

THESIS

BALD EAGLE SPACE USE IN AN URBANIZING LANDSCAPE

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ABSTRACT

BALD EAGLE SPACE USE IN AN URBANIZING LANDSCAPE

Rapid human population growth has led to an increase in urbanization globally. Urbanization extends beyond the boundaries of city limits to include the conversion of natural areas into energy production (such as coal, solar, and wind), the damming and diversion of rivers, and agriculture and forestry to feed and house urban residents. This land use change is a major driver of biodiversity loss and significantly impacts wildlife space use. While many species are unable to persist in urban environments, some species of raptors are frequently found using the urban matrix. Bald Eagles (*Haliaeetus leucocephalus*) are an iconic North American species that was once near extinction but are now commonly observed in and around cities. Here, I examined how urbanization influenced Bald Eagle home range size and habitat selection in the northern Front Range of Colorado, a semi-arid region currently experiencing rapid growth in both eagle and human populations.

In my first chapter, I investigated home range size and core-use areas of 24 territorial Bald Eagles affixed with a GPS/GSM transmitter. Specifically, I examined home range size and core-use area at five different nest stages of the annual cycle (pre-nesting, incubation, nestling, post-fledge, and non-nesting) and for both sexes. Home ranges and core-use areas were created using a dynamic Brownian bridge movement model. I then used a mixed-effects linear regression model to identify the land cover characteristics influencing these areas. My research shows that Bald Eagle home ranges and core-use areas vary in size and are often discontinuous, frequently containing one to three separate areas. Home ranges were fifteen times or more larger than core-use areas. Smaller home ranges were positively correlated with water, herbaceous wetlands, and human development while greater canopy cover was associated with

larger home ranges. Similarly, water was positively associated with smaller core-use areas while greater canopy cover was associated with larger core-use areas. Home ranges and core-use areas tended to be larger during the pre-nesting and non-nesting stages and smaller during the nestling and post-fledge stages, with these differences being more pronounced in females. Male home ranges were smallest during the post-fledge stage ($43.89 \text{ km}^2 \pm 98.67$) and largest during the non-nesting stage ($117.31 \text{ km}^2 \pm 177.04$). Females generally had smaller home ranges, which were smallest during the nestling stage ($2.86 \text{ km}^2 \pm 2.14$) and largest during the incubation stage ($70.31 \text{ km}^2 \pm 183.48$).

In Chapter One, I mapped eagle home ranges throughout the annual cycle and analyzed what habitat features are associated with smaller home ranges, which may indicate higher quality habitat. In my second chapter I built on these findings to assess habitat selection within and beyond the home ranges calculated in chapter one. To examine habitat selection I used a logistic regression model during the same five nest stages, for both sexes, and at two different scales: within home range and within study area. My findings indicate that Bald Eagle habitat selection is influenced by nest stage, sex, spatial scale, land cover, and human development. Generally, eagles selected for herbaceous wetlands, grasslands, and habitats near water. They avoided agriculture and dense canopy cover. Overall eagles avoided development; however, they used low to moderately developed landscapes when in close proximity to water. Eagles had a higher probability of using developed areas within their home range than within the study area and during the incubation and nestling stages. Female eagles were also more likely to use developed areas than male eagles. At all nest stages, eagles were more likely to use areas with low levels of development than areas with high levels of development.

My findings suggest that the space-use patterns of Bald Eagles are complex and vary throughout the annual cycle. Eagles are capable of thriving in urban environments, where their smaller home ranges suggest that they can find quality habitat. Conservation efforts in urbanizing regions should focus on

protecting habitats close to water, in herbaceous wetlands, and with open canopy cover. It is also important to recognize that while Bald Eagles readily use urban environments with these habitat features, they prefer areas with low to moderate development. Additionally, conservation strategies should account for the fact that Bald Eagles have disconnected home ranges with critical foraging sites located away from their nests. Together, these recommendations could help guide policy and practice for sustaining Bald Eagle populations during their full annual cycle in urbanizing landscapes.

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Chapter 1: Bald Eagle Home Range Size and Core-Use Areas in an Urbanizing Landscape

Introduction

Urbanization is a leading driver of land-use change globally (Ramalho & Hobbs, 2012; Jiang & O'Neill, 2017). The structure and function of urban ecosystems are fundamentally different from natural areas, which has consequences for biodiversity (Czech et al., 1997; McKinney, 2006; Russell & Franson, 2014). Many species are not able to persist in urban environments, but others tolerate urbanization or even thrive in cities (Czech et al., 1997; McKinney, 2006; Glista et al., 2009). For example, some raptor species, such as the Red-tailed Hawk (*Buteo jamaicensis*), Cooper's Hawk (*Accipiter cooperii*), American Kestrel (*Falco sparverius*), and Peregrine Falcon (*Falco peregrinus*), are especially well adapted to living in human dominated landscapes (Cade et al., 1996; Hogg & Nilon, 2015; Rosenfield et al., 2018). In particular, Cooper's Hawks are now more commonly found in suburban and urban areas than in natural habitats (Rosenfield et al., 2018). With more raptors living within the urban matrix, it is important to understand how human development is affecting their space use. Evaluating the relationship between home range size and core-use areas, development, and land cover can help identify the landscape characteristics associated with habitat quality, and inform management and policy to promote co-existence in an urbanizing world.

Home ranges are the areas required by an animal to survive, including the resources needed for foraging, mating, and raising young (Burt, 1943). Core-use areas are the parts of the home range that have the highest concentrated use (Samuel et al., 1985; Seaman et al., 1990). While many factors can influence their sizes, in general, home ranges and core-use areas that consist of higher quality habitat tend to be smaller than those that consist of lower quality habitat because they provide more concentrated resources, allowing the animal to move less in search of food, shelter, and mates

(Rolando, 2002; Smith et al., 2017a). Although urban areas are often considered poor habitat for most native plants and animals relative to natural areas, some studies have found that raptors in urban areas have a smaller home range than their more rural conspecifics (Morrison et al., 2016; Rosenfield et al., 2018; O'Donnell & delBarco-Trillo, 2020). This suggests that urban areas provide ample food and habitat for prey species (Peery, 2000; Morrison et al., 2016; Rosenfield et al., 2018). However, in other cases, raptor home ranges did not differ or were larger in urban areas relative to rural landscapes (Andersen et al., 1990; Rolando, 2002). For example, Bald Eagle responses to urbanization are mixed (Mathisen 1968; Stalmaster & Newman, 1978; Wood et al., 1989), yet expanding understanding of their use of urban spaces is particularly important given their conservation status.

