Breeding Ecology of Golden Eagles in Western Washington

Leif Hansen

A thesis

submitted in partial fulfillment of the

requirements for the degree of

Master of Science

University of Washington

2017

Committee:

John Marzluff, Chair

Aaron Wirsing

Marco Restani

Program Authorized to Offer Degree:

School of Environmental and Forest Sciences

University of Washington

Abstract

Breeding Ecology of Golden Eagles in Western Washington

Leif Hansen

Chair of the Supervisory Committee:
Dr. John Marzluff
The School of Environmental and Forest Sciences

Raptors breeding in novel environments must find sufficient food resources to survive and reproduce. Available prey and landscapes surrounding territories can influence aspects of parental care and reproductive output. I investigated the influence of prey size and landscape on parental care and territory occupancy, respectively, in western Washington, where as many as 86 Golden Eagle (*Aquila chrysaetos*) territories have been described. Much of the region is dominated by closed-canopy forests and lacks the typical prey communities commonly associated with Golden Eagle diets in North America. I provide support for the prey size hypothesis in a study of Golden Eagles utilizing a novel prey species. I utilized direct observation of occupied nests in the Cascade Mountains of Washington, U.S.A to record prey use and parental care. Over 70% of prey items delivered to nests were mountain beaver

(*Aplodontia rufa*), and nearly 88% of prey deliveries were made by the male parent. Relative prey mass was among the largest reported in similar studies of prey use and parental care. Consequently, female confinement was longer than reported in other studies of Golden Eagle parental care and approximately equal to what was predicted by the prey size hypothesis. Greater asymmetry in patterns of parental care may select for further reversed size dimorphism in raptors. I also investigated the effects of land cover, topography, and land use on occupancy of Golden Eagle territories ($n = 19$) using historic survey records and remotely-sensed aspects of the landscape. I found that territory occupancy is positively associated with elevation and elevation range, and negatively associated with forest cover. That is, a breeding territory was more likely to be frequently occupied if it occurred at a higher elevation, included a larger range of elevations, or included less forest cover. Forest management including timber harvest is likely providing suitable foraging habitat for Golden Eagles breeding in the region.

KEYWORDS: Golden Eagle, *Aquila chrysaetos*, parental care, western Washington, *Aplodontia rufa*, forestry, territory occupancy

TABLE OF CONTENTS

ACKNOWLEDGEMENTS

Thank you to my coworkers and managers at West Fork Timber Company and Sierra Pacific Industries for access to the study area and for encouraging and supporting this research. Thank you to my committee members, J. Marzluff, A. Wirsing, and M. Restani for their guidance on study design and editorial feedback. Thanks to the members of the Marzluff and Wirsing labs for their support throughout the process. I extend my deepest gratitude to my wife, Heide, for her support and motivation, and for staying up with our newborn son on so many nights so that I could complete another nest watch the next day. This work was funded in part by contributions from West Fork Timber Company and Sierra Pacific Industries.

CHAPTER 1: PREY USE AND PARENTAL CARE BY GOLDEN EAGLES IN WESTERN WASHINGTON

ABSTRACT

Raptors exhibit asymmetric parental care of offspring in the nest, with females in most species providing the majority of care for eggs and nestlings and males providing prey. How the division of parental care between male and female parents is determined in raptors for which the sexes share parenting has been studied and debated for some time. The prey size hypothesis suggests that as prey size increases, females will care for offspring in the nest for a longer period of time to assist offspring feed on larger prey that requires more handling time. Here I show support for the prey size hypothesis in a study of Golden Eagles (*Aquila chrysaetos*) utilizing a novel prey species. I utilized direct observation of occupied nests in the Cascade Mountains of Washington, U.S.A to record prey use and parental care. Over 70% of prey items delivered to nests were mountain beaver (*Aplodontia rufa*), and nearly 88% of prey deliveries were made by the male parent. Relative prey mass was among the largest reported in similar studies of prey use and parental care. Consequently, female confinement was longer than reported in other studies of Golden Eagle parental care, and approximately equal to that predicted by the prey size hypothesis. Greater asymmetry in patterns of parental care select for further reversed size dimorphism in raptors.

KEYWORDS: Golden Eagle, *Aquila chrysaetos*, parental care, western Washington, *Aplodontia rufa*

In most bird species both parents provide care to developing offspring in the nest (Clutton-Brock 1991), including 75% of species with known parental care strategies (Cockburn 2006). In many of these species, however, the division of parental duties is unequal. Females generally are responsible for the majority of incubation, brooding, and tending of offspring at the nest, whereas males provide prey for the offspring and female and only occasionally incubate or brood young (Ketterson and Nolan 1994). The full range of variation in parental care is seen within monogamous birds of prey. At one extreme is the Sharp-shinned Hawk (*Accipiter striatus*), whose males do not provide any care in the nest beyond delivering food (Delannoy and Cruz 1988). At the other extreme are Bearded Vultures (*Gypaetus barbatus*), whose females and males share incubation and brooding nearly equally (Margalida and Bertran 2000). The majority of raptor species fall somewhere between these two extremes, with females providing the majority of care in the nest while occasionally being relieved by males, who mostly provide prey (Newton 1979).

How the division of parental care between male and female parents is determined in raptors for which the sexes share parenting has been studied and debated for some time. Slagsvold and Sonerud (2007) hypothesized that the size and type of prey included in a raptor's diet influences parental care. They postulated that prey items that are larger and require more processing before nestlings consume them should require that the female parent remain in the nest for longer periods of time to assist young with feeding, leaving the male responsible for more of the burden of foraging (Fig. 1). Consequently, raptor species that utilize prey with longer handling times will show greater differences in parental care between sexes.

The prey size hypothesis has been tested both within and across species (Sonerud et al. 2014a, b). The length of time that females spent in nests to feed young (i.e. female confinement

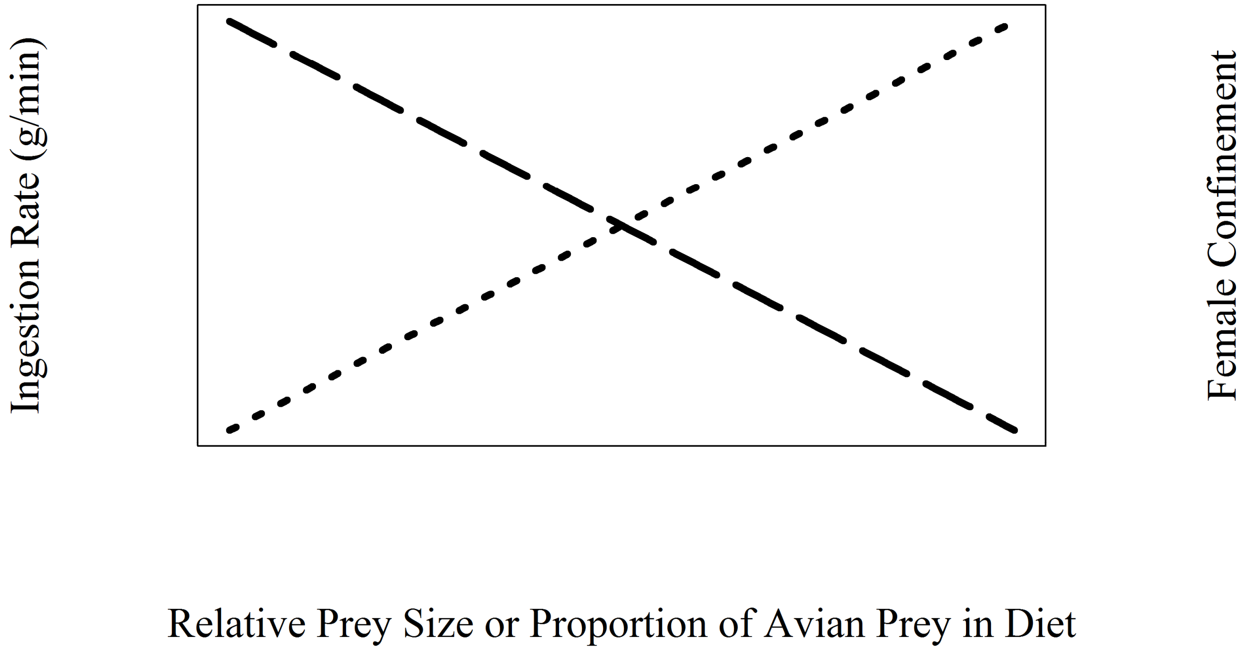

Figure 1. Expected relationship between a raptor’s diet and the duration of female care at the nest. Relative prey size is measured as prey mass divided by the mass of males of the focal raptor. The dashed line represents the ingestion rate of a chick feeding unassisted. The dotted line represents female confinement, or the proportion of the chick-rearing period that females will feed young and remain on the nest relative to a chick’s age at independence for the focal species.

to nest) was calculated by determining the age at which offspring were equally likely to self-feed as they were to be fed by a female relative to the age of total offspring independence. Within species, nestlings were less likely to ingest larger prey without assistance from a parent. When nestlings did feed unassisted, ingestion rates were slower for larger prey and avian prey, which had to be disarticulated or plucked before consumption. Across species, female confinement was not related to the amount of birds included in the diet across species (Fig. 2; $r^2 = 0.05$, $p = 0.26$). However, females assisted nestlings in partitioning prey items and thus were confined to the nest for a longer portion of the nestling period as relative prey size (i.e. the mean mass of prey relative to mass of a male of the focal raptor species) increased (Fig. 3; $y = 0.157+1.013x$, $r^2 = 0.59$, $p < 0.01$). The resulting greater asymmetry in parental care between the sexes and additional selection for a small male adapted to hunt and provide prey to his offspring and mate may partly explain the patterns of reversed sexual size dimorphism that in part underlie the division of parental care observed in raptors.

In this chapter I describe a study of Golden Eagle (*Aquila chrysaetos*) nests in western Washington, USA to investigate the influence of prey use on parental care in this region. Golden Eagles in this region nest on cliffs and in large coniferous trees, usually near fields or even-aged timber harvest units (i.e. clearcuts, Bruce et al. 1982). Prey use by Golden Eagles in western Washington has been documented sporadically and opportunistically. Published observations of prey use include mountain beaver (*Aplodontia rufa*) and anecdotal reports of other small- to medium-sized mammals, as well as carrion (Servheen 1978). However, Golden Eagle prey use in western Washington remains largely unquantified and the prey species typical of other regions are not present or abundant. Generally diets of Golden Eagles in North America are composed of Leporidae (hares and rabbits), Sciuridae (squirrels and marmots), and Tetraonidae (grouse and

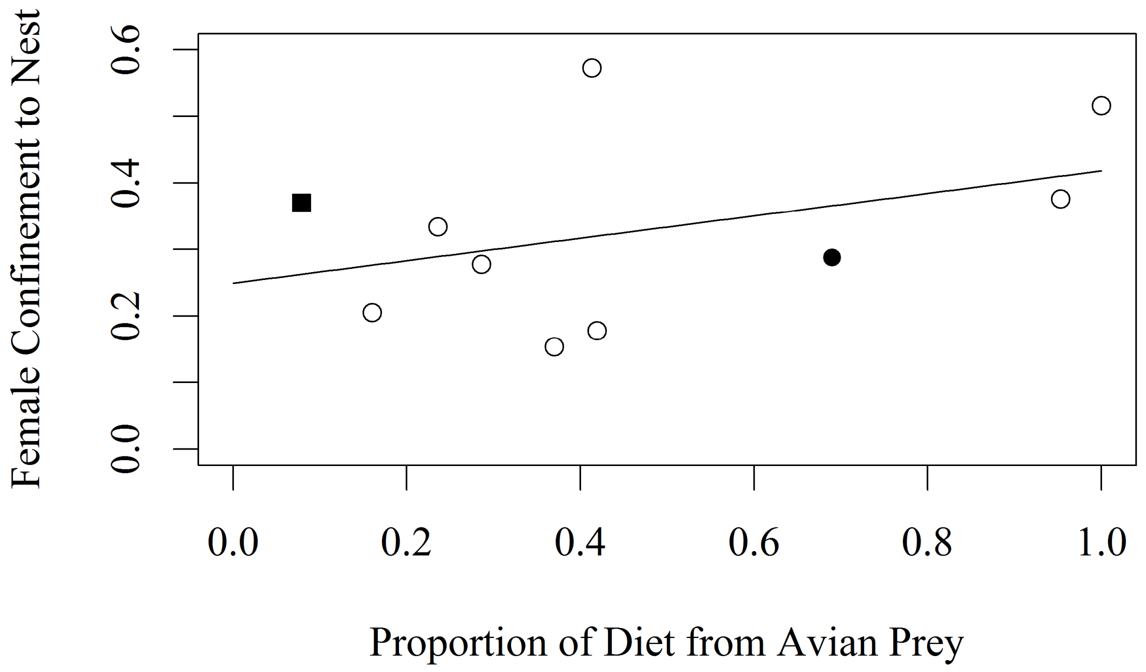

Figure 2. The relationship between female confinement (the period of time that chicks depend on females to feed them in the nest relative to the age of independence) and the proportion of diet from avian prey. Circles are from data on nine raptor species in Sonerud et al. (2014b); square is from data on Golden Eagles in Collopy (1984); filled points are data from Golden Eagles, and unfilled points are for other raptor species. The line represents a linear regression of all datapoints.

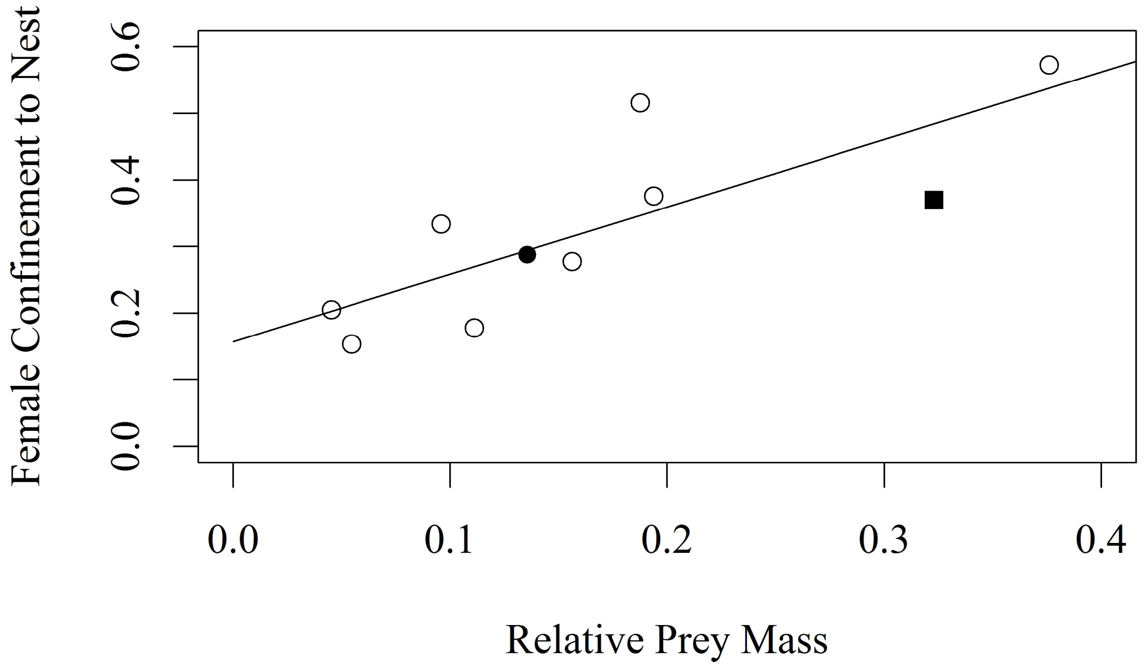

Figure 3. The relationship between female confinement (the period of time that chicks depend on females to feed them in the nest relative to the age of independence) and relative prey mass (mean mass of prey relative to the mass of a male of the focal raptor species). Circles are from data on nine raptor species in Sonerud et al. (2014b); square is from data on Golden Eagles in Collopy (1984); filled points are data from Golden Eagles, and unfilled points are for other raptor species. The line represents the linear regression of all datapoints.

ptarmigan) (Watson 2010). Other species of birds, mammals and reptiles are regularly found in Golden Eagle diets, and fish or eggs are occasionally taken as well (Brown 1992, Valutis and Marzluff 1997). These prey species are generally between 500 g and 2 kg in mass, but prey as small as 63 g and as large as 4 kg are found in diets as well (Watson 2010).

Parental care by Golden Eagles in western Washington has not been studied before. Studies of parental care elsewhere have shown that, like most raptor species, female Golden Eagles are responsible for most of the incubation, sheltering, and feeding of offspring, while males mainly hunt and deliver prey to the nest (Ellis 1979, Collopy 1984, Aoyama et al. 1988, Sonerud et al. 2014b). Females do hunt and deliver prey to the nest later in the nestling period, however, and males briefly incubate and brood to relieve females. Despite the variety of locations where these studies have been conducted and the varying prey taken between regions, the same general pattern of parental care has emerged in each case. However, the degree to which prey mass influences how much and how long the female is confined to the nest to assist young has been investigated in few studies.

Golden Eagles in western Washington offer a unique opportunity to study the influence of prey size on parental care because larger mammals (e.g. hares and rabbits) and birds (e.g. grouse and ptarmigan) do not occur in the same abundance as in other areas where this holarctic predator nests (Sonerud et al. 2014b). The mountain beaver, however, is ubiquitous in forests from sea level to timberline in this region (Carraway and Verts 1993) and could represent a major portion of the diets of Golden Eagles in the area. Mountain beavers are smaller than most mammals reported in previous studies of diet and parental care (mean mass = 1110 g, Appendix 1 Fig. A-1), but are larger than typical avian prey. Mountain beavers represent a relative prey mass of 0.31 compared to the reported mass of a male Golden Eagle (Cramp 1985). This relative prey mass is greater than the relative prey mass of many other studied raptors including avian-dependent Golden Eagles in Norway (Sonerud et al. 2014b), and similar to the relative prey mass of mammal-dependent Golden Eagles in Idaho (Collopy 1984; Fig. 2, 3). The prey size hypothesis predicts that the period of time that females remain at their nest in this region is positively related with prey size. Assuming mountain beavers are the primary prey for Golden Eagles in western Washington, female confinement in this region may be among the highest values reported by Sonerud et al. (2014b) and Collopy (1984).

I test the following hypotheses: 1) the diet of Golden Eagles in this region differs from diets in other regions because of the novel prey community; and 2) female confinement at the nest is positively related to prey mass.

