become used nests at some future time). This includes occupancy of nests constructed but not used in previous years. In a 41-year study at the Morley Nelson Snake River Birds of Prey National Conservation Area in Idaho, Kochert and Steenhof (2012) found that 86% of alternative nests were used at least one breeding season, and time until re-use ranged from 1 to 39 years. Protecting alternative nests for 10 years after the last known use would not have protected 34% of all 300 nests that were re-used during their study; this proportion rose to 49% for 37 alternative nests monitored for 41 years (Kochert and Steenhof, 2012). Re-use of nests does not appear to be associated with the prior year's success (Boeker and Ray, 1971; Kochert and Steenhof, 2012), but some studies suggest re-use of alternative nests may be associated with disturbance or persecution at another previously used nest (Smith et al., 2010; Watson, 2010).

3.1.3. Does the probability alternative nests will be re-used for nesting in future years vary spatially or by nest type?

We found few studies that investigated whether probability of alternative nest re-use was affected by nest substrate or that it varied spatially. Palmer (1988) noted that tree nests might not be as durable as cliff nests, and therefore may not persist to be available as long for re-use. Hunt (1998) noted that for raptors in general, persistence of a nest site is probably inversely related to the abundance of cliffs or trees suitable to support a nest; where suitable nests sites are limited, those sites that do exist are likely maintained and used frequently. Where the potential for golden eagles to build nests is limited, probability of re-use of the available alternative nests is likely greater than if opportunities for building nests are plentiful.

3.2. What is the conservation significance of alternative nests in vacant golden eagle nesting territories?

3.2.1. How often are vacant territories occupied in subsequent years and what makes territories desirable for reoccupancy?

As noted previously, golden eagles have a high annual rate of nesting territory occupancy; the literature also shows a high rate of reoccupancy of nesting territories after a hiatus in use. McIntyre and Adams (1999) and, subsequently, McIntyre and Schmidt (2012) reported that annual occupancy of ∼80 golden eagle nesting territories in Alaska over a 22-year period ranged from 81% to 93%; annually, during this period, the proportion of occupied nesting territories with used nests varied greatly, from 14% to 88%. Occupancy of 36 nesting territories in Idaho from 1971 to 1994 ranged from 78% to 100% (Kochert et al., 1999; Steenhof et al., 1997). Prey availability is a major influence on occupancy of nesting territories by pairs of golden eagles, and especially on the likelihood nests are used. Over a 23-year period in southwestern Idaho, rabbit abundance influenced nearly all measures of golden eagle reproductive success, and black-tailed jackrabbit (*Lepus californicus*) abundance along with weather had the greatest effect on the number of golden eagle pairs that laid eggs (Beecham and Kochert, 1975; Steenhof et al., 1997). McIntyre and Schmidt (2012) found that probability of a golden eagle nesting territory containing a used nest in Denali National Park, Alaska, was strongly and positively influenced by snowshoe hare (*L. americanus*) abundance. Murphy (1975) reported that during years of high prey abundance in central Utah, used nests occurred in more occupied nesting territories than in years of low prey abundance, and the distance between used nests decreased. Nystrom et al. (2006) stated that the "…number of occupied golden eagle territories in the study area [Sweden] was unaffected by prey population fluctuations. This was not surprising as golden eagles in the study area are resident and highly territorial, limiting population growth even during good food conditions". However, the authors found that the proportion of pairs that attempted nesting (i.e., laid eggs) increased coincident with increased abundance of main prey species. Marzluff et al. (1997) noted that home range size of breeding golden eagles in Idaho varied with prey availability; ranging and foraging behavior of the eagles reflected attributes of prey habitat near nests. In Scotland, Watson et al. (1992) showed that golden eagle "…nesting density was positively correlated with one source of food, namely carrion, and that breeding success was positively correlated with another, live prey".

As with other long-lived birds (Janiszewski et al., 2013), the quality of a golden eagle nesting territory also likely plays a role in the probability of its occupancy in a given year, especially in years of low prey abundance. Although prey availability is probably the major determinant of territory quality, other factors like the greater foraging proficiency of certain individuals, availability of high quality nesting habitat, and extent of disturbance and persecution may contribute to differential territory quality (Newton, 1979; Whitfield et al., 2006). Regardless of the mechanism(s), it seems logical that high quality nesting territories have greater likelihood of occupancy than lower quality ones.

Occupancy status of a golden eagle nesting territory often can be misclassified in a particular year, especially if the territory does not contain a used nest. (We address this issue further in Section 3.2.2.) However, in cases where an historical golden eagle nesting territory is truly vacant, some of its components may be used by other golden eagles for non-reproductive purposes (e.g., foraging). Whitfield et al. (2006) described the 11-year history of 20 golden eagle nesting

territories in Scotland and concluded that many alternative nests and parts of vacant territories were claimed by pairs in adjacent occupied territories in some years. Kochert et al. (1999) found presence of a neighboring vacant nesting territory to be a strong positive predictor of breeding success among golden eagles in Idaho after a wildfire reduced prey availability. This implied that vacant territories were incorporated into, and contributed to the success of, the remaining occupied territories.