Bald Eagles (*Haliaeetus leucocephalus*) are an iconic species of conservation concern. They are the only eagle endemic to North America and their range spans from northern Mexico through northern Canada and the entire width of the contiguous United States, as well as Alaska. They occupy many different habitats including grasslands, riparian corridors, coastal regions, and forests (Andrew & Mosher, 1982; Curnutt & Robertson, 1999; Mundahl et al., 2013). In the contiguous United States in 1963, there were 417 known breeding pairs of Bald Eagles (U.S. Fish and Wildlife Service, 2020). They were listed as federally endangered when the Endangered Species Act was enacted in 1973. Through careful monitoring, protection, and the banning of the pesticide DDT, the Bald Eagle population recovered and was delisted in 2007. By the year 2019, there were over 73,000 known breeding pairs in the contiguous U.S. (U.S. Fish and Wildlife Service, 2020).

Understanding how Bald Eagle home range sizes and core-use areas vary across urban-rural gradients is essential as their breeding range increasingly overlaps with human development. Historically, they were found in areas with little development and an abundance of water such as along rivers, lakes, and seashores (Anthony et al., 1982; Fraser et al., 1985; Buehler et al., 1991). However, this species is increasingly breeding in urban areas, as well as throughout the urban-rural gradient. Previous

studies showed little difference in nest success between urban and natural areas (Fraser et al., 1985; Smith et al., 2017a; Gedir et al. 2023), but the effects of urbanization on home range size and core-use areas remain less understood. This knowledge gap, combined with the recent expansion of Bald Eagles into more developed and semi-arid landscapes, makes Bald Eagles an ideal species for studying the impacts of urbanization on home range size.

Home range size of breeding Bald Eagles across their range varies considerably from 1.2 to 12,500 km², with an average of 22 km² (Harmata, 1984, Gerrard et al., 1992; Garrett et al., 1993; Thompson & McGarigal, 2002; Watson, 2002; Smith et al., 2017a; Slankard et al., 2021). Their core-use areas are also variable, ranging from 0.04 to 20.5 km² (Watson, 2002; Smith et al., 2017a). In south central Colorado, wintering Bald Eagles during the non-nesting season had a mean home range of 311 km² (Harmata, 1984). This substantial variation in home range sizes across the range could be attributed to access to food resources. High quality habitat with good access to food was associated with smaller home ranges for Bald Eagles in western Washington (Watson, 2002). Elliot et al. (2006) also found that landfills were associated with smaller home ranges for subadult eagles, but they suspected that this was due to microclimate (landfills are protected from the wind and are warmer than surrounding areas) rather than food availability.

There is little consensus as to what drives within-population variation in home range size. One study found sex and nest stage to have the greatest correlation with home range size, which was larger for males during the non-nesting stage (Gerrard et al., 1992). However, other studies did not agree and some found no differences between males and females (Garrett et al., 1993; Watson, 2002; Smith et al., 2017a; Kocina & Aagaard, 2021). Very few studies have examined the drivers of home range size in Bald Eagles, beyond nest stage and sex. While both male and female eagles incubate and tend to nestlings, females spend a greater percentage of their time at the nest (Gerrard et al., 1979; Wallin, 1982), resulting in a decreased ability to travel far from the nest, which could lead to smaller home ranges than

males. During the non-nesting season when Bald Eagles are less territorial and do not have young to attend, they have a greater ability to leave the nest for longer periods of time, which could lead to a larger home range size (Grier, 1982).

The objective of this study was to examine the factors influencing home range size and core-use areas of breeding Bald Eagles in a rapidly urbanizing landscape. Specifically, we evaluated whether home range size and core-use areas were associated with development intensity, land cover, sex, and nest stage. We focused on land cover types that we expected to be positively or negatively associated with food resources and nesting habitat for Bald Eagles: water, herbaceous wetlands, canopy cover, grassland, and agriculture (National Land Cover Database 2021, Colorado Department of Transportation 2012). We hypothesized that Bald Eagle home ranges would be smaller in areas with higher development intensity, higher canopy cover, and a greater extent of herbaceous wetlands and water (e.g., reservoirs and rivers), because many raptor species have smaller home ranges in urban environments, trees provide good habitat for nesting and perching, and water provides habitat for fish and waterfowl, which are important food resources for this species. Bald Eagles are generalists and can eat a wide variety of prey, but their diet mainly consists of fish, waterfowl, and small mammals (Hunt et al., 1992; Hunt et al., 2002; Bove et al., 2024). We predicted that grassland and agriculture, which may offer fewer food resources, would be associated with larger home ranges. While prairie dogs are commonly found in grasslands, a large portion of grasslands does not contain prairie dogs and may have less prey for Bald Eagles (Boal et al., 2006). We also hypothesized that female eagles would have smaller home ranges than male Bald Eagles due to higher rates of nest attendance, and that home ranges would be smaller during the nesting season when both sexes attend to the nest.

Methods

Study Site

This study occurred in the northern Front Range of Colorado (U.S.A), which is comprised of Adams, Arapahoe, Boulder, Broomfield, Denver, Douglas, Jefferson, Larimer, and Weld Counties (Figure 1.1). This area has a semi-arid climate and encompasses elevations ranging from 1388 – 2005 m. It includes urban city centers, small rural towns, open prairie, agriculture, foothills, natural areas, reservoirs, and riparian corridors. Land ownership includes a mix of private and public land, including some protected areas. The most rural county (Weld County) in the study site had 32.03 ppl/km² while the most urban county (Denver County) had 1804.76 ppl/km². Colorado currently has the 6th highest human population growth rate in the US with a 14.8% increase between 2010 and 2019, with 95% of the growth occurring in the Front Range (US Census Bureau, 2020).