METHODS

I studied Golden Eagles nesting on territories located on forestlands in the Cascade Mountain foothills of western Washington (46° 36’ N, 122° 28’ W; Fig. 4). The study area includes intensively-managed commercial tree farms and public forestlands where timber management practices have created a mosaic of stands of ranging from early to late seral stages. Dominant tree species include Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), Pacific silver fir (*Abies amabilis*), and noble fir (*Abies procera*). Elevation in the area ranges from approximately 300 m to 1650 m.

I use the following terminology as suggested by Steenhof and Newton (2007) to describe Golden Eagle breeding: breeding season, fledging, incubation period, nest, nestling period, nesting territory, and territory occupancy. Early in the 2015 and 2016 breeding seasons, I

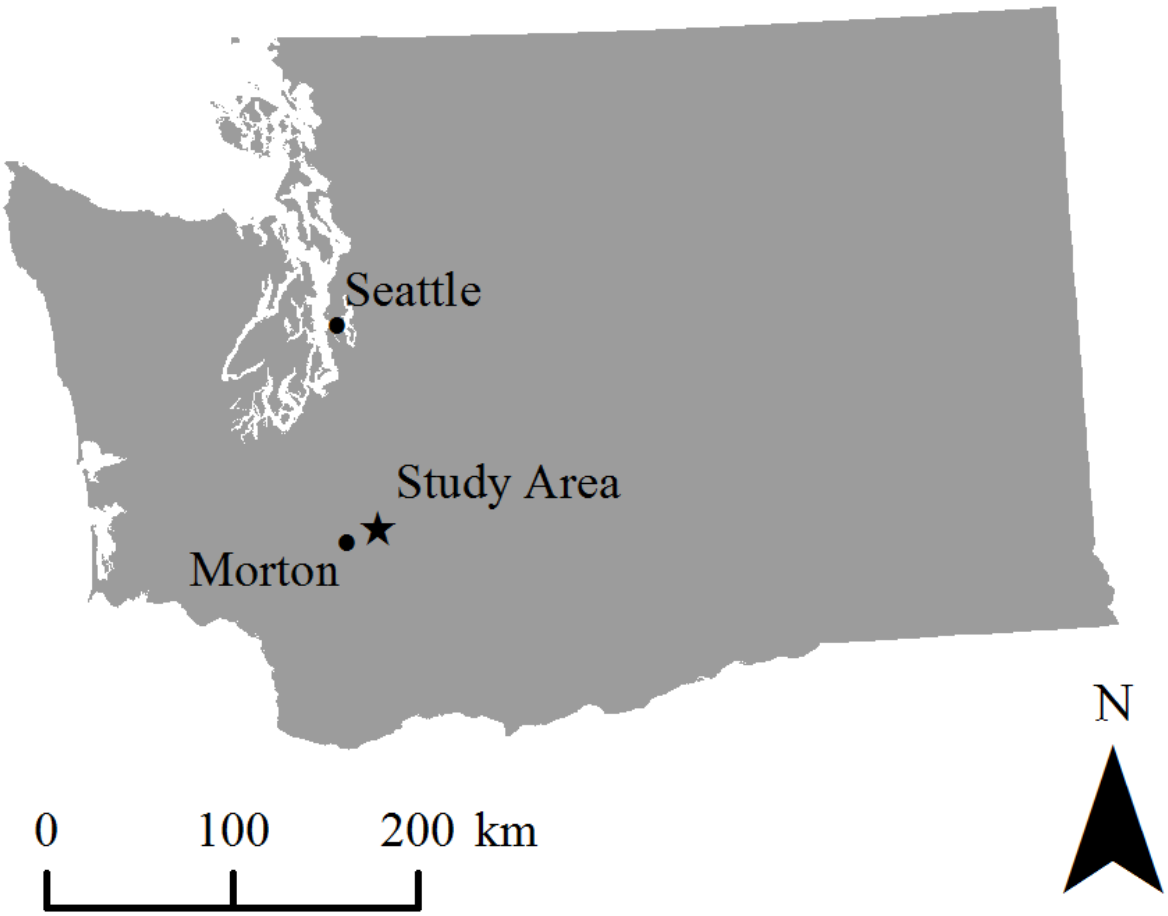

Figure 4. Location of study area in the context of Washington State. Locations of cities are provided for reference.

determined occupancy and nesting status at four nesting territories in the study area during the courtship phase. I searched cliffs and trees known to support Golden Eagle nests from viewpoints located 400 to 2000 m from the nest with a spotting scope to search for signs of occupancy and nest maintenance (Johnson 1972, Pagel et al. 2010). Areas surrounding known nests and potential nest substrates were also searched for adult Golden Eagles displaying territorial behavior (e.g. undulating flight; Harmata 1982).

After I determined a territory was occupied by a nesting pair, I began weekly direct observations of nests to document parental care during the incubation and nestling periods. To limit disturbance early in the nesting season, I established viewpoints providing a clear line of sight to the nest as far from the nest as possible (100 to 1400 m from nests) and used a spotting scope to aid observations. After hatching and as nestlings became able to thermoregulate, I moved to viewpoints closer to the nest (100 to 200 m from nests). I constructed blinds in stands of mature timber or watched from a vehicle on forest roads. I watched nests for 10 hr in daylight beginning near sunrise or concluding near sunset. In some cases observation periods were shorter because of weather (fog or precipitation obstructing views). When I determined a nest had failed, I stopped watching the failed nest and began observing remaining active nests up to two times per week. I concluded the observation season when I found evidence that nestlings fledged for the first time.

Prey Use

I recorded prey deliveries made by adult eagles during the nest observations described above. Prey items delivered to nests were identified as closely to species as possible. Observed prey deliveries were summarized for each species and taxonomic group by their frequency and percent biomass (Marti et al. 2007). I used published adult masses for most species to make estimates about biomass (Maser 1998, Sibley 2003), and for mountain beaver biomass I used the mean mass of carcasses that were trapped in the area for unrelated animal damage control efforts (Appendix 1 Figure A-1). I also calculated the average mass of all prey items delivered to nest using these values for mass.

Parental Care

I employed all-occurrences sampling to capture all aspects of parental care at the nest and recorded bouts of incubation, sheltering, food provisioning, and general nest attendance (Gaibani and Csermely 2007). I recorded each prey item delivered to the nest, identifying each prey item and the sex of the delivering parent. I determined sex of the adult Golden Eagle using their behavior, relative size, position during copulation, and unique plumage characteristics of individual birds. I calculated the duration of time and the proportion of each observation period that I observed each adult incubating eggs or sheltering young, feeding young, and attending the nest. I also calculated the number of deliveries of prey made by each adult during each observation period and compared the frequency of deliveries made by the female versus male adult. To test for differences in care between male and female parents, I used a Wilcoxon signed-rank test because small sample size precluded parametric analysis (Zar 1984). I described the trend in female behavior at the nest and prey deliveries over time by conducting linear regression (Zar 1984). I set significance for these tests at $p < 0.10$ because of small sample size. I also modeled the probability that a chick self-fed in a feeding bout as a function of chick age using logistic regression (Zar 1984), and calculated odds ratios to interpret the output of this logistic regression, specifically how the odds that a chick self-fed increased each week.

To compare my results to other prey and parental care studies, I calculated female confinement (Sonerud et al. 2014b) as the age at which the probability of a chick self-feeding and a chick being fed by an adult are equal, divided by the age when fledglings become independent from parents (140 d, Soutullo et al. 2006). Relative prey mass was calculated as the mean mass of prey delivered to the nests divided by the reported mean mass of male Golden Eagles (3572 g, Cramp 1985). The proportion of avian prey in the diet was determined as the frequency of avian prey items divided by the frequency of all prey items. I used R software for all statistical analysis (R Core Team 2015).

RESULTS

I watched four nesting attempts at three nesting territories in the study area during the 2015 and 2016 breeding seasons for a total of 382 hr during 41 observation periods. Two of the nesting attempts were successful, each fledging one bird. The remaining two nests failed during the nestling period.

Prey Use

I observed 49 prey deliveries during observation periods; between 5 and 25 deliveries were observed per nesting attempt. In all cases, identifiable prey items were delivered to the nest whole. The most commonly observed prey species was the mountain beaver, and other prey species included Sooty Grouse (*Dendragapus fuliginosus*) and unidentifiable small mammals (Fig. 5). The relative contributions of each prey species were unchanged when calculated by frequency or by total biomass contributed by the species (Fig. 6). The estimated average mass of all prey delivered to nests was 1035 g. I could not definitively identify 10 prey items because of poor visibility or birds in the nest obstructing my view.

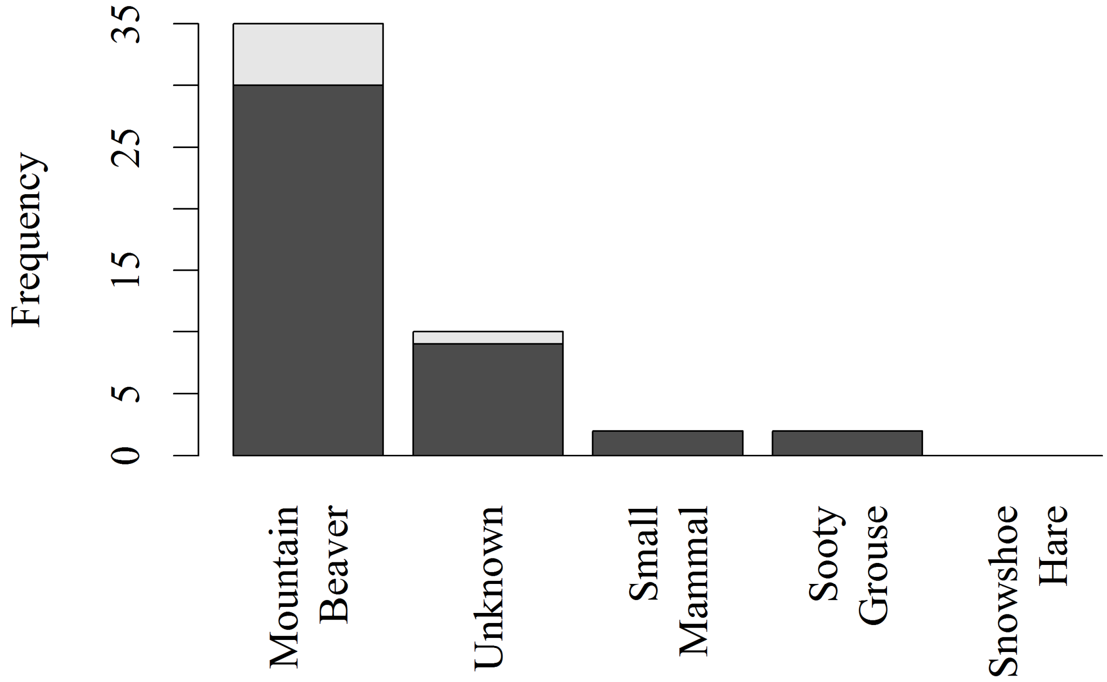

Figure 5. Frequency distribution of prey items delivered to Golden Eagle nests. Dark bars represent deliveries by males (*n* = 43), and light bars represent deliveries by females (*n* = 6).

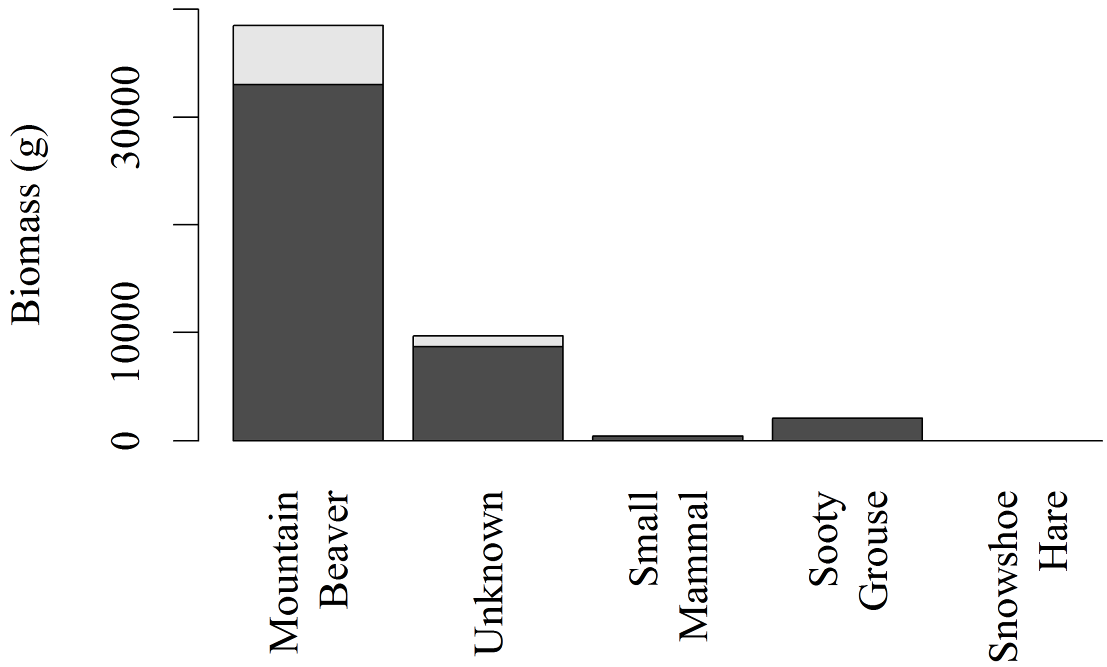

Figure 6. Estimated biomass of prey items delivered to Golden Eagle nests. Dark bars represent deliveries by males, and light bars represent deliveries by females. I used the following prey masses to estimate biomass: mountain beaver, 1110 g (Appendix 1 Fig. A-1); unknown, 967 g (average of other 4 prey types); small mammal, 225 g (Maser 1998); Sooty Grouse, 1043 g (Sibley 2003); snowshoe hare (*Lepus americanus*), 1500 g (Maser 1998)

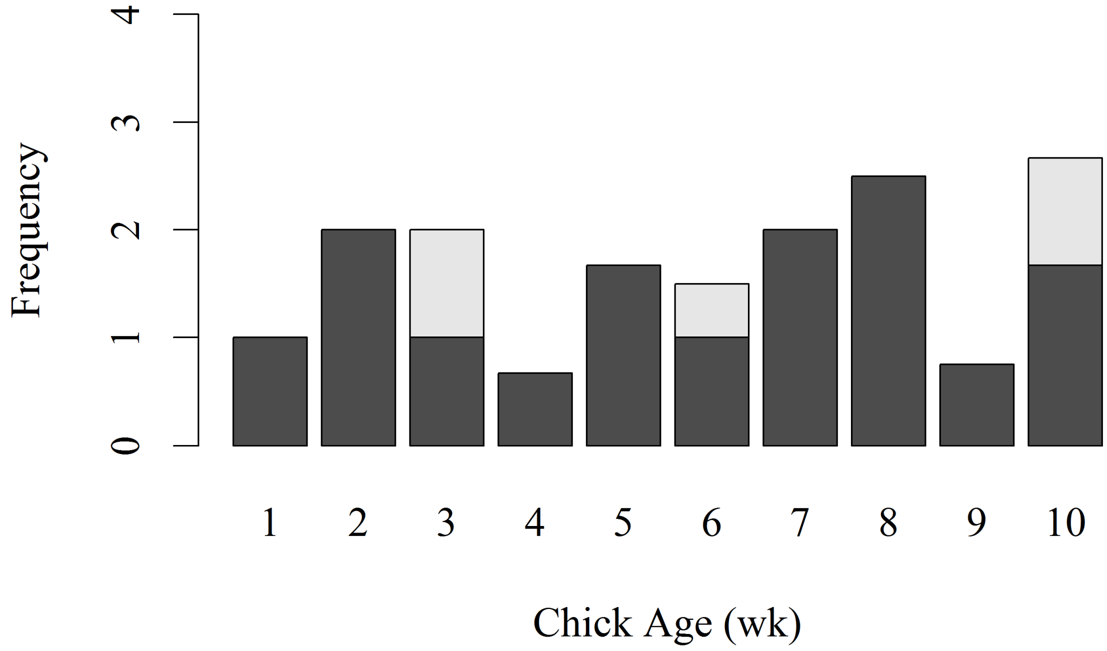

Figure 7. Mean prey deliveries per observation period during each week of the nestling period. The dark bars represent deliveries by the male, and the lighter bars represent deliveries by the female.

Male eagles were the main providers of prey, bringing 43 of 49 prey items delivered to nests during observation periods (Fig. 5). There did not appear to be a difference in prey species delivered by each parent beyond the frequency of deliveries. Prey deliveries observed per day increased slightly over the course of the nestling period (Fig. 7; $y = 1.17 + 0.068x$, $r^2 = 0.06$, $p = 0.29$).

Parental Care

During incubation I observed nests for a total of 113.2 hr over 12 observation periods. At least one adult was present at the nest nearly all of the observed time, with nests left unattended only 3.9% of observed time. Female eagles provided the majority of care in the nest, being present in the nest 86.4% and incubating 78.2% of each observation (Fig. 8; $W = 10$, $p = 0.06$). Conversely, male eagles attended nests 10.4% of each observation period and spent nearly all of that time incubating. Males relieved females on average 1.25 times per observation period. I observed only 2 prey deliveries to nests during incubation, both made by males. On several more occasions I suspected but could not confirm that females left the nest for a nearby perch where the male had delivered prey.