3.2.2. How accurate are assessments that nesting territories are vacant?

As noted in Section 3.2.1, a major consideration when classifying occupancy status of a golden eagle nesting territory in a given year is the probability of correctly ascertaining adult presence. To reach the stage of having a used nest, holders of a territory must have successfully completed pair bonding and obtained enough food for the female to be physiologically prepared to produce eggs (Newton, 1979). The probability that occupancy of a nesting territory will be confirmed by surveyors increases with each stage of nesting in a given year; potentially occupied territories in which no eggs are laid are the hardest to classify correctly, territories with unsuccessful nests risk being misclassified, and those with successful nests are the easiest to classify correctly (Steenhof and Newton, 2007).

In our review we found scant information on the probability of correctly classifying occupancy status of golden eagle nesting territories. In southwestern Alaska, Booms et al. (2010) used replicate aerial surveys to derive detection probabilities of 0.68 and 0.69 for golden eagles occupying nesting territories in two study areas. However, both fixed-wing aircraft and helicopters were used to survey eagle territories in the two areas, confounding comparison between areas and survey methods. Detection probability was estimated to be 11%–15% higher for observers considered to be experienced than for inexperienced observers (Booms et al., 2010). Martin et al. (2009) used up to four helicopter and ground-based surveys per season to detect golden eagle nesting territory occupancy in Denali National Park, Alaska; they estimated that detection probability ranged between 0.9 and 1.0 across 20 years. Neither Booms et al. (2010) nor Martin et al. (2009) modeled effects of the presence of used nests on detection probability. Robust approaches for addressing imperfect detection of nesting territory occupancy (and nest success) are available (e.g., Nichols et al. (2007)); it would be informative to apply such approaches when analyzing data from surveys of territory occupancy by golden eagles. We surmise that for species of raptors that, like golden eagles, often forego reproduction when prey are scarce, the problem of misclassifying an occupied nesting territory as vacant is not inconsequential and could lead to inadequate protection of nesting territory holders from mortality and disturbance.

3.2.3. Do nests, or the associated habitat features (cliff, perches, surrounding foraging habitat) that initially facilitated or prompted nest-building, serve as attractants for non-breeding eagles?

We did not find specific information to address this question for golden eagles in our literature review. Conspecific attraction plays an important role in the distribution of colonial and semi-colonial raptors (Sergio and Penteriani, 2005), and as we previously noted, floating, non-territorial juvenile spotted owls and adult peregrine falcons aggregate around occupied nesting territories (Hunt, 1998; Lahaye et al., 2001). However, Caro et al. (2011) stated that golden eagle floaters on southwestern Europe's Iberian peninsula used "settlement areas" outside of occupied nesting territories. The fact that golden eagles in subadult plumage do occasionally occupy nesting territories and successfully reproduce suggests they must monitor the status of nesting territories and take advantage of openings when they can (Kochert et al., 2002; Steenhof et al., 1984). This implies some level of spatial proximity between subadult eagles and nesting territories, at least during early stages of pair formation. This important question would benefit from further investigation.

3.2.4. Do patterns in territory occupancy vary predictably geographically or with habitat?

As we noted in Section 3.2.1, the literature indicates that probability of a golden eagle nesting territory being occupied and, more importantly, that there is a used nest, is related to prey availability and other aspects of territory quality. In regions where annual prey abundance fluctuates temporally, territory occupancy and the frequency with which a given nest may be used likely varies more than in regions with less annual variation. For example, Millsap (1981) noted that most pairs of golden eagles on nesting territories in the Sonoran and Mojave deserts of west-central Arizona did not lay eggs every year; these deserts likely represent an extreme breeding environment for the species. Whether territory owners remained present during years when breeding was forgone was unknown. As with other aspects of nesting territory occupancy, the question of geographic variability in occupancy rates would benefit from further study.

4. Summary and conclusions

Our review of the literature shows that alternative nests are a common feature of golden eagle nesting territories across the species' range. They serve an important biological function. Alternative nests directly and indirectly attract both current territorial residents and residents of current or newly established, adjacent territories during territorial boundary adjustments or population expansion. For some other species of raptors, occupied nesting territories can attract non-breeders, though we found no direct information on this topic for golden eagles. At a given territory in a given year, the greatest activity area of a breeding pair of golden eagles includes alternative nests. Data from PTT-monitored golden eagles in JW's and RM's Pacific Northwest and New Mexico studies indicate that annual core use areas (50% utilization distributions) within larger home ranges (95% utilization distributions) of territory holders typically include all known alternative nests, even in years when no nest in the nesting territory is used.