Bald Eagles are designated as a Species of Greatest Conservation Need in Colorado (Colorado Parks and Wildlife 2015); however, the statewide eagle population has exhibited rapid growth over the past decade. The first recorded Bald Eagle nest in the study area was found in 1986, and by 2024 there were over 130 known active eagle nests (Colorado Parks and Wildlife Statewide Raptor Nest Database). Bald Eagles in the study area had an estimated 76% average apparent nest success rate between 2020 and 2024, excluding 2022 which had a lower success rate, likely due to an outbreak of Highly Pathogenic Avian Influenza in the study area (Conrey et al., 2024, Conrey personal communication, Oct 4th, 2024). A Bald Eagle territory typically contains one to three alternate nests, but only one nest is used for breeding purposes in a given year (Buehler et al., 2022). Bald Eagle movement patterns vary depending on location and life stage. Some eagles migrate, some maintain high site fidelity year-round, and some wander (Wheat et al., 2017; Buehler et al., 2022). In our study area, breeding eagles stay on their territories year-round, although some will take brief hiatuses of a few days to a few weeks from their territory during the post-fledge and non-nesting seasons.

Nest Monitoring

The study occurred between the years 2020 and 2024. The Bird Conservancy of the Rockies' volunteer program, Bald Eagle Watch, has been monitoring nests in the Front Range since 1986; Colorado Parks and Wildlife (CPW), City, and County staff and volunteers also monitored nests. Starting in 2020, additional data were collected by CPW Avian Research staff. We aimed to visit all nests in the study area at least once every two weeks beginning in mid-January to early February, prior to the initiation of incubation, through nest completion, which is usually in June or July if nests are successful. When feasible, we monitored a subset of the nests until the young had dispersed. A nest attempt was considered complete when either the nest failed or at least one young fledged. Observers maintained a sufficient distance from the nest such that they did not influence the behavior of the eagles.

Telemetry

To estimate home ranges, we captured and affixed transmitters to Bald Eagles in this population. We targeted one member of the breeding pair for this project and also tagged several non-breeding adults and fledged juveniles for CPW's larger study; those data on non-territorial eagles are not presented here. We selected birds based on our ability to gain landowner permission and to represent a rural to urban gradient. Favorite perches were determined prior to trapping through nest monitoring. Before attempting to trap an adult during the nesting season, we waited until the nestlings were at least 3 weeks old, because they can self-thermoregulate starting at 2 weeks of age (Warnke et al., 2002). When trapping during the non-nesting season, we ensured that only the breeding pair (and no other eagles) were present. Eagles were trapped on the ground near nests or favorite perches using a modified leg-hold trap safe for raptors and baited with cottontail rabbit, jackrabbit, duck, or fish. The trap was monitored by a remote camera and attended to as soon as a bird was caught.

Following capture, a GPS/GSM (Global Positioning System/Global System for Mobile Communications) transmitter from Cellular Tracking Technologies was affixed to Bald Eagles with good

body condition, using a specially designed backpack harness that breaks away in case of being snagged or not tolerated. The transmitters collected data via satellite on location, time, activity, and accuracy and relayed the data via cell towers once a day. The rate at which the transmitters collected points varied from one point every 4 seconds to four fixes per day, with the most common setting being once every 15 minutes while resting and once every 30 seconds while flying. The frequency of the data collection was altered based on the voltage of the solar-powered battery. Feather coverage, angle of the sun, and individual variation in the transmitters themselves affected the transmitters' ability to charge and maintain a charge. No points were collected from dusk to dawn to save battery power, as eagles usually roost at their nest or are otherwise sedentary during this time. The transmitter and harness weighed 50 - 70 g (due to variation in the tag model available from the manufacturer), which is 1 - 2% of the total weight of an adult male eagle (Figure 1.2). The harnesses were designed to degrade and fall off after 5 years.

Annual cycle

The annual cycle of Bald Eagles can be divided into five nest stages: pre-nesting, incubation, nestling, post-fledge, and non-nesting. Each nest stage was defined individually per eagle from nest observation data. Pre-nesting starts December 1st (Colorado Parks and Wildlife, 2020) and lasts until eggs are laid. Incubation begins when the first egg is laid and continues until hatch (Maestrelli & Wiemeyer, 1975). The nestling stage lasts from hatch until fledge, when the eaglets are capable of flight. The post-fledge stage is the six weeks following fledging when eaglets are capable of flight but are still dependent on their parents for survival. In Colorado, this post-fledging period lasts six weeks on average (D. Bove, personal communication, May 7, 2024). From the end of post-fledge through December 1st is the non-nesting period (Colorado Parks and Wildlife, 2020). If the nest failed during incubation, no nestling or post-fledge home ranges were calculated. If the nest failed during the nestling stage, no post-fledge home ranges were calculated. In both cases, the non-nesting stage was extended. If the eagle was

territorial and maintained a nest but did not lay eggs, only the pre-nesting and non-nesting stages were calculated. The pre-nesting stage ended on the average date when incubation began for other eagles in the study area who made a nesting attempt that season.

Home Range Size and Core-Use Area

Separate home range and core-use areas were calculated for each eagle and for each nest stage of the annual cycle. Only stages for which we obtained complete temporal coverage were calculated. Since most eagles were captured mid-nest stage, home ranges and core-use areas were calculated starting with the following stage, eliminating capture bias as the eagles were tagged for at least a week before the start of analysis. To calculate the home ranges and core-use areas, we used a dynamic Brownian Bridge movement model (DBBMM; Kranstauber et al., 2012). All statistical modeling was performed in Program R (R Core Team 2023; V 4.3.2). The move package (V 4.2.2; Kranstauber et al., 2023) was used to calculate the DBBMMs. Error was set to 40 m and calculated by measuring the cloud of points around unmoving GPS units. Before calculating home ranges, we removed erroneous locations, defined as any GPS location with an HDOP (horizontal dilution of precision) above three or a latitude of 0.000. HDOP values < 3 are considered relatively accurate (Isik et al., 2020). We thinned the data to one location per minute to reduce computational time. A 90% utilization distribution (UD) was considered to be the home range, while a 50% utilization distribution was considered to be the core-use area (Heikkilä et al., 1996; Börger et al., 2006). A 90% utilization distribution was used in place of the standard 95% because Bald Eagles frequently have extra-territorial movement, and anything above 90% would result in areas the eagle visited only once being included as part of the home range.