During the nestling period, I observed nests for a total of 268.8 hr over 29 observation periods. Two nests failed early in the nestling period. Nests were unattended more often than during incubation, especially as offspring grew closer to fledging. Like the incubation period, female eagles continued to provide the majority of care in the nest, being present in the nest 46.2% of total observed time and sheltering young 22.9% of total observed time, compared to 0.9% and 0.2% for males, respectively (Fig. 9; $W = 10$, $p = 0.06$)). Whereas the amount of time females attended the nest or sheltered eggs during incubation remained high throughout incubation, these behaviors decreased over the course of the nestling period (Fig. 10 and 11; nest

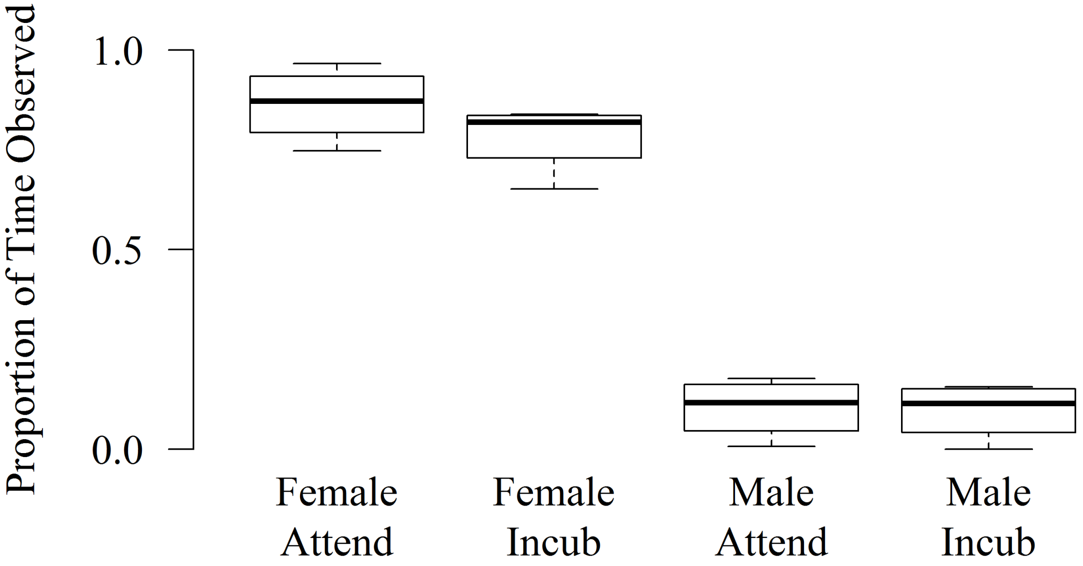

Figure 8. Proportion of each observation during the incubation period that parents attended the nest or incubated eggs. The dark bar represents the median value, the extent of the boxes represents lower and upper quartiles, and the whiskers represent 1.5 times the inter-quartile distance.

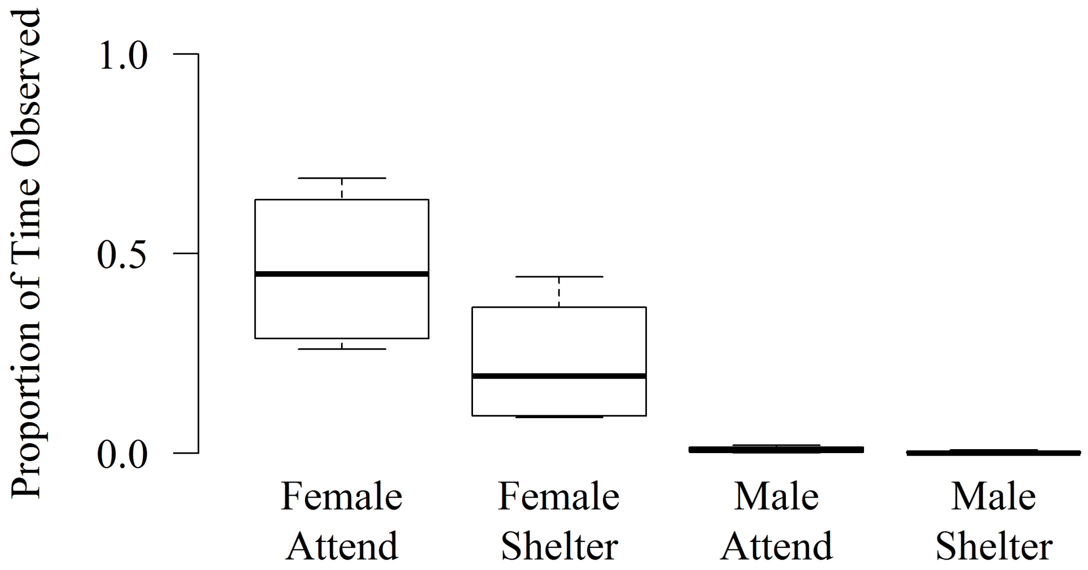

Figure 9. Proportion of each daily observation period that parents attended the nest or sheltered offspring. The dark bar represents the median value, the extent of the boxes represents lower and upper quartiles, and the whiskers represent 1.5 times the inter-quartile distance.

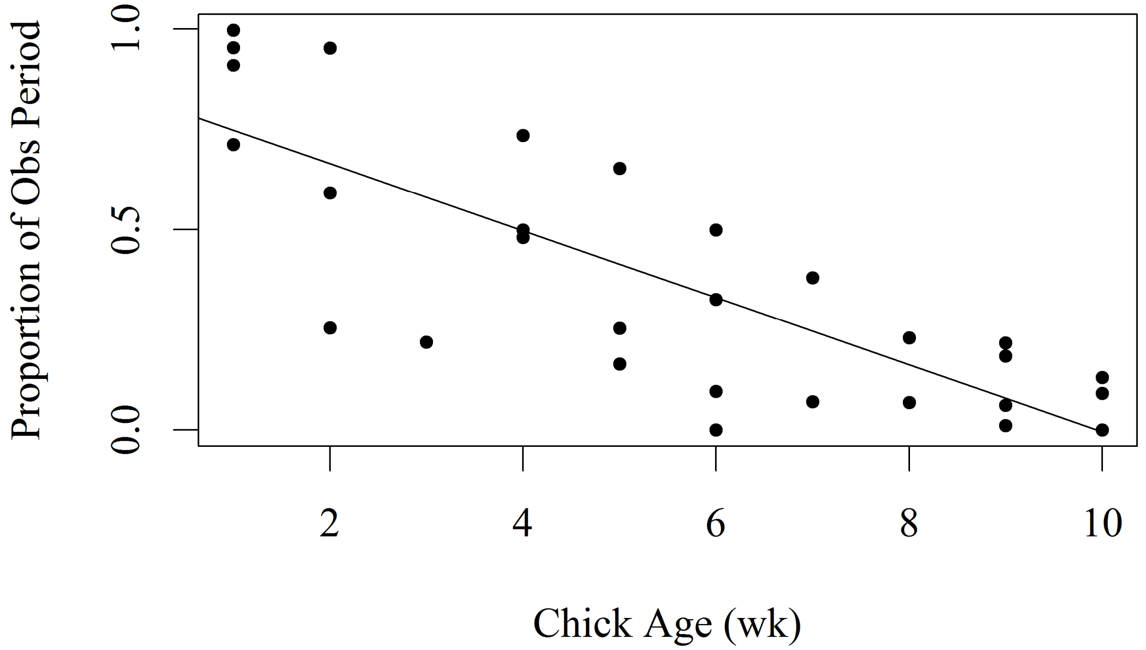

Figure 10. The proportion of each observation period that the adult female was present on a nest during the nestling period. The trendline represents the trend in female attendance from hatching (week 0) to fledging (week 10).

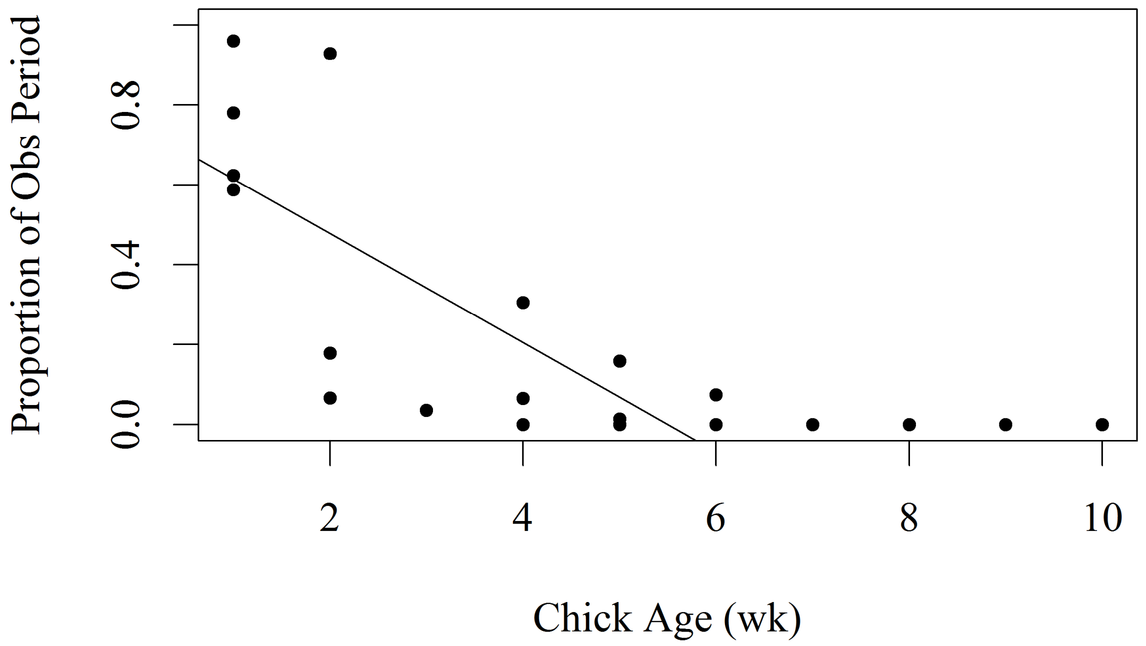

Figure 11. The proportion of each observation period that the adult female was present on a nest and sheltering young during the nestling period. The trendline represents the change in sheltering behavior from hatching (week 0) to the time when no more sheltering was observed (week 6).

attendance: $y = 0.83145-0.08359x$, $r^2 = 0.64$, $p \leq 0.0001$; sheltering: $y = 0.7516 - 0.1366x$, $r^2 = 0.59$, $p \leq 0.001$). Females did not shelter young after the sixth week of development. In 96.8% of instances of parental feeding the female was the parent that fed the chicks. The time that adults fed young decreased after the fifth and sixth week of chick development, when chicks began to effectively tear prey and self-feed more often (Fig. 12). The probability that a chick was self-fed during an observed bout of feeding increased over the course of the nestling period; however, chicks were not entirely independent in terms of feeding by the time they fledged (Fig. 12, intercept = -4.6441, $\beta = 0.5844$, odds ratio = 1.794). The odds ratio indicates that for each week a chick aged, the odds that it fed unassisted increased by 79%. The logistic regression predicted that when 7.9 wk old, chicks were equally likely to self-feed as they were to be fed by a female. A similar pattern emerged when considering the amount of time chicks self-fed compared to the overall time they were fed in each observation period.

The degree of female confinement was close to that predicted by the prey size hypothesis given the large relative prey size value from these nests (Fig. 13, relative prey size = 0.29). The relationship between the amount of avian prey in the diet and female confinement at these nests provided further support against a relationship between the amount of avian prey in the diet and female confinement (Fig. 14).

DISCUSSION

In general, parental behavior was similar to other published studies of Golden Eagles despite marked differences in diets between the regions, however this finding is not unexpected, for the pattern seems to be conserved among Golden Eagles across their wide range (Watson

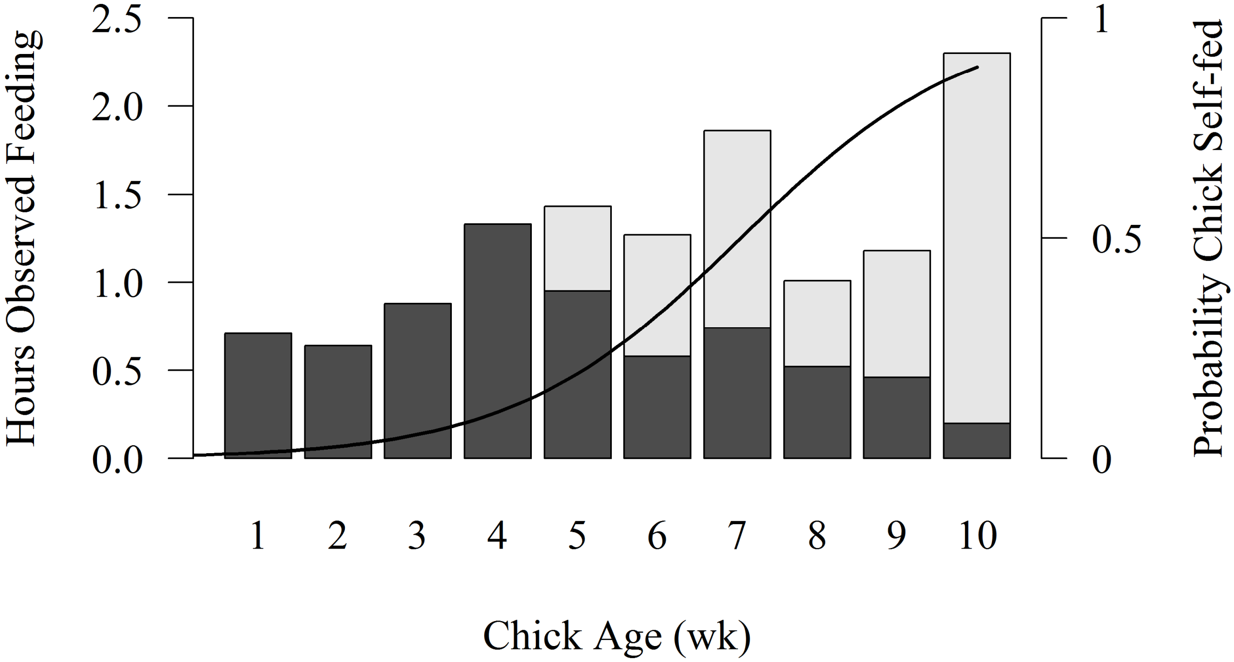

Figure 12. The amount of time that chicks were fed during the nestling period. Values shown in bars represent the mean of all observation periods made during each week of chick development. Dark shaded bars represent instances when the female fed offspring, and light shaded bars represent instances when chick was self-feeding. Feeding by the adult male was negligible. The curve shows the probability based on logistic regression that a chick on the nest was self-fed in a given feeding bout over the course of the nestling period, based on the mean frequency of observed bouts of parents feeding and chicks self-feeding each week (*n* = 97 bouts).

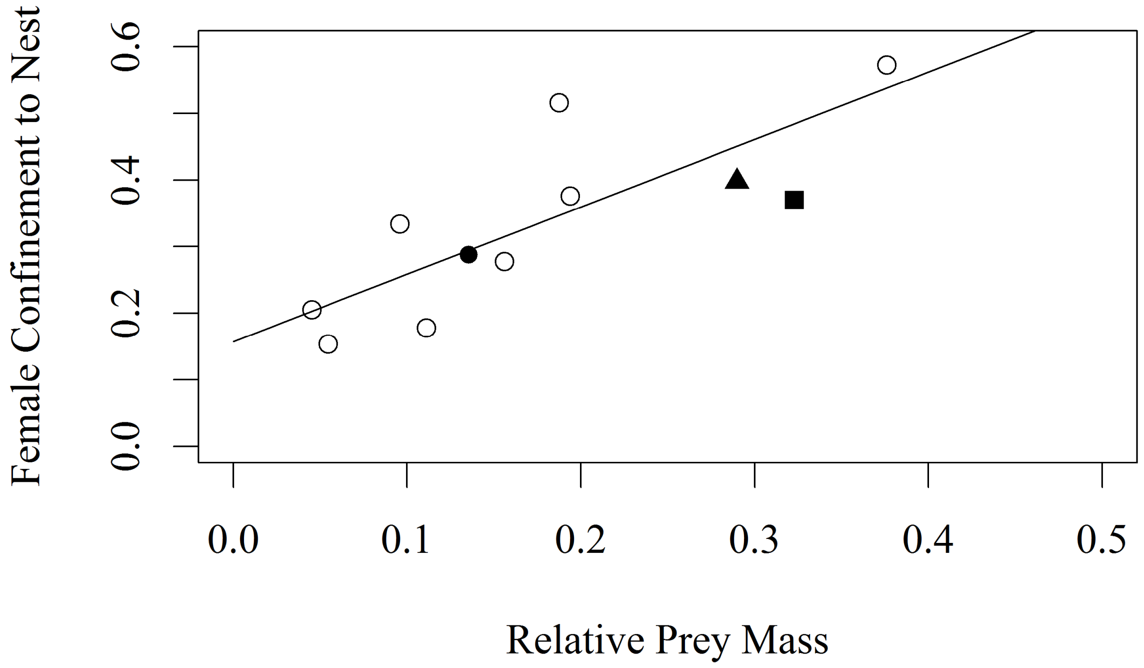

Figure 13. The relationship between female confinement and relative prey mass. Triangle is from this study, square is from Collopy (1984), and circles are from Sonerud et al. (2014b). Filled shapes are from Golden Eagle nests, unfilled shapes are other raptor species. The line represents a linear regression of all datapoints from Collopy (1984) and Sonerud et al. (2014b).

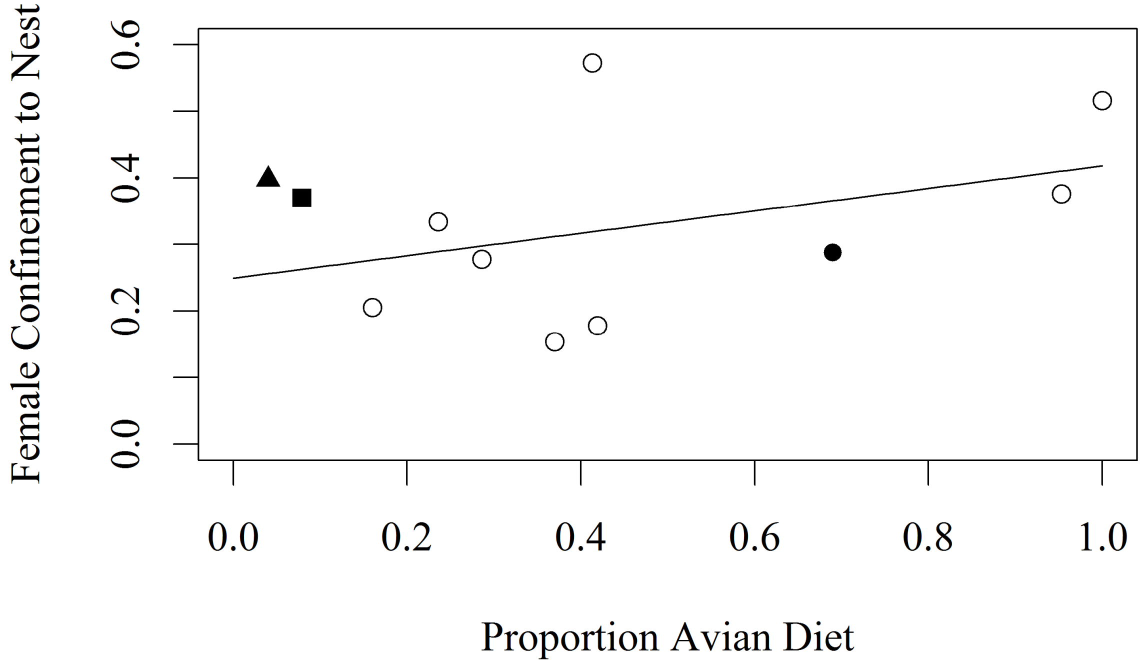

Figure 14. The relationship between female confinement and the amount of avian prey in the diet. Triangle is from this study, square is from Collopy (1984), and circles are from Sonerud et al. (2014b). Filled shapes are from Golden Eagle nests, unfilled shapes are other raptor species. The line represents a linear regression of all datapoints from Collopy (1984) and Sonerud et al. (2014b).