Literature we reviewed indicates a golden eagle nest not used in a given year likely will be used in the future. The probability of re-use appears related to the nesting territory's quality, especially availability of prey, which affects how often there is a used nest. Another factor is availability and distribution of suitable nesting sites. For example, where cliffs and large trees are scarce in a landscape otherwise suited for golden eagles, alternative nests are likely fewer and more likely to be used than in places where suitable nesting sites are more numerous and widespread. We believe both of these factors vary geographically, though evidence for this is sparse and the topic warrants additional study.

Annual occupancy of golden eagle nesting territories tends to be very high, on the order of 80%–100% in studies we reviewed. However, long-term, published studies may have focused on larger or higher-density populations, and occupancy may be more intermittent in marginal habitats or smaller populations. We found only two studies that estimated probability of correctly classifying occupancy status of nesting territories (Booms et al., 2010; Martin et al., 2009). Although detection probability for occupancy in breeding areas with used nests was high in these studies, we surmise detection probability is likely much lower for occupied nesting territories lacking used nests. Comparisons within, and between, these two studies in open terrain in Alaska suggest that detection probabilities likely vary with factors such as survey methods, number of surveys per breeding season, study area characteristics, and observer experience (Booms et al., 2010; Martin et al., 2009). Given this and the high rate with which apparently vacant nesting territories are reoccupied, classification of an historical golden eagle nesting territory as permanently vacant should be undertaken with due care and only after a period of many years has passed with no sign of occupancy; in most cases, such territories are best regarded as potentially occupied. Published information indicates that a substantial proportion of alternative golden eagle nests can undergo ten or more years of disuse before being used again. Implications of this finding may extend to protection of entire nesting territories. Granted, unless potential nest sites are scarce, reoccupancy of nesting territories is more likely than re-use of a given alternative nest, but 10 years may still be insufficient time to "confirm" that a golden eagle nesting territory is permanently vacated.

Inter-year variation in breeding activity (e.g., presence of a used nest) in golden eagle nesting territories varies more than territory occupancy, ranging from 14%–100% in studies we reviewed. In general, nesting territory occupancy and breeding activity of golden eagles are directly linked to prey availability, but the relationship is stronger for breeding activity than for occupancy. Moreover, in one study we reviewed, the food resource that influenced breeding density differed from that which influenced breeding success (Watson et al., 1992).

Increased reoccupancy of nesting territories by golden eagles in a given area leads to increased nesting densities, and, consequently, concurrent decreases in nesting territory size. In periods of reduced prey availability, fewer golden eagle nests are used, and pairs with used nests may subsume within their territories portions of neighboring nesting territories with no breeding activity. As we mentioned above, there is greater tendency to re-occupy historical sites rather than pioneer new sites during increases in availability of prey. Golden eagles in habitats and regions with temporally consistent moderate to high levels of prey availability tend to have more stable, higher rates of nesting territory reoccupancy and breeding activity.

Our review indicated there is little information available to address questions of spatial and structural variation in the probability of nest re-use, and the degree to which alternative nests attract non-breeding golden eagles. We believe these are important questions, and suggest they are ripe topics for future research. Although they will not be easy questions to answer, retrospective reviews of existing nest-use data sets for golden eagle populations that use different nest support structures, and detailed analyses of existing spatial-use information from satellite-tagged non-breeding eagles are important next steps. Additionally, we believe more effort should be devoted to quantifying probability of detection of territory occupancy and nest use. Such data could help improve the design of monitoring efforts to assess golden eagle presence and reproductive status.

With respect to our initial questions, we conclude that: (1) alternative nests of golden eagles are attractive features in that they or the associated habitats are components of core areas used by golden eagles occupying nesting territories; (2) alternative golden eagle nests likely will be re-used; (3) probability of an alternative nest becoming used is greatest in areas where consistent and moderate to high levels of available prey support frequent breeding, and availability of alternative nests is limited; (4) probability of annual occupancy of golden eagle nesting territories typically is very high, as is the probability of reoccupancy of potentially vacant nesting territories; and (5) prey availability is probably the most important determinant of nesting territory occupancy and especially the probability that a nesting territory will be used in a given year. We surmise that a golden eagle nesting territory that is occupied but lacks a used nest is more prone to being misclassified as vacant than one with a used nest. Based on our review, we recommend alternative golden eagle nests be treated with the same deference as used nests in land use plans. We justify this recommendation on the basis of existing scientific information reviewed here, which suggests take, as defined by the Act and implementing regulations, is as likely to occur at alternative golden eagle nests as at used nests.

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