Many of the eagles took a hiatus from their territory during the post-fledge and non-nesting stages. This was not migration as it is not regular movement, can occur multiple times throughout the year, and is different every year. To account for this, we created a circular buffer using a displacement function (Fleming et al., 2018), which considered how far the eagle traveled during the incubation and

nestling stages, when the eagles did not take hiatuses, and calculated a buffer using that distance. Anything within the buffer was considered a part of the home range (Figure S1.1).

Covariates

We evaluated the relationship between eight covariates (sex, nest stage, development, water, herbaceous wetlands, tree cover, agriculture, and grasslands) and home range size and core-use area (Table 1.1). Sex was determined by weight, culmen, tarsometatarsus, and hallux claw length of the eagle at time of capture (Bortolotti, 1984). Nest stage was determined through nest monitoring efforts. We used the Human Development Index (Theobald et al., 2020) to represent the intensity of human development. This index combines diverse types of human modification to the natural landscape into a continuous value between 0 and 1 (no development to high development). This index included reservoirs, buildings, agricultural lands, all forms of power generation, oil and gas production, mines and quarries, all roads, power lines, railways, logging, and air pollution (Theobald et al., 2020). Although reservoirs are created by people and thus a developed resource, they are perceived as similar to natural water bodies by eagles (Hunt 2002). Therefore, we replaced Human Development Index values (most > 0.95) for reservoirs with a value of 0.

We used the 2021 National Land Cover Database (NLCD) open water classification, combined with the Colorado Department of Transportation (CDOT) 2012 rivers and streams layer, to consider the association between water and home range size and core-use area. All water bodies are stocked with fish in the study area, and most support waterfowl. However, data on fish and waterfowl abundance were not available at the resolution needed to include in our models; thus we view water as a coarse proxy for these food resources (A. Treble, personal communication, April 11, 2023). In Colorado, most Bald Eagles nest in cottonwood trees; however, a spatial layer for cottonwood does not exist for the entirety of our study region, so we used herbaceous wetlands (2021 NLCD emergent herbaceous wetlands) as a proxy for this land cover type. We also evaluated overall tree canopy cover (NLCD 2021

USFS Tree Canopy Cover) as a covariate, because other tree species can also provide nesting and perching habitat. We used the 2021 NLCD pasture/hay and cultivated crops classifications to evaluate the association between agriculture and home range size and the 2021 NLCD grassland/herbaceous classification for grasslands. Water, herbaceous wetlands, and agriculture were calculated as percentages of the home range, while canopy cover was the average canopy cover throughout the home range. We were unable to include prairie dogs, an important food resource for Bald Eagles, as a covariate because activity status, size, and extent of prairie dog colonies change frequently, and these data were not consistently available at the temporal and spatial scale of this study.

Other covariates that were explored but not used include distance to nearest nest (CPW Statewide Raptor Nest Database), human population density (Colorado State Demography Office Home Page, 2022), and nest fate (field data). When examining distance to nearest nest we found that larger home ranges were closer to more nests. This was uninformative as a larger area naturally encompasses more nests by chance. Human population density was closely correlated ($r = 0.71$) with the Human Development Index. The sample size for failed nests was too small to draw conclusions, as most eagles were tagged during the nestling stage of successful breeding seasons.

Modeling

All analyses were performed in Program R (R Core Team 2023; V 4.3.2). Before running models, we first checked for correlations among the covariates and chose the better performing covariate of any pair with a correlation coefficient greater than 0.70. We log transformed home range sizes and core-use areas to account for any skewedness in the data and used eagle ID as a random effect for all models. Using the lme4 package (V 1.1-35.3; Bates et al., 2015), we ran a univariate mixed effect linear regression model for each covariate separately. Next, we ran a mixed effect linear regression model containing every covariate that had a coefficient p-value < 0.05 from the univariate models, plus an interaction between sex and nest stage. We included an interaction between sex and nest stage, as

preliminary data exploration showed home range size changed differently among nest stages for each sex. Using the dredge function from the MuMin (V 1.47.5) package (Bartoń, 2023), we evaluated all possible additive combinations of coefficients plus the interaction between sex and nest stage and the random effect of eagle ID. We then ran a new model using only the coefficients from the top model, as well as the interaction between nest stage and sex, with eagle ID as a random effect.

Results

A total of 24 territorial Bald Eagles were outfitted with a GPS/GSM transmitter. Of those 24 eagles, 13 were male and 11 were female. A separate home range and core-use area was calculated for each eagle and nest stage, totaling 135 different home ranges and core-use areas. The mean duration for collection of telemetry data was 438 days, and the number of days of data collection varied among eagles from 42 to 1371 days. Hiatuses had to be accounted for in 31% of the home ranges during the post-fledge and non-nesting stages combined. Reasons for data collection ending prior to the end of the study period included death of the eagle (n=6), loss of territory (n=5), removal of transmitter by the eagle (n=4), GPS malfunction (n=2), and 3G sunset (n=1). The first transmitter deployed used the 3G cellular network, which was discontinued in the study site in 2021. Five male eagles transitioned from territorial to non-territorial during the study period due to the loss of a mate, competition from another eagle, or unknown reasons. Location data from these eagles were excluded from the home range analysis after they no longer maintained a defined home range. One female eagle maintained a territory but did not make a nesting attempt for the first two years while affixed with a transmitter. The third year she had a successful nesting attempt.