2010). The Golden Eagles in my study area are utilizing mountain beaver as their primary prey species; nearly three-quarters of prey items delivered to nests were mountain beavers. Average mountain beaver mass (1110 grams, Appendix 1 Fig. A-1) falls within the range of masses for prey predominantly taken in North America (Watson 2010) but is less than the average mass of black-tailed jackrabbits (*Lepus californicus,* 2300-3200 g, Maser 1998), one of the primary prey observed by Collopy (1984). Although mountain beavers are smaller than primary mammalian prey consumed outside of western Washington (e.g. jackrabbits), the average mass of prey delivered to nests in my study (1035 g) was only slightly less than what was reported by Collopy (1983a, 1153 g) and greater than what was reported by Sonerud et al. (2014b, 483 g). The smaller size of mammalian prey consumed in western Washington (mountain beaver) compared to Idaho (Collopy 1983a) should require less processing and handling time by females and enable nestlings to self-feed more often as they get closer to fledging. This in turn should reduce the amount of time females spend feeding young, reduce the time the female is at the nest, and enable the female to leave the nest to forage and deliver prey to their offspring.

The nestlings I watched continued to take prey offered by the female up until fledging though the amount of time females fed decreased. Chicks became competent at self-feeding but did not reach total independence in that regard by the time they fledged. In contrast, feeding by parents was rare after the seventh week in Idaho and Norway (Collopy 1984, Sonerud et al. 2014b). Females at Washington and Idaho nests stopped sheltering young when chicks were 6 weeks old. Direct comparisons in nest attendance cannot be made because of differences in how data on parental care were recorded and reported, but Idaho females spent less time at the nest than Washington females as evidenced by their increased prey contributions in weeks 7 through 9; females in Idaho contributed 43% of the total biomass delivered during weeks 7 through 9 when nestling food consumption peaked (Collopy 1984). Washington females, despite having smaller mammalian prey than Golden Eagles in Idaho and theoretically less of a need to partition prey for young, did not increase prey deliveries to the nest over the nestling period.

It appears that nesting raptors with diets including larger prey experience more and longer female feeding behavior and attendance at the nest to facilitate the feeding of offspring. Though my study does support the hypothesis that prey size influences the degree of female feeding and confinement in the nest overall, the relationship between my findings and those of Collopy (1984) warrants further review. It could be the case that prey ecology and the ability of a solo-hunting male Golden Eagle to successfully hunt mountain beaver are also shaping the patterns of parental care in western Washington. Hunting for mountain beavers is a different prospect than hunting hares or grouse. Mountain beavers are territorial, non-colonial, fossorial mammals that rarely travel on the surface (Carraway and Verts 1993). When above ground they are generally foraging near a burrow entrance or making longer movements while dispersing (Arjo et al. 2007). Historically, mountain beavers were thought to only venture above ground nocturnally, but recent research (Arjo et al. 2007) as well as my own observations of mountain beavers being delivered to eagle nests throughout the day suggest that they are active and above ground at all hours. Their diurnal activity that increases predation risk is likely driven by their poorly functioning kidneys that require nearly constant water intake (Carraway and Verts 1993). Golden Eagles likely forage for this species using contour-flight with short glide attacks and low flight with slow descent attacks (Watson 2010). Foraging eagles would rely on surprising mountain beavers that were out of their burrow and taking them before escape to the safety of a burrow was possible.

In comparison, the prey species observed in other study areas are predominantly not burrowing animals (e.g. hares and grouse). These prey species rely on vegetative cover and may be susceptible to other hunting strategies such as tandem hunting. This behavior has been observed in Golden Eagles hunting prey with well-developed escape responses, including jackrabbits (Collopy 1983b). In tandem hunting, one eagle strikes and captures the prey as the other eagle diverts the attention of the prey. Most tandem hunting in Golden Eagles involves larger prey (Kochert et al. 2002). Other raptor species are known to employ tandem hunting including the Aplomado Falcon (*Falco femoralis*), which tandem hunts largely when pursuing birds that are elusive to capture (Hector 1981). Using this technique Aplomado Falcons experienced lower capture success than hunting alone but recorded a higher number of hunting attempts, resulting in more successful hunts of avian prey. It could be the case that female confinement in Idaho is shortened by a need for the female to participate in tandem hunts.

The importance of mountain beavers in the diet of western Washington Golden Eagles is also worth considering. Mountain beavers are found in many types of forest in the region but are most prolific in areas with higher amounts of shrub and low vegetative cover (Arjo et al. 2007). Densities in closed canopy forests seldom exceed 4 animals per hectare (Anderson and Borrecco 1980) but can exceed 15 to 20 animals per hectare in areas of early seral conditions following timber harvest and during stand establishment (Neal and Borrecco 1981). Mountain beavers can cause considerable damage to seedlings in regenerating stands, and significantly slow seedling establishment and reforestation efforts. The economic damage to first year regenerating stands caused by mountain beavers on all private timberlands in Oregon was estimated to be as high as $6.8 million annually (Nolte and Dykzeul 2000), assuming that no damage control efforts were employed. Nonetheless, the economic cost is substantial.

In an attempt to limit damage, efforts are often employed by forest managers to reduce mountain beaver densities and encourage stand regeneration. Reductions in prey abundance and availability can impact breeding success in a variety of ways (Newton 1979). The impact depends on the timing and severity of abundance reduction, as well as the availability of alternative prey. During the pre-breeding season, female raptors need to build body reserves to develop eggs and to withstand lean times during incubation and the nestling period. Food shortages pre-breeding can lead to failure or impact the timing of breeding, as has been shown in Cooper's Hawks (*Accipiter striatus*) in Arizona (Snyder and Wiley 1976). Food abundance is also important during the early nestling period, when male raptors are responsible for the majority of prey items delivered. Prey needs to be abundant and available enough for the male to feed himself, the female, and any young on the nest. Prey also needs to be available for young birds after they fledge, as these birds are inexperienced hunters that will starve if insufficient prey is captured. Reductions in mountain beaver densities, though desirable for forest managers, could be problematic for breeding Golden Eagles if numbers are reduced enough over a wide enough area to limit total biomass available to eagles, especially if reductions occur during critical periods of the breeding season. Golden Eagle management plans for western Washington should take this into account, with considerations made for maintaining adequate prey numbers in Golden Eagle home ranges to limit impact on breeding success.

Golden Eagles breeding in the forests of western Washington appear to be utilizing a unique prey species- the mountain beaver. Moreover, the length of time adult females remained on the nest to feed young was consistent with the prey size hypothesis given the size of this novel prey species. The relationship between prey size and female care in the nest was maintained in populations of Golden Eagles in two other regions utilizing very different prey, and appears to hold across other species of raptor as well. However, only a small number of studies have specifically investigated this relationship. Many studies of Golden Eagles and closely related species have employed nest watches to document prey use, yet only a few studies have recorded or reported patterns of parental care in a manner that allows for analysis of the relationship between parental care and prey use. Future studies of prey use by raptors should report on the extent and duration of females feeding young in the nest so that direct comparisons can be made and the prey size hypothesis can be evaluated using the results of these studies.

CHAPTER 2: ON THE EDGE: THE EFFECT OF LAND COVER ON GOLDEN EAGLE TERRITORY OCCUPANCY IN WESTERN WASHINGTON

ABSTRACT

Predators, including raptors, adjust their spatial movements to increase encounters with vulnerable prey and establish breeding territories where sufficient resources are available, even when occupying novel environments. The Golden Eagle (*Aquila chrysaetos*) typically breeds in open or semi-open landscapes where prey species are abundant and available. Yet as many as 46 Golden Eagle breeding territories have been described in western Washington, where closed canopy forests dominate the landscape in the absence of disturbance or forest management. I investigated the effects of land cover, topography, and land use on occupancy of Golden Eagle territories ($n = 19$) using historic survey records and remotely-sensed information about the landscape. I found that territory occupancy is positively associated with elevation and elevation range, and negatively associated with forest cover; that is, a breeding territory was more likely to be frequently occupied if it occurred at a higher elevation, included a larger range of elevations, or included less forest cover. Forest management including timber harvest is likely providing suitable foraging habitat for Golden Eagles breeding in the region. Future efforts should focus on identifying existing unknown territories in the region and systematically surveying territories for occupancy and reproductive outcomes.

KEYWORDS: Golden Eagle, *Aquila chrysaetos*, western Washington, forestry, territory occupancy

Predators adjust their range and movements to increase access to critical prey resources (Krebs 2001). Often, these adjustments require nuanced use of the landscape to hunt where prey are not only available, but also safely accessible. For example, gray wolves (*Canis lupus*) in northern British Columbia use vast landscapes in a manner that maximizes encounters with prey, while minimizing the cost of travel (Milakovic et al. 2011). To do so, wolves travel along edges and areas covered by shrub communities that increased encounter rates of elk (*Cervus elaphus*) and moose (*Alces alces*), while avoiding areas of dense spruce forest that entailed greater travel costs. In contrast, female Pacific fishers *(Martes pennanti*) on the Olympic Peninsula of Washington, USA tended to avoid areas of open habitat to reduce predation risk and meet reproductive requirements (Lewis et al. 2016). Space use by lions (*Panthera leo*) in the Serengeti was consistently related to landscape attributes that increased prey vulnerability, regardless of prey taken or the season (Kittle et al. 2016). In the wet season when prey were scarce lions spent more time near embankments that facilitate ambush of prey, whereas in the dry season they concentrated use near the limited water sources that attracted high numbers of prey animals.

Likewise, avian predators, though able to easily move throughout their range, also respond to variation in land cover, land use, and terrain. These aspects of the landscape affect prey abundance and accessibility, which raptors respond to through changes in habitat use (Bechard 1982, Kochert et al. 1999, Rullman and Marzluff 2014). Raptors also respond to changes resulting from human land use, which can determine what types of management and forms of disturbance occur in an area. For example, policies encouraging the development of forest can cause reduced densities of raptors that forage in more open environments (Pedrini and Sergio 2001) or cause shifts in raptor diet (Murgatroyd et al. 2016), whereas recreational activities can affect occupancy and colonization of territories (Kaisanlahti-Jokimaki et al. 2008, Martin et al. 2009, Spaul and Heath 2016). Terrain characteristics like elevation and topography may affect the density or structure of vegetation and ground cover or create updrafts that provide lift for foraging birds (McGrady et al. 2002). These characteristics together determine the quality of an area as breeding habitat and can impact the occupancy of a territory by avian predators, such as Golden Eagles (*Aquila chrysaetos*), especially where density of the species is low and habitat is heterogeneous (Ferrer and Donazar 1996, Watson 2010). However, the landscape characteristics that impact territory occupancy can vary among species and regions, and this variation has yet to be investigated in novel settings.

In this paper I describe the landscape of Golden Eagle territories in western Washington in terms of terrain, land use, and land cover. The region of Washington State west of the Cascade Mountains offers a unique setting to study breeding Golden Eagles, a species that typically breeds in areas containing open and semi-open habitats including tundra, shrublands, grasslands, and coniferous forests (Kochert et al. 2002). Yet as many as 86 territories have been documented in western Washington (Hayes 2013), where much of the landscape is generally dominated by closed-canopy coniferous forest which is usually avoided by the species (Singh et al. 2016). Approximately half of Washington is forested, and public agencies manage roughly two-thirds of this forested area (Washington Forest Protection Association 2006). By area, approximately 20% of public forestlands in Washington are designated as National Parks, National Wilderness Areas, and State Conservation Areas and have limitations on land management (Washington Forest Protection Association 2006). Much of the forest outside of preserves, both public and private, is subjected to forest management. In Western Washington, the primary method of timber harvest is even-aged management, which has replaced fire and wind as the main disturbance agent that creates and maintains gaps in forest cover (Agee 1993). Where Golden

Eagles and close relatives do occur in forested lands they often associate with clearings where prey are most available (Leopold and Wolfe 1970, Servheen 1978, Bruce et al. 1982). The mountain beaver (*Aplodontia rufa*), a primary prey species of Golden Eagles in western Washington, occurs at higher abundance in early seral forest stands that have not yet achieved canopy closure (Neal and Borrecco 1981), and Golden Eagle core use areas are expected to include areas of early seral habitat. However, the characteristics of the landscape and land cover types surrounding Golden Eagle territories has not been previously quantified in western Washington, and the relationship between landscapes and territory occupancy has not been investigated. I test the hypothesis that territory occupancy is positively associated with prey vulnerability, which I expect to increase with reduced forest cover and on managed lands where timber harvest is frequent.

METHODS

I obtained from the Washington Department of Fish and Wildlife a database of locations of known Golden Eagle nests from all identified territories in western Washington (Fig. 1, *n* = 46). These territories were west of the crest of the Cascade Mountains at elevations ranging from sea level at the Pacific Coast to approximately 2700 m above sea level in the Cascade and Olympic mountain ranges. Western Washington contains a variety of land uses and cover types including urban centers, agricultural lands, timberlands, and alpine environments. Vegetative communities vary widely but are dominated largely by coniferous forest (Franklin and Dyrness 1973).

The database included occupancy and productivity values for these territories, with some records dating back to 1965. Recent efforts have emphasized standardized occupancy and

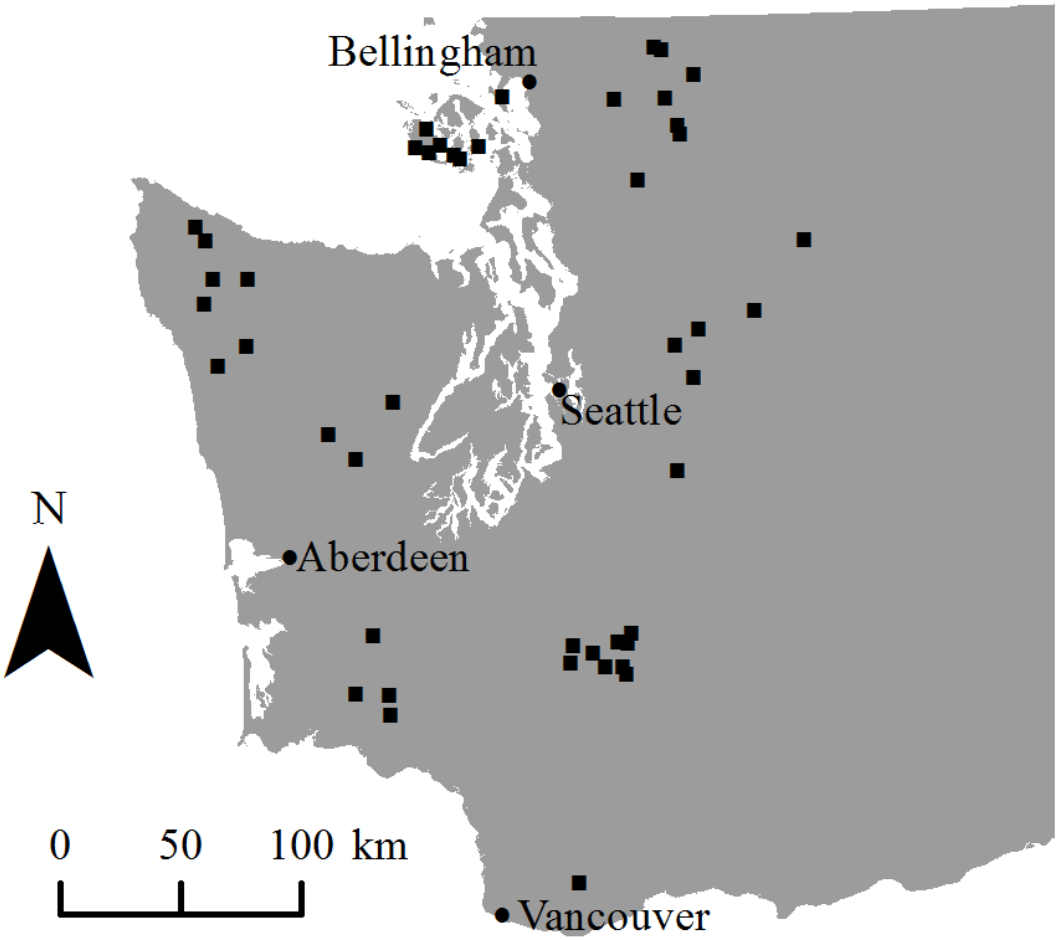

Figure 1. Squares represent the locations of Golden Eagle territories in western Washington (*n* = 46). Circles show the locations of cities for reference.

productivity survey protocols (Pagel et al. 2010, Hayes 2013), but this was not done for all years included in the database. Generally, occupancy values were determined by making at least one visit to a known nest or territory and checking for signs of occupancy such as nest repairs, breeding behaviors, and territorial behaviors. The database does not indicate if observers made at least two visits before a territory was considered unoccupied, as recent standards recommend (Pagel et al. 2010).

Territory Centers

I conducted my analysis at the territory scale. For each territory, I computed an activity centroid as the geometric mean of all nests recorded in the database belonging to the same territory. In the absence of empirical home range data from this region of Washington, I created a hypothetical core use area by creating a 3 km buffer around the territory center (Kochert et al. 1999, Whitfield et al. 2001, McIntyre et al. 2006). This distance has been suggested as a simplistic representation of the area of most importance and highest use to Golden Eagles breeding in Alaska, Idaho, and Scotland. When neighboring territory centers were less than 3 km apart, I created Thiessen polygons so that a boundary was placed equidistant between adjacent territory centers.

Terrain

I calculated several elevation values for each territory using DEM rasters including elevation of the territory centroid, mean elevation of core use area, and range of elevation in core use areas. To assess the ruggedness of core use areas I calculated the terrain ruggedness index (TRI) of each territory (Riley et al. 1999, R Core Team 2015, Hijmans 2016), which assesses the differences between adjacent pixels in a DEM and summarizes those differences for a focal area as a numerical index, where 0 is completely flat and increasing values represent more rugged terrain.

Land Use

I used spatial data describing public land to calculate the proportion of core use areas on public ownership for each territory. I also calculated the proportion of the core use area lying within a preserve that would restrict land use in that area (e.g. National Wildlife Refuge, National Park, National Wilderness Area).

Land Cover

I assumed that important resources, especially food resources, for Golden Eagles would be linked to land cover types due to the effects on prey abundance and availability (Watson 2010). Using the core areas developed around territory centers, I used data from the National Land Cover Database (NLCD) for 1992, 2001, 2006, and 2011 to characterize the surrounding landscape using ArcMap (Fry et al. 2007, Homer et al. 2007, Fry et al. 2011, Homer et al. 2015). I reclassified some land cover classes into pooled categories (Table 1). The 2011 dataset lacked coverage for open water areas more than 300 m from shorelines at 8 territories and consequently the amount of non-water coverage in these core use areas was inflated. To correct this issue I determined the difference between the total 2011 pixel count and the average pixel counts from the other three years at each affected territory, then added the difference to the open water pixel count for that territory. I calculated proportions of land cover using these adjusted values at these eight territories.

I calculated the proportion of each cover type in each core use area and used these values

Table 1. Land classification schemes used in National Land Classification Database (NLCD) and in this analysis.

1992 COVER TYPE	2001-2011 NLCD COVER TYPE	THIS ANALYSIS
Open Water	Open Water	Open Water
Perennial Snow/Ice	Perennial Snow/Ice	Perennial Snow/Ice
Agricultural Land Barren Grasslands/Shrub	Barren Herbaceous Hay/Pasture Cultivated Crops Shrub	Open/Shrub
Forest	Deciduous Forest Evergreen Forest Mixed Forest	Forest
Wetland	Woody Wetlands Emergent Herbaceous Wetlands	Wetland
Urban	Developed Open Developed Low intensity Developed Mid Intensity Developed High Intensity	Urban

in subsequent analyses. Using the latest NLCD 2011 dataset, I summarized the landscape currently surrounding territory centers. I also summarized land cover using the other NLCD data and recorded the average values for each cover type within each territory across all four NLCD datasets. Measures included the number of territories containing each cover type, mean, standard error, and 95% confidence intervals of the proportion of the territory covered by each cover type.

Landscape and Territory Occupancy

I used historic nest survey data to investigate relationships between landscape characteristics and territory occupancy. I limited my analysis to territory occupancy because more precise estimates of productivity were not reported for nearly a third of occupied territories. Within the survey database, I pooled and summarized results from nest surveys by territory to obtain one record per territory in a given year. I excluded from this analysis records that were inconclusive regarding occupancy status (i.e. season summary code = 900) and limited the analysis to data from years after 1987 so that a NLCD dataset would be no more than 5 years out of date for occupied territories. The resulting data included 202 records from 19 territories, all with at least 5 years of reported occupancy. Naïve occupancy rates were calculated for these territories as the number of years occupied divided by the number of years monitored.

Based on naive occupancy rates I grouped territories into low and high occupancy classes, separating those occupied more than half of the years surveyed from those occupied less often. I then tested for relationships between home range attributes and observed occupancy rates using boxplots (Johnson 1999) and logistic regression (R Core Team 2015). Home range attributes included the land use and land cover data and the terrain characteristics elevation, elevation range, and TRI. I used the average values of the four NLCD years to incorporate cover types from all years considered when calculating naïve occupancy rates.

Based on differences in central tendencies observed in boxplots, I included the following covariates in stepwise logistic regression development and evaluation: elevation mean, elevation range, and forest cover. I did not include the amount of open or shrub cover as a predictor variable in the logistic regression because the proportions for this cover class were highly negatively correlated with forest cover ($r^2 = -0.98$, $n = 19$, $p < 0.0001$). Similarly, I did not include centroid elevation in the model because these values were positively correlated with elevation mean ($r^2 = 0.81$, $n = 19$, $p < 0.0001$). To ease interpretation of model parameters, I divided elevation values by 100 and entered forest cover values as the percentage of the core area covered by forest. I compared model fits using AIC and considered models with $\Delta\text{AIC} \leq 2$ as competitive, and interpreted the parameter estimates using odds ratios. All statistical analysis was conducted using R (R Core Team 2015).

RESULTS

Terrain

Territories occurred across a wide range of elevations; territory centroid elevations and mean elevations of core use areas were similar and ranged from near sea level to roughly 2200 m above sea level (Fig. 2, 3). The elevation ranges within core use areas were normally distributed (Fig. 4), and were positively correlated with centroid elevation ($r^2 = 0.866$, $p < 0.001$, $n = 46$). The terrain ruggedness index (TRI) varied from 0.282 to 5.520 with a mean of 3.106 (Fig. 5).

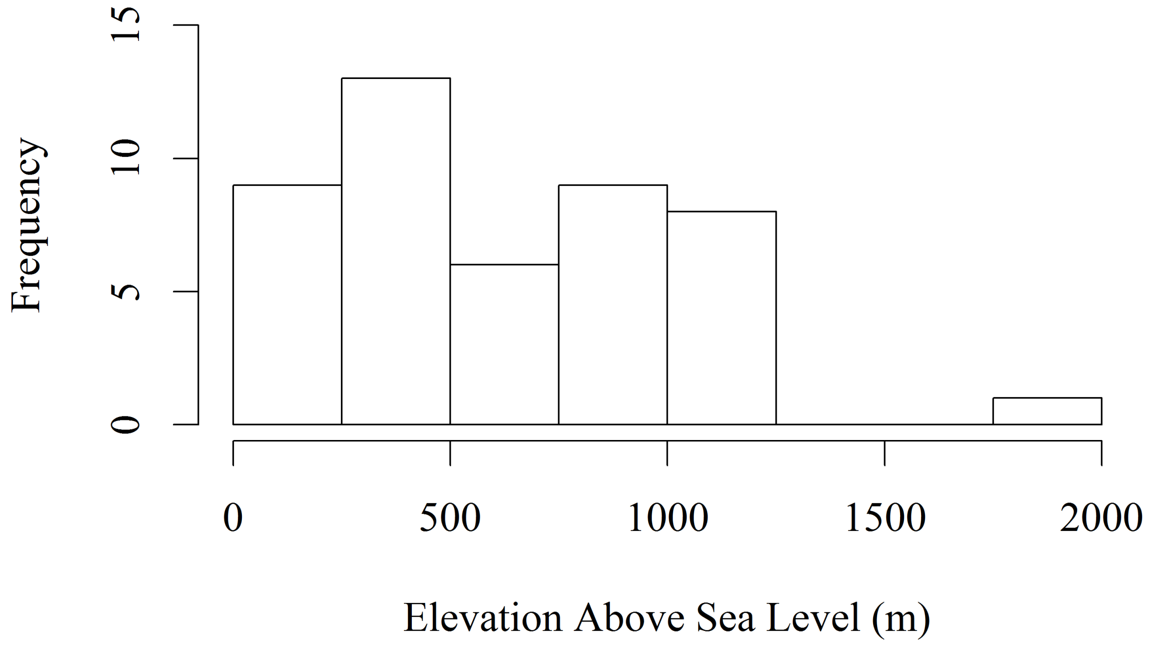

Figure 2. Frequency distribution of mean elevations of Golden Eagle territory core use areas (*n* = 46).

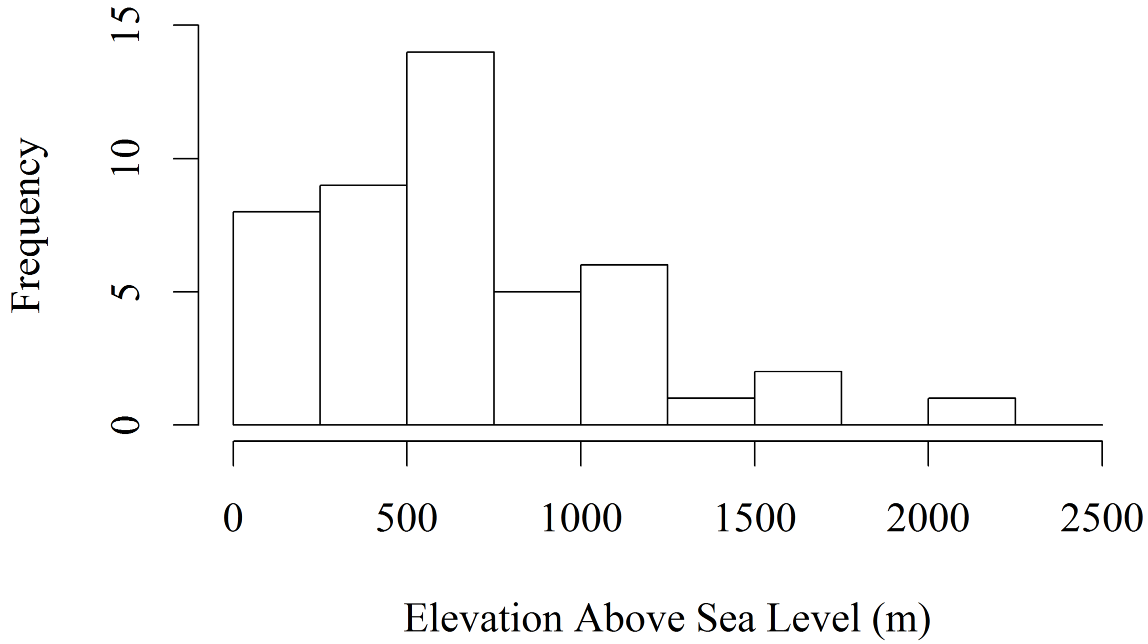

Figure 3. Frequency distribution of elevations of territory centroids (*n* = 46).

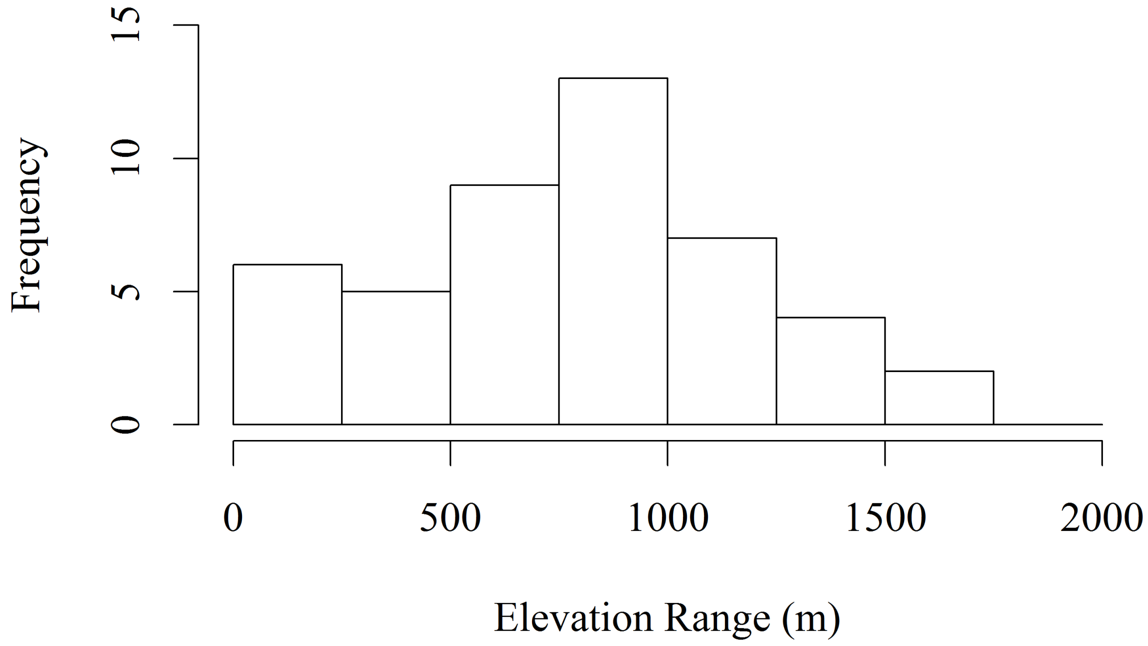

Figure 4. Frequency distribution of elevation range (the difference between maximum and minimum elevations) within territory core use areas (*n* = 46)

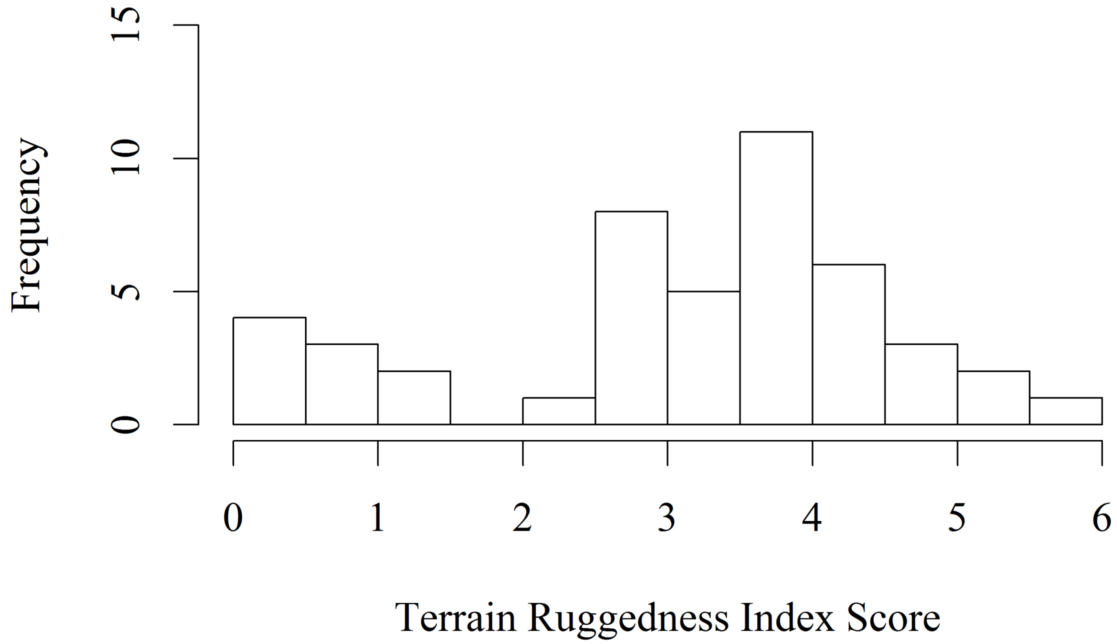

Figure 5. Frequency distribution of terrain ruggedness index (TRI) scores of territory core use areas ($n = 46$). A score of 0 indicates a completely flat landscape, and increasing values indicate more rugged terrain.

Table 2. The percentage of each territory core use area in western Washington that occurred on preserved or public land.

LAND USE	*n*	$\bar{x}$	SE	95% CI
Preserve (%)	14	31.3	10.2	9.3-53.3
Public Land (%)	41	64.8	6	52.6-77.0

Land Use

Only 14 territories had core use areas containing preserved land; these included National Wilderness areas, a National Wildlife Refuge, and a State Conservation Area (Table 2). Public lands were present in the core use areas of 41 territories, and included Federal, State, and County ownerships with a variety of land use designations (Table 2).

Land Cover

Every territory included some forest cover in its core use area based on the 2011 land cover data (Fig. 6). Shrub and open cover types were also present in all core use areas, though generally to a lesser degree than forest (Fig. 6). Urban and wetland cover types were present in almost all core use areas, but accounted for very little of the overall home range (less than 5% and 2% of these areas on average, respectively; Fig. 6). Roads (both paved and forest roads) accounted for nearly all observed areas of urban cover. Open water covered an average of 13% of 24 core use areas; however, all but the eight home ranges located in the San Juan Islands contained less than 3% open water (Fig. 6). Perennial snow was not common and accounted for less than 2% of core use areas where present (Fig. 6).

Landscape and Territory Occupancy

Nineteen territories had at least 5 yr of occupancy records since 1987; six of these territories were occupied in at least 50% of the years in which they were monitored since 1987 and categorized as High Occupancy, and the remaining 13 territories were categorized as Low Occupancy (Table 3). High occupancy territories tended to have lower forest cover and higher open/shrub cover than low occupancy territories (Fig. 7, Appendix 1 Table A-2). The amount of the other four cover types (water, snow, urban, and wetland) was negligible in the 19 territories

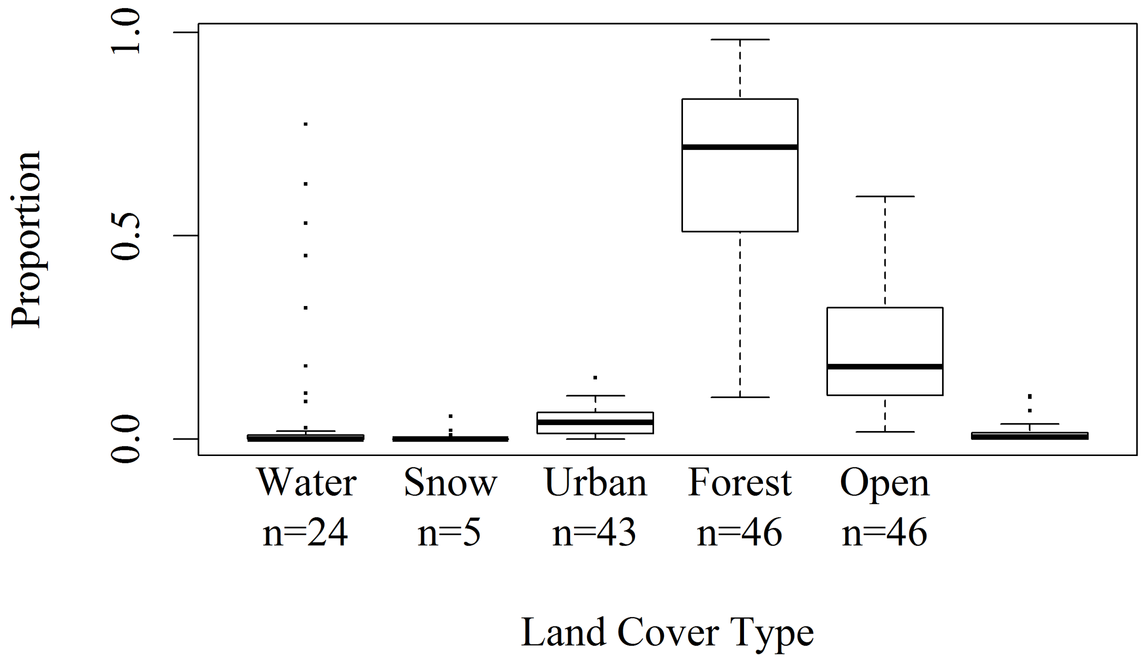

Figure 6. Land cover of core use areas in all western Washington territories (*n* = 46), based on 2011 NLCD data. The frequency of territories where cover types occurred are displayed below each cover type. Water includes areas of open water, Snow includes areas of perennial snow or ice, Urban includes developed areas, Forest includes areas with vegetation > 5 m in height, Open includes areas lacking vegetation or where vegetation < 5 m in height, and Wetland includes forested and non-forested wetlands. The dark bar represents the median across all territories, the extent of the boxes represents lower and upper quartiles, the whiskers represent 1.5 times the inter-quartile distance, and points represent outliers. Values displayed are from Appendix 1 Table A-1.