The overall mean home range size (90% UD) for all birds was $60.75 \pm 119.16 \text{ km}^2$, which was over fifteen times larger than the overall mean core-use area size (50% UD), which was $3.95 \pm 8.92 \text{ km}^2$ (Table 1.2). The mean home range size for male eagles ($79.8 \pm 126.23 \text{ km}^2$) was almost double the mean female home range size ($40.24 \pm 107.59 \text{ km}^2$). The mean size of male core-use areas ($5.86 \pm 10.64 \text{ km}^2$)

was triple the mean size of female eagles' core-use areas ($1.89 \pm 5.79 \text{ km}^2$). There was considerable variation in both home range sizes (0.58 - 708.21 km^2) and core-use areas (0.01 - 56.59 km^2). There was no correlation between mean home range size and mean nest stage length (Figure S1.2). The mean, minimum, and maximum sizes of home ranges and core-use areas across all sexes and nest stages are reported in Tables S1.1 and S1.2. Many of the home ranges and core-use areas were not contiguous and consisted of multiple disconnected areas (Figure 1.3).

Although home range sizes differed among nest stages for both males and females, the difference was only statistically significant for females ($p < 0.05$; Figure 1.4A). For females, home ranges during the stages associated with the latter part of the breeding period (nestling and post-fledge) were smaller than the home ranges in the stages associated with the non-breeding period (pre-nesting and non-nesting). Home ranges in the incubation nest stage were closer in size to that of the non-breeding period than to the nestling and post-fledge stages. For males the smallest home range sizes were observed during the post-fledge nest stage while the largest were the incubation and non-nesting nest stages. On average males had larger home ranges and core-use areas than females; however, the difference was only statistically significant during the nestling and post-fledge stages (Figure S1.3). For all nest stages and both sexes, home range sizes were quite variable and the size distribution was heavily skewed towards smaller home range sizes. The differences in core-use area between nest stage and sex were similar to patterns in home range size for females, except that core-use area during the nestling stage was significantly smaller than the other nest stages, while core-use area during the incubation stage was more similar to the other nest stages in the breeding period than the non-breeding period (Figure 1.4B). For males, core-use area was smallest during the three breeding nest stages. Both home range sizes and core-use areas were right skewed and had means that were larger than the medians and outside of the interquartile range.

The covariates included in the top linear regression model ($r^2 = 0.75$) for home range size were nest stage x sex, human development index, percent water, percent herbaceous wetlands, and average canopy cover (Tables 1.3a, S1.3). Smaller home ranges were associated with higher levels of human development, water cover, and herbaceous wetlands, while larger home ranges were associated with higher levels of canopy cover (Figure 1.5a). The covariates included in the top linear regression model ($r^2 = 0.63$) for core-use areas were nest stage x sex, percent water, and average canopy cover (Table 1.3b, Table S1.4). Water cover was associated with smaller core-use areas, while average canopy cover was a weak predictor for larger core-use areas (Figure 1.5b). Human development was not included in the top model for core-use area, but was weakly positively associated with larger core-use areas. Agriculture and grasslands were not in the top models for either home range size or core-use area (Tables 1.3, S1.3, S1.4).

Discussion

Bald Eagles are increasingly observed within human dominated areas, but the consequences of this trend for this iconic species are not well known (Jones et al., 2013; Goulet et al., 2021). To understand the landscape characteristics associated with habitat quality, and to better inform management and policy that promotes co-existence in an urbanizing world, this study evaluated the relationship of Bald Eagle home range size and core-use area with sex, nest stage, human development, and land cover. We found that home ranges and core-use areas of territorial Bald Eagles are quite variable in size and often discontinuous over space. Home ranges and core-use areas were generally larger during the non-breeding stages (pre-nesting and non-nesting) and smaller during the later parts of the breeding stages (nestling and post-fledge). On average males had larger home ranges and core-use areas than female eagles, although these differences were only statistically significant during the nestling and post-fledge stages. Furthermore, smaller home range sizes, which could indicate higher

quality habitat (Rolando, 2002; Smith et al., 2017b), were positively associated with human development, water, and herbaceous wetlands, and negatively associated with canopy cover.

Bald Eagle home range sizes in this study region, Colorado's Northern Front Range, ranged widely but were generally on the smaller end of those reported from other regions (1.2 - 12,500 km²; Gerrard et al., 1992.; Garrett et al., 1993; Watson, 2002; Smith et al., 2017a; Kocina & Aagaard, 2021; Slankard et al., 2021). However, the size of our core-use areas exceeded what has previously been reported (0.4 - 20.5 km²; Watson, 2002; Smith et al., 2017a). It is possible that despite the relative lack of water, the northern Front Range of Colorado provides quality habitat for Bald Eagles relative to other regions, though the variable sizes of core-use areas may indicate not all home ranges are equal in quality.

On average, Bald Eagle home ranges and core-use areas were larger for males than for females. However, this difference was only statistically significant during the nestling and post-fledge nest stages. These findings are in contrast to other studies which have found no significant difference between home range size in males and females (Watson, 2002; Smith et al., 2017a; Kocina & Aagaard, 2021). While both sexes incubate, during the first 3 weeks of the nestling stage the female spends 90% of her time at the nest while the male is present only 50% of the time (Wallin, 1982). Since the male spends longer periods away from the nest, this allows the male to travel farther (Wheat et al. 2017) and have a larger home range and core-use area than the female while brooding young nestlings. Less literature is available on which sex spends more time with the young during the post-fledge stage; in our study, both males and females sometimes took a hiatus from their territory during this period while the young and other adult were still observed at the nest. However, our findings suggest that females may attend to the young more than males during the post-fledge stage, especially at the beginning when the new fledglings are more dependent on their parents (Wallin, 1982). Males and females did not have statistically different home range sizes or core-use areas during the pre-nesting, incubation, or non-

nesting stages. During the non-breeding season (pre-nesting and non-nesting) when there are no young or eggs to tend, both males and females have equal ability to spend time away from the nest. Both sexes incubate and forage for food and have the same ability to fly and leave the nest during the incubation stage as well.

Bald Eagle home ranges and core-use areas were dynamic and changed in size throughout the year depending on nest stage. In general, the sizes during the non-breeding stages (pre-nesting and non-nesting) were larger than the sizes during the later parts of the breeding stages (nestling, and post-fledge), with the difference being more pronounced in females than in males. The literature is mixed on whether time of year is correlated with home range and core-use size. A literature review on raptor home range size found no significant difference in size between breeding and non-breeding periods for Bald Eagles (Kocina & Aagaard, 2021). Another study focused on non-migratory eagles found that half of their eagles had larger home ranges during the non-breeding period, while the other half had smaller home ranges during the non-breeding period (Garrett et al., 1993). However, this study took place in a coastal area where the ocean does not freeze, providing eagles with a more consistent source of fish and waterfowl. In contrast, similar to our study, studies in Louisiana and Saskatchewan found season to be correlated with home range size and core-use area (Gerrard et al., 1992; Smith et al., 2017a). During the breeding season in our study, the incubation nest stage was larger than the other two stages (nestling and post-fledge). In Colorado, incubation starts between February and March when there is reduced access to resources as many water bodies are still frozen, prairie dogs are less active during periods of inclement weather (Harlow et al., 1986), and many non-resident eagles are present and competing for limited resources. This study did not look at the timing of the availability of these resources, but this decrease in resources and increase in competition could in part explain the larger size of the home range during incubation. The nestling and post-fledge stages had the smallest home range size and core-use areas, with the post-fledge stage being smaller. During the post-fledge stage the young

are particularly vulnerable as they have limited ability to fly, with as many as half of the first flight attempts being unsuccessful, leaving young eagles grounded for up to a few weeks before being able to fly successfully (Kussman, 1977). These young are still cared for by the parents and are more vulnerable to ground predation than when in the nest (Kussman, 1977). Even once the eaglets are able to fly, they are still dependent on their parents for all food before learning how to hunt on their own (Gerrard et al., 1992; Kussman, 1977). In the northern Front Range of Colorado, the post-fledge stage typically lasts six weeks after the young leave the nest (D. Bove, personal communication, May 7, 2024). Even if the nest is destroyed after eaglets fledge, they may still be tied to the area. One nest in the study area fell out of the tree shortly after the young fledged. Over a month later, the fledglings were still within 250 m of their former nest site. This continued dependency on their parents and increased vulnerability due to being on the ground likely limits the adults' ability to move and likely decreases the post-fledge home range size and core-use area.

Higher levels of human development were associated with smaller home range sizes but larger core-use areas. This suggests that at the home range scale, urban areas can provide quality habitat for eagles. Urban areas often have high abundance of prey species that cohabit with humans, including small mammals, such as rabbits, raccoons, and squirrels, and birds that are attracted by bird feeders (Hager, 2009; Tomiałojć, 2017). In addition, many waterfowl species were either intentionally introduced to cities or originated from escaped domestic populations, providing valuable prey resources to urban eagles (Tomiałojć, 2017). However, a study that occurred in a subset of our study area found that eagles nesting in the Colorado Front Range often select natural areas that are less developed than the surrounding area, with the number of buildings within a 0.5 km² buffer (400 m radius) of the nest being 13 times lower than within a 0.5 km² buffer of random points (Bove et al., 2024). This buffer is on the small end of the core-use areas we calculated, though it is larger than female core-use areas during the nestling and post-fledge stages. Other studies have also found that eagles nest in locations with less

development than the surrounding area (Andrew & Mosher, 1982; Saalfeld & Conway, 2010; Mundahl et al., 2013). This could in part explain why larger core-use areas are associated with development. Although at a landscape scale developed areas can provide high quality habitat, at the smaller scale of core-use areas, natural areas are still higher quality habitat than developed areas. A nest in a natural area surrounded by development may be limited in the areas where the territorial adults can forage. A home range in a developed area may contain fewer but more intensely concentrated resources than a home range in a natural area with more dispersed resources. This may result in the eagle having a smaller home range, but using a larger part of it more intensely than an eagle whose home range is in a natural area.

We found that both water and herbaceous wetlands were associated with smaller home ranges for Bald Eagles, which suggest that these habitat types increase habitat quality (Rolando, 2002; Smith et al., 2023). Bald Eagles are known to be associated with water, which provides important food sources (e.g., fish and waterfowl; Anthony et al., 1982; Fraser et al., 1985; Buehler et al., 1991). Herbaceous wetlands, characterized by cottonwood trees in the study area, often surround rivers and reservoirs and provide good nesting and perching sites in a landscape which otherwise consists largely of grass and shrubland. However, at the same time, increasing canopy cover was associated with larger home ranges. Eagles prefer open forests with uneven canopy height and open patches for ease of flight and for better visibility (Gerrad et al., 1979; McEwan & Hirth, 1979; Anthony & Isaacs, 1989). While trees increase habitat quality by providing nesting and perching sites, areas with dense canopy cover may be too dense and difficult to fly through and have limited visibility, leading to a decrease in habitat quality.

Although this study provides new insights into Bald Eagle space use in an urbanizing landscape, there were some limitations to the project, which highlight opportunities for future research. This study evaluated the overall effect of development on Bald Eagle home range and core area sizes; however, different types of development may affect eagles differently. When hunting, eagles spend 90% of their

time perching (Stalmaster, 1984). Power lines through prairie dog colonies that otherwise would not have trees may increase habitat quality, but they may also increase mortality risk due to electrocution. City parks and other artificial habitats, like planted trees, may increase suitable habitat for prey, such as small mammals and birds (Rosenfield et al., 2018) and lead to an increase in habitat quality for eagles. However, urban areas may decrease habitat quality by removing important habitat for other types of prey (e.g., prairie dog colonies converted to residential or commercial development, or building around reservoirs leaving no room for eagles to build nest sites). Other types of development like sand and gravel mining may initially decrease habitat quality by removing natural habitat and increasing human disturbance but later improve habitat quality by resulting in a pond where eagles can fish. Urbanization also leads to increased disturbance for Bald Eagles. Eagles have been shown to avoid shorelines with year-round residents (Mcgarigal et al., 1991). To better understand how development is affecting Bald Eagles, it would be beneficial to investigate each type of development separately rather than as a combined index, as well as examine how eagles respond to different types of human activities. Such a study would require collecting spatially-explicit data on human-activity levels during all nest stages, and disaggregating and ground-truthing existing development layers.