Table 3. Naïve occupancy rates from 1987-2016 at 19 Golden Eagle territories in western Washington.

		OCCUPANCY RATE (%)		
OCCUPANCY CLASS	*n*	$\bar{x}$	SE	RANGE
High	6	95	3.14	83-100
Low	13	18	4.77	0-42

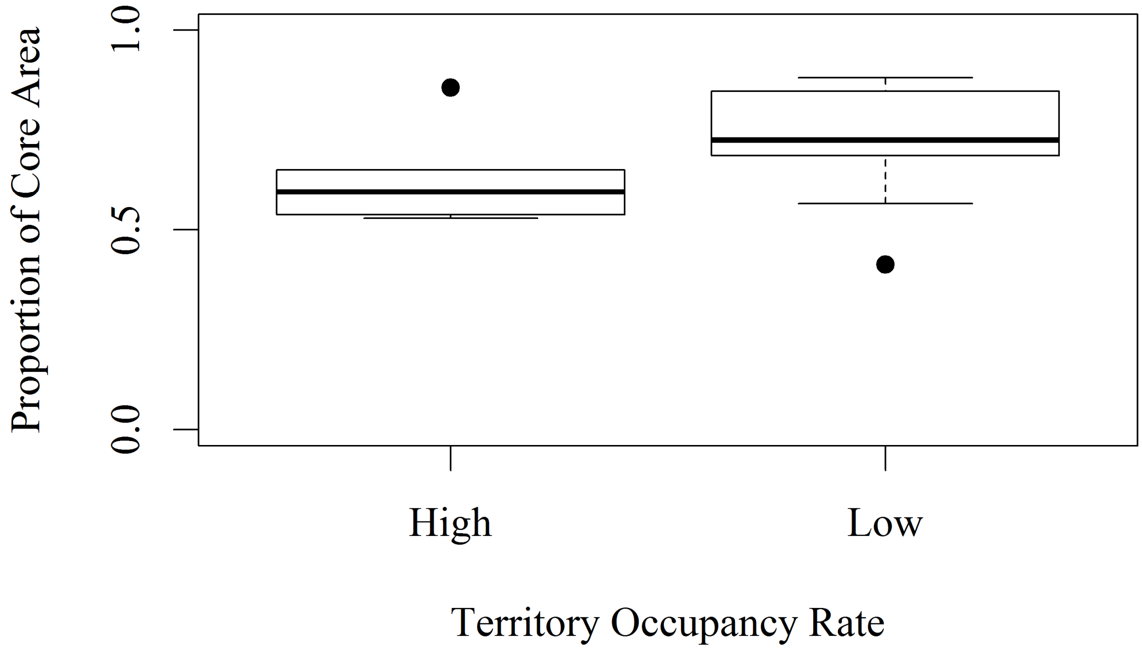

Figure 7. Comparison of forest cover in Golden Eagle territories with high (*n* = 6) and low (*n* = 13) occupancy histories. The dark bar represents the median across all territories, the extent of the boxes represents lower and upper quartiles, the whiskers represent 1.5 times the inter-quartile distance, and points represent outliers. Plot is based on values displayed in Appendix 1 Table A-2.

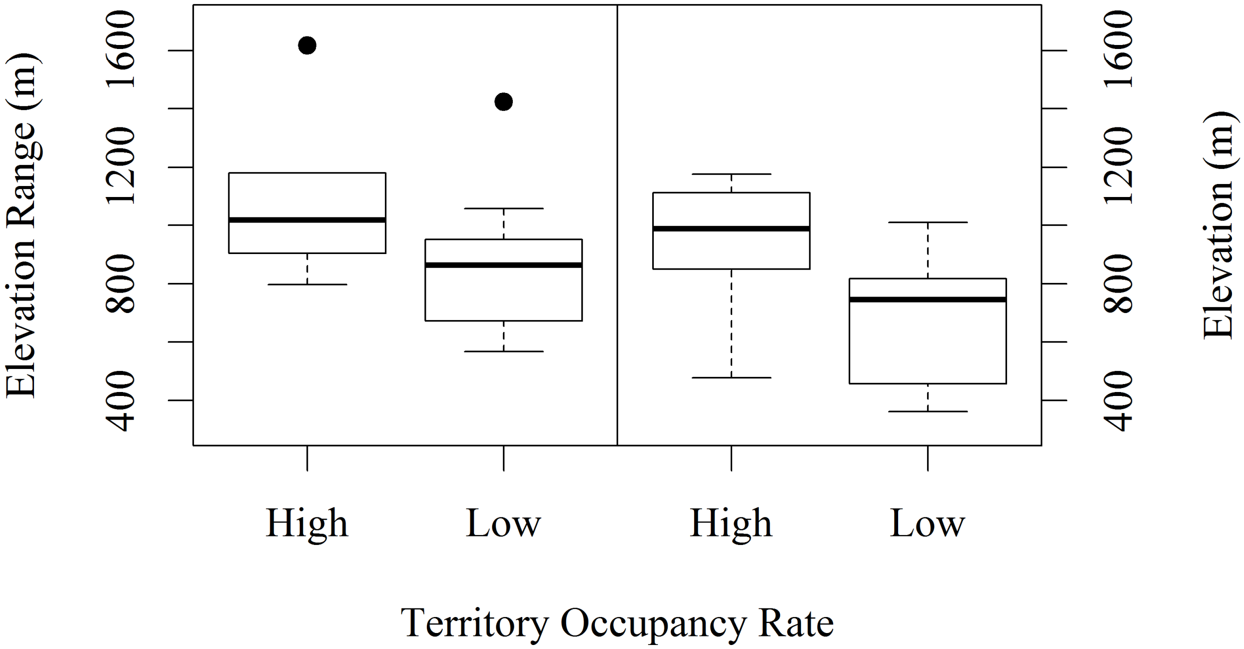

Figure 8. Comparison of elevation range (left axis) and territory elevation (right axis) values at Golden Eagle territories with high (*n* = 6) and low (*n* = 13) historic occupancy rates. The dark bar represents the median across all territories, the extent of the boxes represents lower and upper quartiles, the whiskers represent 1.5 times the inter-quartile distance, and points represent outliers. Values are displayed in Appendix 1 Table A-2.

Table 4. Comparison of logistic regression models and parameters. Values of elevation mean (ElevMean) and elevation range (ElevRange) are the calculated values divided by 100. Values for forest cover are percentage points indicating the amount of forest cover in territory.

MODEL	PARAMETER	ESTIMATE	ODDS RATIO	AIC	ΔAIC
5	Intercept	-5.7661		21.906	0
	ElevMean	0.6187	1.8565		
4	Intercept	-2.44		22.902	0.996
	ElevMean	0.57445	1.7761		
	ForestCover	-0.04345	0.957		
2	Intercept	-6.5274		23.655	1.749
	ElevMean	0.5525	1.7375		
	ElevRange	0.1325	1.1417		
6	Intercept	-4.1376		24.561	2.655
	ElevRange	0.3502	1.4194		
1	Intercept	-3.2093		24.745	2.839
	ElevMean	0.5196	1.6813		
	ElevRange	0.1106	1.1169		
	ForestCover	-0.0415	0.9594		
3	Intercept	-0.3479		25.009	3.103
	ElevRange	0.3195	1.3764		
	ForestCover	-0.0514	0.9499		
7	Intercept	3.4944		25.186	3.28
	ForestCover	-0.0628	0.9391		
8	Intercept	-0.7732		25.699	3.793

included in this analysis (Appendix 1 Table A-2). No relationships between occupancy rate and terrain ruggedness, amount of preserve, or amount of public land were evident. High occupancy territories tended to include a greater range of elevations and higher average elevation than those occupied rarely (Fig. 8).

Elevation of the territory and the amount of forest cover in the core use area were related to territory occupancy (Table 4). Competitive logistic regression models (Table 4; models 2, 4, 5) consistently included average elevation, which also had a significantly positive coefficient in the top model (Model 5). The effects of each parameter were consistent across all models. Golden Eagle territories with higher observed occupancy histories occurred at higher elevations, and included less forest cover within 3 km of the territory center. Odds ratios of the top three models indicated that an increase of 100 m in elevation increased the odds that a territory had a high occupancy history by 73-85%, and that an increase of 1 percentage point of forest cover decreased the odds a territory had a high occupancy history by more than 4%.

DISCUSSION

When predators are found in atypical environments they may not experience the prey and type of land usually encountered by conspecifics, but pioneering individuals still adjust their movements to encounter areas of local prey abundance and availability, as cougars (*Puma concolor*) did in a residential landscape in western Washington (Kertson et al. 2011). The results of my study show that Golden Eagles breeding in forested areas of western Washington, which is atypical for the species, are more likely to occupy breeding territories located at higher elevations and that contain less forest cover. Increasing elevation has been suggested to be correlated with decreasing vegetative cover and less human disturbance in central Alaska

(McIntyre and Schmidt 2012). The suggestion that greater availability of prey due to a lack of vegetative cover at higher elevations might lead to higher occupancy and reproductive output at those territories was only weakly supported in the Denali study, however, and effects from human disturbance were found to be minimal in the remote Alaskan wilderness. I also found no correlation between elevation and the amount of forest cover in western Washington (r^2 = -0.29, n = 46, p = 0.22). The mean elevation values for all territories included in the occupancy analysis were below 1200 m, and only one of all western Washington territories was located above 1250 m. These elevations are not likely high enough to be above the tree line in this area, so the effect proposed for alpine environments in central Alaska likely may not be as strong in the territories I studied. However, characteristics of the forest such as structure may change at higher elevations, increasing prey susceptibility, but this is outside the scope of the land cover data I used.

Reduced exposure to human disturbance at higher elevations may in part explain the observed patterns between occupancy and elevation. In western Washington, urban and developed areas are largely confined to the Puget Trough and associated valleys, with development decreasing at higher elevations. Fewer interactions with humans at higher elevations could decrease disturbance to Golden Eagles, encouraging higher occupancy rates at these territories. Nearly all territories in my study contained a small amount of urban land cover, which largely consisted of roads. While no relationship was evident between the amount of roads in a core use area and the likelihood a territory was occupied more often, the degree of road use could be less in areas at higher elevations that are more distant from human population centers, decreasing the likelihood of early season disturbances that negatively affect territory occupancy (Spaul and Heath 2016).

Forest cover was negatively associated with occupancy of Golden Eagle territories in western Washington, which is likely related to prey accessibility. Forest cover in the NLCD includes forest greater than 5 m in height, which generally coincides with canopy closure. The time of canopy closure is thought to be of great importance for Golden Eagles because eagles cannot easily fly through vegetation to capture prey, and because closed canopy stands generally support fewer prey species at lower abundances (Whitfield et al. 2007). The selection of open foraging habitat by Golden Eagles in forested areas has long been suspected, and has been demonstrated recently through telemetry of breeding Golden Eagles in Sweden, where foraging adults selected for forest clearings within their home range, presumably to take advantage of increased abundance and detectability of prey (Singh et al. 2016). Studies of Golden Eagle territories in Scotland showed that afforestation of previously unforested territories affected prey abundance and availability (Watson 2010), where initial increases in prey abundance brought about by development of ground cover during stand establishment were followed by a decrease in prey availability as trees grew and the canopy closed approximately 15 yr later. Overall the breeding success of pairs in areas experiencing significant afforestation declined, however the complex relationship between forest cover and Golden Eagle productivity was influenced by other factors including experience of the pair, habitat quality, and proximity to vacant territories (Watson 1992, Whitfield et al. 2001, Whitfield et al. 2007).

Within western Washington, recent clearcuts and younger forest stands offer peak abundance and availability of mountain beavers (*Aplodontia rufa*), the primary prey of Golden Eagles in this region (Chapter 1). The mountain beaver occupies forests of all ages and height classes (Anderson and Borrecco 1980, Appendix 1 Fig. A-2), yet their abundance is usually highest in recent clearcuts with developing ground vegetation; densities in closed canopy forests seldom exceed 4 animals per hectare (Anderson and Borrecco 1980) but can exceed 15 to 20 animals per hectare following timber harvest and during stand establishment (Neal and Borrecco 1981). The combination of higher densities and reduced cover likely makes clearcuts and open, young forest ideal foraging habitat for Golden Eagles. Consequently, a lower proportion of forested area in core use areas likely increases territory quality, as suggested by the observed negative relationship between forest cover and occupancy in the region.

Changes in land cover can affect historical distributions and typical breeding patterns of Golden Eagles. The negative effects of afforestation through land abandonment and a variety of land-conversion programs on Golden Eagle territory occupancy and productivity have been demonstrated in Scotland, Italy, and Japan (Pedrini and Sergio 2001, Whitfield et al. 2007, Watson 2010). Changes in shrub communities caused by intensive grazing or increased fire regimes have been implicated in reduced Golden Eagle reproductive output in Scotland and Idaho (Kochert et al. 1999, Whitfield et al. 2007). The effects on Golden Eagle occupancy have been varied in these cases, but generally the density of breeding pairs decreased as increases in forest cover or reduction of native shrubs affected prey abundance or availability (Marzluff et al. 1997). Afforestation is likely not a threat in western Washington, however, where forest management will continue to create and maintain open areas in an otherwise forested landscape.

Land ownership and the policies that inform management of those lands are varied in western Washington; however land ownership alone did not predict which territories had higher occupancy rates. Roughly a third of all known territories overlapped preserve lands and nearly all included at least some public land. The presence and amount of preserved areas did not affect occupancy of the sites included in this analysis, and neither did the amount of public land ownership within core use areas. Much of these public lands were public forests managed by the

Washington Department of Natural Resources and US Forest Service for revenue generation, primarily through even-aged harvest and thinning, and generally experience the same disturbance forces as private timberlands. However, harvest rates may be reduced or harvest rotations may be longer to meet land management plans specific to these agencies. Regardless of ownership, clearings created through forest management would likely have positive effects on occupancy of nearby Golden Eagle territories.

Beyond the benefits of creating ideal foraging habitat, forest management may negatively affect Golden Eagles. Loss of nest trees represents a threat to continued occupancy, as potential nest sites are generally limited for large raptors (Newton 1979). However, protection of nest sites is afforded by several laws including the Bald and Golden Eagle Protection Act and the Migratory Bird Treaty Act. Potential sources of disturbance during the pre-laying, incubation, and nestling periods on timberlands include harvest and stand management operations. The potential for these disturbances to affect occupancy or reproductive output should be evaluated in a context-specific manner. For example, helicopters are used to apply herbicide to regenerating stands to reduce competition for young trees. Disturbance from aircraft has long been a concern for the conservation of nesting raptors (Fyfe and Olendorff 1976), but some Golden Eagles have been found to tolerate intermittent helicopter flights near active nests during the breeding season with no effects on breeding success evident (Grubb et al. 2010). Considering the timing, duration, and frequency of management activities could lead to better estimates of potential impacts to eagles breeding in this area.

While this analysis of the effects of landscape on occupancy of Golden Eagle sites in western Washington is exploratory, I did identify elevation and the amount of forest cover as important covariates in predicting territory occupancy. Future investigations should be conducted as more site-specific resource-use data and longer, more standardized survey histories become available. The 3 km-radius theoretical core area was used in this analysis following the recommendations of Whitfield et al. (2001) and McIntyre et al. (2006) because of the lack of site-specific resource use data. Obtaining accurate estimates of range use in western Washington during the breeding season through telemetry would provide a more accurate estimate of resource use in the area as well as test the assumptions of resource selection used in this analysis. Quality of breeding habitat (Marzluff et al. 1997) and resource availability (Whitaker et al. 2006) have been shown to influence range size. Telemetered eagles in forested regions of Sweden and eastern North America, both areas of limited foraging area, were reported to have home ranges much larger than reported from typical Golden Eagle breeding areas (Moss et al. 2014, Singh et al. 2016, Miller et al. in review). Thus, telemetry data will likely reveal that eagles in this region of Washington with limited open foraging habitat also increase range size to incorporate more foraging habitat.

The data from the WDFW database come from many years of unstandardized surveys and efforts. Though I limited the analysis to only territories with at least 5 yr of reported occupancy results since 1987, survey efforts across those surveys may have varied widely. Four of the six territories with high occupancy occur on a private tree farm managed under a Habitat Conservation Plan that includes annual occupancy and productivity surveys of Golden Eagle territories (Beak Consultants Incorporated 1995). Surveys at these territories included multiple checks from the ground throughout each breeding season and have been conducted for up to 23 yr. Other territories only just met the minimum number of surveyed years to be included in the analysis, often with multiple years between surveys. The survey results may have been inadequate if, for example, only one visit was conducted each year and the territory was reported as unoccupied, as multiple visits spaced at an adequate interval of time are required to confidently determine a territory as unoccupied (Pagel et al. 2010). The variability in survey efforts may have also led to alternate nests within one territory being described as adjacent unique territories (Hayes 2013). More accurately describing known territories and searching suitable habitat for additional territories through standardized surveys in Washington has been identified as a priority in the in the future.

APPENDIX 1

Table A-1. Land cover of all Golden Eagle core use areas in western Washington. Mean, SE, and 95% CI are reported as the percentage of a circle with 3 km radius.

COVER	n	$\bar{x}$	SE	95% CI
Forest	46	64.90	3.21	58.43-71.38
Open/Shrub	46	13.68	2.13	18.00-26.61
Urban	43	4.59	0.50	3.59-5.60
Wetland	41	1.53	0.38	0.76-2.30
Water	24	13.29	4.69	3.59-22.99
Snow	5	1.81	1.03	-1.06-4.68

Table A-2. Comparison of landscape attributes for high occupancy territories (n = 6) and low occupancy territories (*n* = 13) in western Washington.