Directly comparing Bald Eagle home range and core-use area sizes over space and time is limited by differences in methodological approach among studies. We chose to use a DBBMM as it accounts for irregular sampling and temporal autocorrelation (Kranstauber et al., 2012), both of which are present in our data. DBBMMs are more conservative in calculating home ranges and may result in smaller home ranges than other methods (Kranstauber et al., 2012). Studies also vary in what utilization distribution they select (e.g., 90% or 95%; Gerrard et al., 1992; Garrett et al., 1993; Thompson & McGarigal, 2002; Watson, 2002; Smith et al., 2017a; Slankard et al., 2021). A 90% UD can result in smaller estimated home ranges as it excludes extra-territorial movements that would have been included by using a 95% UD. As technology continues to improve and new methods of analyzing home ranges are developed, it will be

increasingly difficult to compare to previous studies. As such, it is imperative that we either standardize or compare methods using a fixed data set in order to make more accurate comparisons over time.

The post-fledge nesting stage is not well understood, and there are few regulations or recommendations protecting Bald Eagle habitat during this period. The current recommendations in Colorado focus on nesting Bald Eagles from the start of pre-nesting (December 1st) through July 31st or nest completion, whichever comes first. There are no formal recommendations for the post-fledge stage, which frequently extends beyond July 31st, in Colorado or other states (Colorado Parks and Wildlife, 2020; U.S. Fish and Wildlife Service, 2007). Young eagles cannot easily leave the nest area in response to human disturbance, as they have limited flying capabilities (Kussman, 1977). Even once they are able to fly, they still use the nest and are dependent on their parents for survival and are frequently within 230 m of the nest before dispersing (Wallin, 1982; Wood et al., 1998). More research is needed to understand how human activity and development affect eagles at this vulnerable stage, and to evaluate whether extending the current recommendations to include the post-fledge period would be beneficial.

Conservation Implications

In this study, Bald Eagle home ranges and core-use areas were often discontinuous, which has implications for policy and practice. Currently Colorado's state wildlife agency recommends no new surface occupancy within 400 m of an active nest (year round) and no new human encroachment within 800 m of an active nest (during the nesting season). If new surface occupancy cannot be avoided and the nest is within an already highly developed area, the recommended buffers are 200 m and 400 m for no new surface occupancy and human activity, respectively. These recommendations are only for nest sites and do not take into account additional core-use areas away from nest sites (Colorado Parks and Wildlife, 2020). The federal recommendation is to protect only foraging areas in view of the nest (U.S. Fish and Wildlife Service, 2007). This study and others have shown that eagles have multiple core-use areas in addition to their nest site that are frequently not in view of the nest (Smith et al., 2017b). These

areas are also likely important to the continued persistence of Bald Eagles. While it is not feasible to identify the location of all core-use areas for every eagle, understanding which landscape characteristics are associated with core-use areas could help identify the resources an eagle needs beyond the nest site. Resources like eBird could also provide valuable insights into the locations of core-use areas. Investigating eBird hot spots for Bald Eagles during the breeding season could lend insights to where these birds are spending time while not at the nest. Protecting these areas could also protect important habitat for other species that are dependent on water and riparian habitat in a semi-arid urbanizing landscape.

Figures and Tables

Table 1.1: The covariates (name, metric, category and source) used to evaluate the association between Bald Eagle home range size and sex, nest stage, development and land cover along the Front Range of Colorado from 2020 to 2024. CDOT refers to Colorado Department of Transportation.

| Variable | Metric | Categorical/Continuous | Source |
|-------------------------|---|-------------------------------|---|
| Human Development Index | Scale index 0-1 | Continuous | Theobald et al., 2020 |
| Sex | Male/Female | Categorical | Field Collection |
| Nest Stage | pre-nesting, incubation, nestling, post-fledge, non-nesting | Categorical | Field Collection |
| Herbaceous Wetlands | % cover | Continuous | National Land Cover Database (NLCD) 2021 |
| Canopy Cover | % cover | Continuous | National Land Cover Database (NLCD) 2021 |
| Agriculture | % cover | Continuous | National Land Cover Database (NLCD) 2021 |
| Grassland | % cover | Continuous | National Land Cover Database (NLCD) 2021 |
| Water | % cover | Continuous | National Land Cover Database (NLCD) 2021, CDOT 2012 |

Table 1.2: The mean, standard deviation, and sample size (N) of home range sizes (90% utilization distribution) and core-use areas (50% utilization distribution) for Bald Eagles along the Front Range of Colorado from 2020 to 2024 for each sex and nest stage, and across sexes and all nest stages. All area measurements are shown in km².

| Nest Stage | Pre-Nesting | | | Incubation | | | Nestling | | |
|-------------------|--------------------|--------------|----|--------------------|--------------|----|-----------------|--------------|-----|
| Sex | Home Range | Core-Use | N | Home Range | Core-Use | N | Home Range | Core-Use | N |
| Male | 77.16 ± 79.95 | 8.48 ± 11.91 | 14 | 88.69 ± 158.43 | 5.26 ± 15.08 | 14 | 77.03 ± 111.6 | 5.44 ± 10.92 | 10 |
| Female | 60.43 ± 108.59 | 5.19 ± 10.67 | 15 | 70.31 ± 183.48 | 0.85 ± 1.53 | 14 | 2.86 ± 2.14 | 0.06 ± 0.09 | 7 |
| Combined | 68.51 ± 94.53 | 6.78 ± 11.21 | 29 | 79.5 ± 168.47 | 3.06 ± 10.75 | 28 | 46.49 ± 91.78 | 3.22 ± 8.63 | 17 |
| Nest Stage | Post-Fledge | | | Non-Nesting | | | Combined | | |
| Sex | Home Range | Core-Use | N | Home Range | Core-Use | N | Home Range | Core-Use | N |
| Male | 43.89 ± 98.67 | 2.09 ± 5.25 | 17 | 117.31 ± 177.04 | 8.51 ± 11.42 | 15 | 79.8 ± 129.73 | 5.86 ± 11.16 | 70 |
| Female | 8.32 ± 7.32 | 0.42 ± 0.49 | 11 | 34.08 ± 24.98 | 1.55 ± 1.54 | 18 | 40.24 ± 101.11 | 1.89 ± 5.44 | 65 |
| Combined | 29.49 ± 78.03 | 1.43 ± 4.13 | 28 | 71.91 ± 125.76 | 4.71 ± 8.41 | 33 | 60.75 ± 118.08 | 3.95 ± 9.07 | 135 |