	HIGH OCCUPANCY			LOW OCCUPANCY		
VARIABLE	$\bar{x}$	SE	95% CI	$\bar{x}$	SE	95% CI
Water (%)	0.0	0.0	0.0- 0.1	0.2	0.1	0-0.4
Snow (%)	0.9	0.9	-1.5-3.4	0	0	0-0
Urban (%)	4.7	1.2	1.7-7.7	4.8	0.7	3.3-6.4
Forest (%)	62.8	5.0	49.9-75.6	73.0	3.7	64.9-81.0
OpenShrub (%)	31.0	4.3	19.9-42.1	21.2	4.0	12.4-30.0
Wetland (%)	0.5	0.3	-0.3-1.3	0.8	0.1	0.5-1.1
Preserve (%)	1.9	1.4	-1.7-5.6	6.8	4.6	-0.3- 16.9
Public (%)	59.8	14.7	22.1-97.5	59.9	12.2	33.4-86.3
TRI	3.682	0.195	3.181-4.183	3.659	0.243	3.129-4.189
Mean Elevation (m)	932	102.1	670-1195	666	55.6	545-787
Centroid Elevation (m)	962	127	637-1288	684	65.2	541.6-825.6
Elevation Range (m)	1090	121	778-1402	857	66.9	711-1003

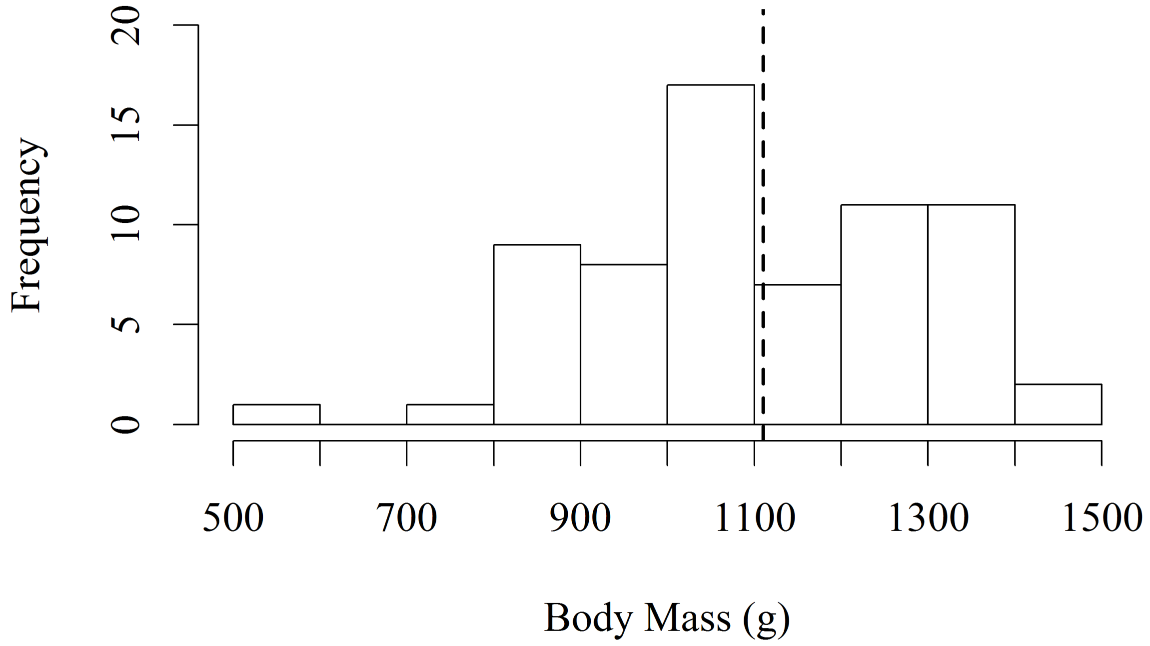

Figure A-1. Frequency distribution of body mass of mountain beaver carcasses obtained on from the study area (n = 67). The vertical dashed line shows the mean from this sample (1110 g). Male mountain beavers were significantly larger than females (Appendix 2).

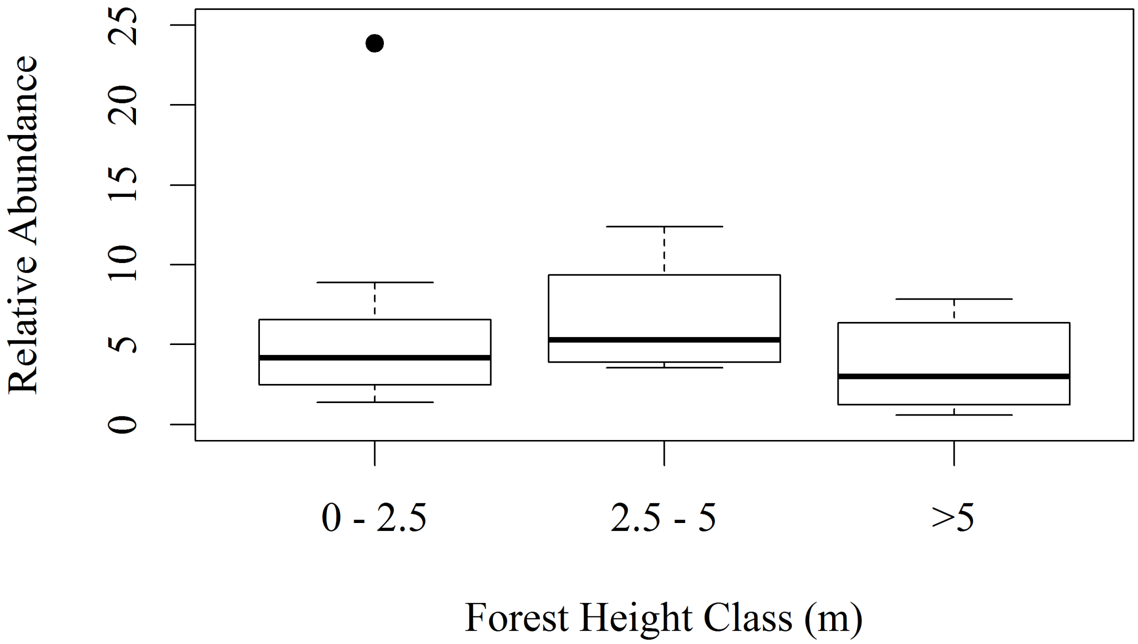

Figure A-2. Relative abundance of mountain beavers in a commercial tree farm in the southwest Cascade Mountains, Washington, based on counts of active mountain beaver burrows observed along transects. I walked transects in seven stands each of the tallest and shortest height classes, and 4 stands in the intermediate height class. I calculated relative abundance as the frequency of active burrows divided by the length of the transect multiplied by 100.

APPENDIX 2. MOUNTAIN BEAVER MASS

To investigate potential selection within the primary prey species observed during my observations, I measured mountain beaver remains I collected from below nests and compared them to measurements from skulls I prepared from whole carcasses. The mountain beaver carcasses had been trapped near the study area under a depredation permit to minimize damage to tree seedlings in young forest plantations.

METHODS

For each carcass I recorded sex, total mass, and mass of the decapitated carcass. The latter measure was made to estimate the consumable mass of the animal, as eagles were frequently seen removing heads and discarding them away from the nest. I then prepared skulls using cold water maceration and measured the following skull characteristics, as defined in Elbroch (2006): greatest length (GL), basilar length (BL), palatal length (PL), breadth of rostrum (BR), mastoid breadth (MB), zygomatic breadth (ZB), interorbital breadth (IB), maxillary toothrow length (MaxT), mandibular toothrow length (ManT), and length of mandible (ManL).

From the trapped carcasses, I calculated mean mass by sex and overall. I tested for sex differences in mass and proportion of body mass in body using a one-tailed and two-tailed t-test, respectively (Zar 1984). I then developed a model predicting the mass of individuals from skull measurements using stepwise linear regression (R Core Team 2015). Using the model I developed from the trapped carcasses and skulls, I estimated mass of the animals that belonged to the skulls I collected under nests. Predicted masses were then evaluated for selection by eagles within this primary prey species.

RESULTS

I measured mass of 67 mountain beaver carcasses that had been trapped through the winter in animal damage control efforts, including 27 females and 40 males. Males were significantly larger than females in mass (Appendix 2 Table A-3, Fig. A-3; $t = 5.62$. $df = 55.98$, $p < 0.001$). Based on measurements from 44 individuals, the mean proportion of mass that was edible (i.e. (total mass-head mass) /total mass) was high, and did not differ significantly between sexes (Appendix 2 Table A-3; $t = -0.52$, $df = 32.0$, $p = 0.62$).

The best linear model based on AIC values to predict mass using skull measurements included palatal length, breadth of rostrum, and interorbital breadth, and zygomatic breadth (Appendix 2 Table A-3; model 4). However Model 6 was comparably robust without the need for a zygomatic breadth measurement, which is ideal considering that very few of the mountain beaver skulls I collected had zygomatic arches intact.

The distribution of predicted masses using model 6, model 4, and model 1 are shown in Appendix 2 Fig. A-4, A-5, and A-6. These figures suggest that most mountain beaver skull and jaw remains collected below nests were from animals with mean masses near the average obtained from trapped carcasses I measured, suggesting that golden eagles did not select for mountain beavers of a particular size while foraging.

Table A-3. Total mass and proportion that is edible of mountain beaver carcasses. Edible proportion was calculated as the decapitated mass divided by the total mass of a specimen.

	TOTAL MASS				PROPORTION OF MASS EDIBLE			
	n	MEAN	SE	95% CI	*n*	MEAN	SE	95% CI
Male	40	1194.8	23.7	1146.8-1242.7	26	0.86	0.005	0.852-0.871
Female	27	985.2	28.8	926.0-1044.4	18	0.87	0.007	0.852-0.880
Total	67	1110.0	22.1	1066.1-1154.4	44	0.86	0.004	0.856- 0.871

Table A-4. Comparison of linear models predicting mountain beaver mass from skull attributes.

MODEL	PARAMETER	ESTIMATE	SE	r^2	AIC	Δ AIC	*n*
1	Intercept	3078.23***	426.71	0.69	539.015	76.159	42
	ManL	85.31***	8.67				
2	Intercept	3080.48***	431.22	0.684	540.871	78.015	42
	ManT	6.99	19.05				
	ManL	82.91***	10.93				
3	Intercept	2218.81***	548.48	0.651	466.212	3.356	38
	PL	28.45*	15.82				
	BR	53.29**	22.03				
	MB	11.57	17.05				
	ZB	16.47	15.91				
	IB	-24.07	16.59				
	MaxT	0.45	27.30				
4	Intercept	2143.54***	517.23	0.667	462.856	0	17
	PL	30.44**	14.53				
	BR	52.85**	21.39				
	ZB	25.29**	9.51				
	IB	-26.92*	15.76				
5	Intercept	2003.70***	620.63	0.599	469.901	7.045	38
	PL	51.17***	14.15				
	BR	65.03***					
	IB	-32.74*	17.14				
	MaxT	14.83	27.30				
6	Intercept	1852.43***	548.84	0.607	468.238	5.382	60
	PL	54.95***	12.19				
	BR	63.91***	22.78				
	IB	-33.59*	16.89				

*p<0.1, **p<0.05, ***p<0.01

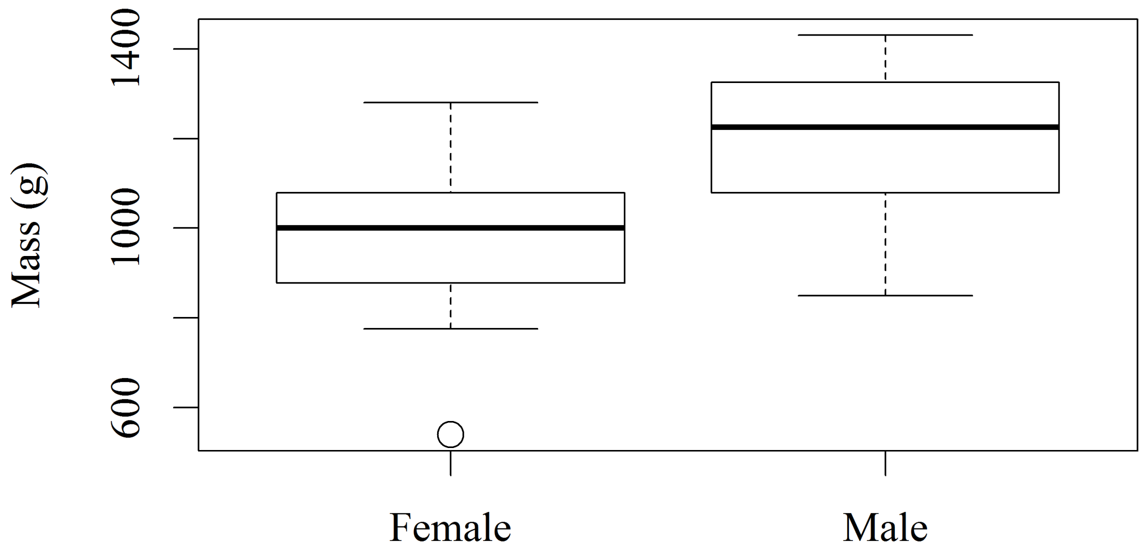

Figure A-3. Total mass of male and female mountain beaver carcasses (*n* = 67)

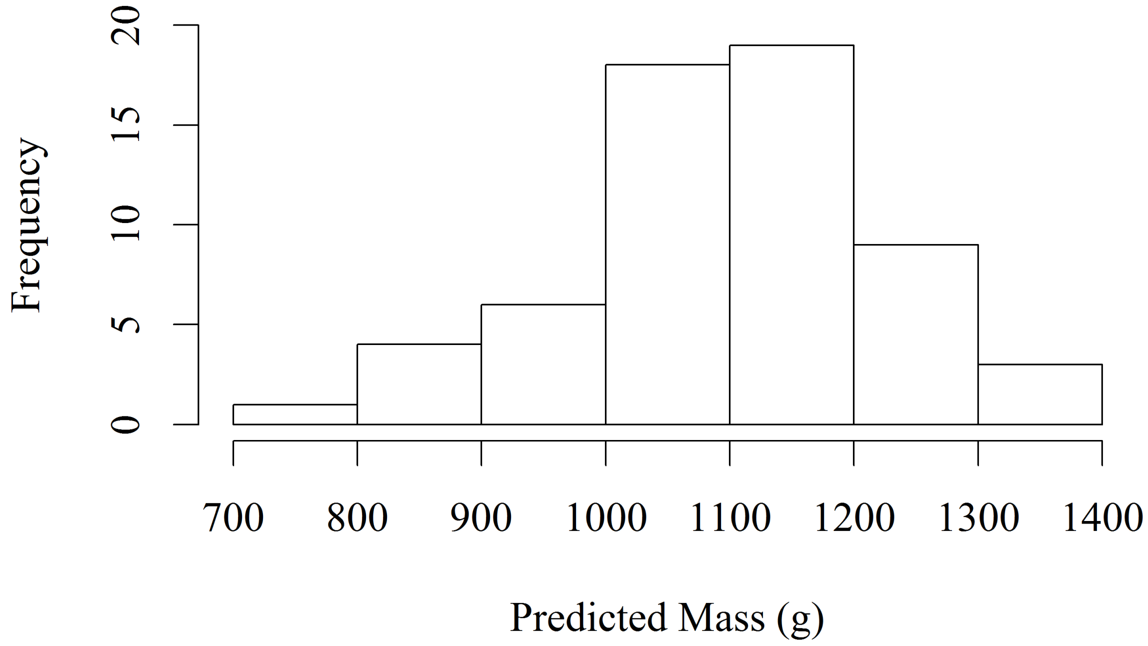

Figure A-4. Frequency distribution of masses predicted from prey remains using Model 6 (*n* = 60).

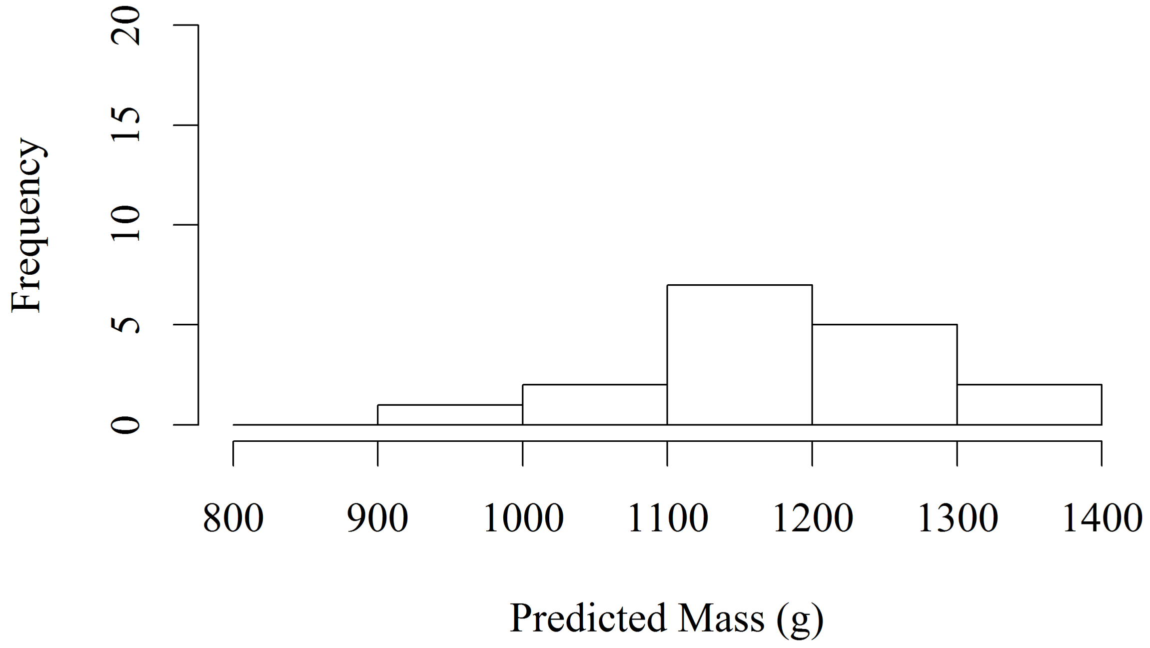

Figure A-5. Frequency distribution of masses predicted from prey remains using Model 4 (*n* = 17).

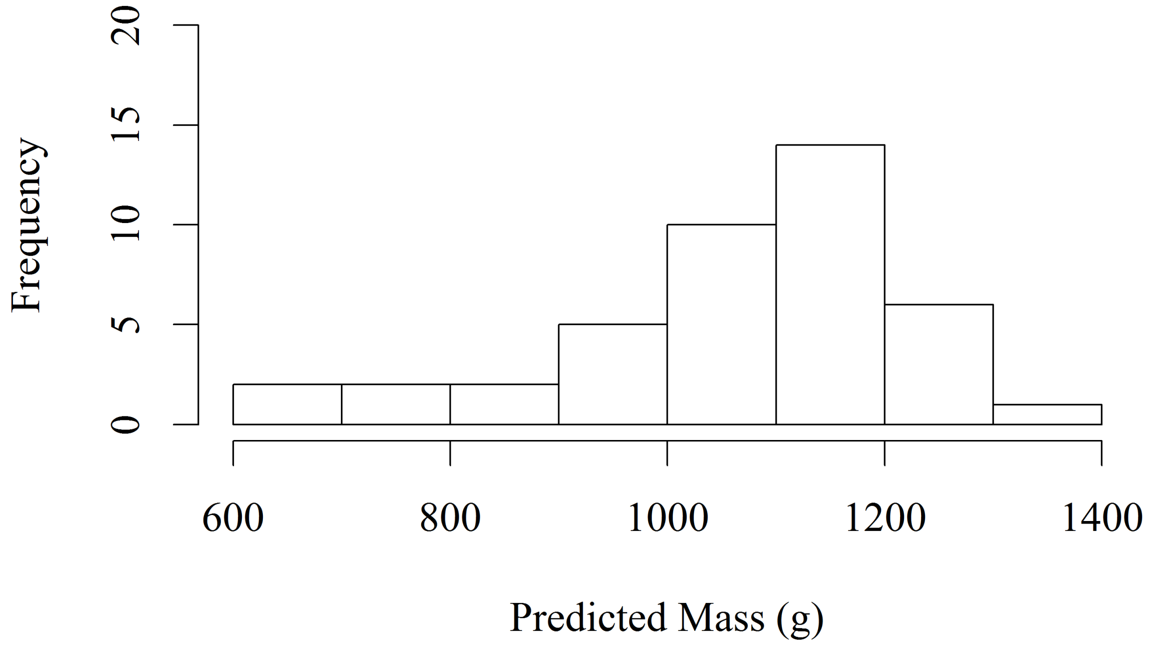

Figure A-6. Frequency distribution of masses predicted from prey remains using Model 1 (*n* = 42).

LITERATURE CITED

AOYAMA, I., F. SEKIYAMA, N. OBARA, G. TAMURA, AND H. SAKAGUCHI. 1988. Breeding biology of a pair of Golden Eagles in the Kitakami Mountains. *Aquila chrysaetos* 6:14-23.

ARJO, W.M., R.E. HUENEFELD, AND D.L. NOLTE. 2007. Mountain beaver home ranges, habitat use, and population dynamics in Washington. *Canadian Journal of Zoology* 85: 328-337.

AGEE, J.K. 1993. Fire ecology of Pacific Northwest forests. Island Press.

BEAK CONSULTANTS INCORPORATED. 1995. Amendment to the habitat conservation plan and incidental take permit PRT-777837 for the Northern Spotted Owl on timberlands owned by the Murray Pacific Corporation, Lewis County, Washington. Prepared for Murray Pacific Corporation, Tacoma, WA.

BECHARD, M.J. 1982. Effect of vegetative cover on foraging site selection by Swainson's Hawk. *Condor* 84: 153-159.

BORRECCO, J.E., AND R.J. ANDERSON. 1980. Mountain beaver problems in the forests of California, Oregon and Washington. *Proceedings of the 9th Vertebrate Pest Conference* Paper 3.

BROWN, B.T. 1992. Golden Eagles feeding on fish. *Journal of Raptor Research* 26:36-37.

BRUCE, A.M., R.J. ANDERSON, AND G.T. ALLEN. 1982. Observations of Golden Eagles nesting in western Washington. *Journal of Raptor Research* 16: 132-134

CARRAWAY, L.N. AND B.J. VERTS. 1993. *Aplodontia rufa*. *Mammalian species*; N 431.

CLUTTON-BROCK, T.H. 1991. The evolution of parental care. Princeton University Press.

COCKBURN, A. 2006. Prevalence of different modes of parental care in birds. *Proceedings of the Royal Society of London B: Biological Sciences* 273: 1375-1383.

COLLOPY, M.W. 1983a. A comparison of direct observations and collections of prey remains in determining the diet of Golden Eagles. *The Journal of Wildlife Management* 47: 360-368.

------ 1983b. Foraging behavior and success of Golden Eagles. *Auk* 100: 747-749.

------ 1984. Parental care and feeding ecology of Golden Eagle nestlings. *Auk* 101: 753-760.

CRAMP, S. 1985. The birds of the western Palearctic. Vol. IV. Oxford: Oxford University Press

DELANNOY, C.A., AND A. CRUZ. 1988. Breeding biology of the Puerto Rican Sharp-shinned Hawk (*Accipiter striatus venator*). *Auk* 105: 649-662.

ELLIS, D.H. 1979. Development of behavior in the Golden Eagle. *Wildlife Monographs* 70:3-94.

FERRER, M., AND J.A. DONAZAR. 1996. Density-dependent fecundity by habitat heterogeneity in an increasing population of Spanish Imperial Eagles. *Ecology* 77: 69-74.

FRANKLIN, J.F., AND C.T. DYRNESS. 1973. Natural vegetation of Oregon and Washington. Oregon State University Press.

FRY, J.A., M.J. COAN, C.G. HOMER, D.K. MEYER, AND J.D. WICKHAM. 2009. Completion of the National Land Cover Database (NLCD) 1992-2001 Land Cover Change Retrofit product: U.S. Geological Survey Open-File Report 2008-1379, 18 p.

------, J., G. XIAN, S. JIN, J. DEWITZ, C. HOMER, L. YANG, C. BARNES, N. HEROLD, AND J. WICKHAM. 2011. Completion of the 2006 National Land Cover Database for the Conterminous United States, *Photogrammetric Engineering and Remote Sensing* 77:858-864.

FYFE, R.W. AND R.R. OLENDORFF. 1976. Minimizing the dangers of nesting studies to raptors and other sensitive species. Occas. Paper No. 23. Canadian Wildlife Service, Ottawa, Ontario, Canada.

GAIBANI, G. AND D. CSERMELY. 2007. Behavioral studies. . In *D.M. Bird and K.L. Bildstein, (Eds.), Raptor research and management techniques* 117-128. Hancock House Publishing.

GRUBB, T.G., D.K. DELANEY, W.W. BOWERMAN, AND M.R. WIERDA. 2010. Golden Eagle indifference to heli-skiing and military helicopters in northern Utah. *Journal of Wildlife Management* 74:1275-1285.

HARMATA, A.R. 1982. What is the function of undulating flight display in Golden Eagles*? Journal of Raptor Research* 16: 103-109.

HAYES, G.E. 2013. Golden Eagles (*Aquila chrysaetos*) nesting in Washington, 2013. Draft Annual Report, December 2013. Washington Department of Fish and Wildlife, Olympia, Washington

HECTOR, D P. 1981. The habitat, diet, and foraging behavior of the Aplomado Falcon, (*Falco femoralis*) (Temminck) Doctoral dissertation, MS Thesis, Oklahoma State University, Stillwater, Oklahoma.

HIJMANS, R. J. 2016. raster: Geographic Data Analysis and Modeling. R package version 2.5-8. http://CRAN.R-project.org/package=raster

HOMER, C., J. DEWITZ, J. FRY, M. COAN, N. HOSSAIN, C. LARSON, N. HEROLD, A. MCKERROW, J.N. VANDRIEL, AND J. WICKHAM. 2007. Completion of the 2001 National Land Cover Database for the Conterminous United States. *Photogrammetric Engineering and Remote Sensing* 73: 337-341.

HOMER, C.G., J.A. DEWITZ, L. YANG, S. JIN, P. DANIELSON, G. XIAN, J. COULSTON, N.D. HEROLD, J.D WICKHAM, AND K. MEGOWN. 2015. Completion of the 2011 National Land Cover Database for the conterminous United States-Representing a decade of land cover change information. *Photogrammetric Engineering and Remote Sensing* 81: 345-354

JOHNSON, D.H. 1999. The insignificance of statistical significance testing. *Journal of Wildlife Management* 63: 763-772.

JOHNSON, D.R. 1981. The Study of Raptor Populations. University Press of Idaho

KAISANLAHTI-JOKIMAKI, M., J. JOKIMAKI, E. HUHTA, M. UKKOLA, P. HELLE, AND T. OLLILA. 2008. Territory occupancy and breeding success of the Golden Eagle (*Aquila chrysaetos*) around tourist destinations in northern Finland. *Ornis Fennica* 85: 2-12

KERTSON, B.N., R.D. SPENCER, J.M. MARZLUFF, J. HEPINSTALL-CYMERMAN, AND C.E. GRUE. 2011. Cougar space use and movements in the wildland–urban landscape of western Washington. *Ecological Applications* 21: 2866-2881.

KETTERSON, E.D. AND V. NOLAN JR. 1994. Male parental behavior in birds. *Annual Review of Ecology and Systematics* 25: 601-628.

KITTLE, A.M., J.K. BUKOMBE, A.R. SINCLAIR, S.A. MDUMA, AND J.M. FRYXELL. 2016. Landscape-level movement patterns by lions in western Serengeti: comparing the influence of inter-specific competitors, habitat attributes and prey availability. *Movement Ecology* 4: 1-18.

KOCHERT, M.N., K. STEENHOF, L.B. CARPENTER, AND J.M. MARZLUFF. 1999. Effects of fire on Golden Eagle territory occupancy and reproductive success. *Journal of Wildlife Management* 63: 773-780.

------, ------, C.L. MCINTYRE AND E.H. CRAIG. 2002. Golden Eagle (*Aquila chrysaetos*), The Birds of North America (P.G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna-org.offcampus.lib.washington.edu/Species-Account/bna/species/goleagDOI: 10.2173/bna.684

KREBS, C.J. 2001. Ecology, 5th Edition. Benjamin Cummings.

LEOPOLD, A.S. AND T.O. WOLFE. 1970. Food habits of nesting Wedge-tailed Eagles (*Aquila audax*) in south-eastern Australia. *Wildlife Research* 15: 1-17.

LEWIS, J.C., K.J. JENKINS, P.J. HAPPE, D.J. MANSON, AND M. MCCALMON. 2016. Landscape-scale habitat selection by fishers translocated to the Olympic Peninsula of Washington. *Forest Ecology and Management* 369: 170-183.

MARGALIDA, A. AND J. BERTRAN. 2000. Breeding behavior of the Bearded Vulture (*Gypaetus barbatus*): minimal sexual differences in parental activities. *Ibis* 142: 225-234.

MARTI, C.D., M. BECHARD, AND F.M. JAKSIC. 2007. Food habits. In *D.M. Bird and K.L. Bildstein, (Eds.), Raptor research and management techniques* 129-49. Hancock House Publishing

MARTIN, J., C.L. MCINTYRE, J.E. HINES, J.D. NICHOLS, J.A. SCHMUTZ, AND M.C. MACCLUSKIE. 2009. Dynamic multistate site occupancy models to evaluate hypotheses relevant to conservation of Golden Eagles in Denali National Park, Alaska. *Biological Conservation* 142: 2726-2731.

MARZLUFF, J. M., S.T. KNICK, M.S. VEKASY, L.S. SCHUECK, AND T.J. ZARRIELLO. 1997. Spatial use and habitat selection of Golden Eagles in southwestern Idaho. *Auk* 31: 673-687.

MASER, C. 1998. Mammals of the Pacific Northwest. Oregon State University Press.

MCGRADY, M.J., J.R. GRANT, I.P. BAINBRIDGE, AND D.R.A. MCLEOD. 2002. A model of Golden Eagle (*Aquila chrysaetos*). *Journal of Raptor Research* 36: 62-69.

MCINTYRE, C.L., M.W. COLLOPY, J.G. KIDD, A.A. STICKNEY, AND J. PAYNTER. 2006. Characteristics of the landscape surrounding Golden Eagle nest sites in Denali National Park and Preserve, Alaska. *Journal of Raptor Research* 40: 46-51.

------, C. L. AND J.H. SCHMIDT. 2012. Ecological and environmental correlates of territory occupancy and breeding performance of migratory Golden Eagles (*Aquila chrysaetos*) in interior Alaska. *Ibis* 154: 124-135.

MILAKOVIC, B., K.L. PARKER, D.D. GUSTINE, R.J. LAY, A.B. WALKER, AND M.P. GILLINGHAM. 2011. Habitat selection by a focal predator (*Canis lupus*) in a multiprey ecosystem of the northern Rockies. *Journal of Mammalogy* 92: 568-582.

MILLER, T.A., R.P. BROOKS, M.J. LANZONE, J. COOPER, K. O'MALLEY, D. BRANDES, A. DUERR, T.E. KATZNER (in review). Space use and habitat use of Golden Eagles (*Aquila chrysaetos*) in eastern North America during breeding season and winter. *Auk*.

MURGATROYD, M., G. AVERY, L.G. UNDERHILL, AND A. AMAR. 2016. Adaptability of a specialist predator: the effects of land use on diet diversification and breeding performance of Verreaux's Eagles. *Journal of Avian Biology* 47: 834-845.

NEAL, F.D., AND J.E. BORRECCO. 1981. Distribution and relationship of mountain beaver to openings in sapling stands [Douglas-fir (*Pseudotsuga menziesii*)]. *Northwest Science*.

NEWTON, I. 1979. Population ecology of raptors. *A and C Black*.

NOLTE, D.L. AND M. DYKZEUL. 2000. Wildlife Impacts on Forest Resources. Human Conflicts with Wildlife: Economic Considerations. Paper 20.

PAGEL, J.E., D.M. WHITTINGTON, AND G.T. ALLEN. 2010. Interim Golden Eagle inventory and monitoring protocols; and other recommendations. Division of Migratory Bird Management*, US Fish and Wildlife Service.*

PEDRINI, P., AND F. SERGIO. 2001. Golden Eagle (*Aquila chrysaetos*) density and productivity in relation to land abandonment and forest expansion in the Alps. *Bird Study* 48: 194-199.

R CORE TEAM. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

RILEY, S.J. 1999. Index that quantifies topographic heterogeneity. *Intermountain Journal of Sciences* 5: 23-27.

RULLMAN, S., AND J.M. MARZLUFF. 2014. Raptor presence along an urban–wildland gradient: influences of prey abundance and land cover. *Journal of Raptor Research* 48: 257-272.

SERVHEEN, C. 1978. Mountain beaver as a prey species of the Golden Eagle. *Murrelet* 59: 77.

SIBLEY, D.A. 2003. The Sibley Field Guide to Birds of Western North America. Alfred P. Knopf, Inc.

SINGH, N.J., E. MOSS, T. HIPKISS, F. ECKE, H. DETTKI, P. SANDSTRÖM, AND B. HÖRNFELDT. 2016. Habitat selection by adult Golden Eagles (*Aquila chrysaetos*) during the breeding season and implications for wind farm establishment. *Bird Study* 63: 233-240.

SLAGSVOLD, T. AND G.A. SONERUD. 2007. Prey size and ingestion rate in raptors: importance for sex roles and reversed sexual size dimorphism. *Journal of Avian Biology* 38: 650-661.

SNYDER, N.F. AND J.W. WILEY. 1976. Sexual size dimorphism in hawks and owls of North America. *Ornithological Monographs* No. 20.

SONERUD, G.A., R. STEEN, L.M. LØW, L.T. RØED, K. SKAR , V. SELÅS, AND T. SLAGSVOLD. 2014a. Evolution of parental roles in raptors: prey type determines role asymmetry in the Eurasian Kestrel. *Animal Behaviour* 96: 31-38.

------, ------, V. SELÅS, O.M. AANONSEN, G.H. AASEN, K.L. FAGERLAND, AND S.K. SKOUEN. 2014b. Evolution of parental roles in provisioning birds: diet determines role asymmetry in raptors. *Behavioral Ecology* 25: 762-772.

SOUTULLO, A., V. URIOS, M. FERRER, AND S.G. PENARRUBIA. 2006. Post-fledging behavior in Golden Eagles (*Aquila chrysaetos*): onset of juvenile dispersal and progressive distancing from the nest. *Ibis* 148:307-312.

SPAUL, R.J. AND J.A. HEATH. 2016. Non-motorized recreation and motorized recreation in shrub-steppe habitats affects behavior and reproduction of Golden Eagles (*Aquila chrysaetos*). *Ecology and Evolution* 6: 8037-8049.

STEENHOF, K., AND I. NEWTON. 2007. Assessing nesting success and productivity. In *D.M. Bird and K.L Bildstein (Eds.). Raptor research and management techniques*. 181-192. Hancock House Publishing.

VALUTIS, L.L. AND J.M. MARZLUFF. 1997. A Golden Eagle eats wild Canada goose eggs. *Journal of Raptor Research*. 31:288-289.

WASHINGTON FOREST PROTECTION ASSOCIATION. 2006. About Washington's forests. Washington Forest Protection Agency, Olympia, WA U.S.A. http://www.wfpa.org/forest-policy/washington-forests/ (last accessed 9 February, 2017)

WATSON, J. 1992. Golden Eagle (*Aquila chrysaetos*) breeding success and afforestation in Argyll. *Bird study* 39: 203-206.

------, J. 2010. The Golden Eagle. Bloomsbury Publishing.

WHITFIELD, D.P., A.H. FIELDING, M.J. GREGORY, A.G. GORDON, D.R. MCLEOD, AND P.F. HAWORTH. 2007. Complex effects of habitat loss on Golden Eagles (*Aquila chrysaetos). Ibis* 149:26-36.

------, D.P., D.R MCLEOD, A.H. FIELDING, R.A. BROAD, R.J. EVANS, AND P.F. HAWORTH. 2001. The effects of forestry on Golden Eagles on the island of Mull, western Scotland. *Journal of Applied Ecology* 38:1208-1220.

ZAR, J.H. 1984. Biostatistical analysis. 2nd Ed. Prentice Hall USA**.**