Table 1.3: Models of A) home range size (90% UD) and B) core-use area (50% UD) for Bald Eagles along the Front Range of Colorado from 2020 to 2024, including the number of parameters (K), $\Delta AICc$, and model weight (> 1%). All models included eagle ID as a random effect as well as sex, season, and the interaction between sex and season as fixed effects in addition to the covariates listed. A full list of models can be found in the appendix. Refer to Table 1.1 to see description of covariates.

A

| Model | K | $\Delta AICc$ | Weight |
|----------------------------------|----------|---------------------------------|---------------|
| Canopy+Development+HerbWet+Water | 9 | 0.00 | 0.859 |
| Canopy+HerbWet+Water | 8 | 3.91 | 0.122 |
| Canopy+Development+Water | 8 | 7.85 | 0.016 |

B

| Model | K | $\Delta AICc$ | Weight |
|--------------------------|----------|---------------------------------|---------------|
| Canopy+Water | 7 | 0.00 | 0.338 |
| Water | 6 | 0.88 | 0.246 |
| Canopy+Development | 7 | 2.19 | 0.128 |
| Canopy+Development+Water | 8 | 2.30 | 0.121 |
| Development+Water | 7 | 3.31 | 0.073 |
| Development | 6 | 4.80 | 0.035 |

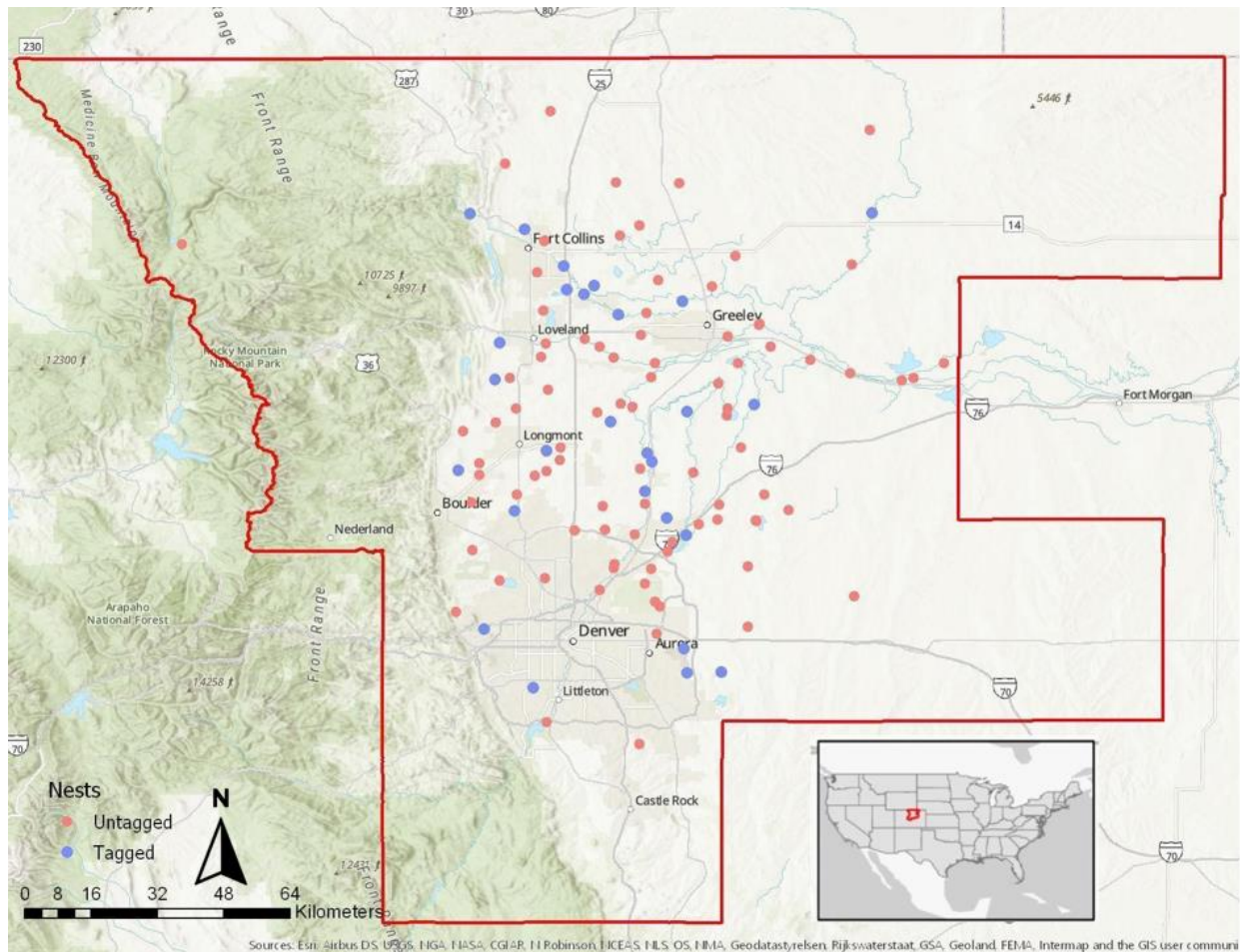


Figure 1.1: Map of study area in northern Colorado showing locations (red and blue dots) of known Bald Eagle nests in 2024. Tagged nests (blue dots) are nests where one adult of a breeding pair was affixed with a GPS/GSM transmitter during 2020 - 2024.



Figure 1.2: An adult Bald Eagle with a transmitter affixed to its back via a backpack harness. Photo credit M. Middleton.

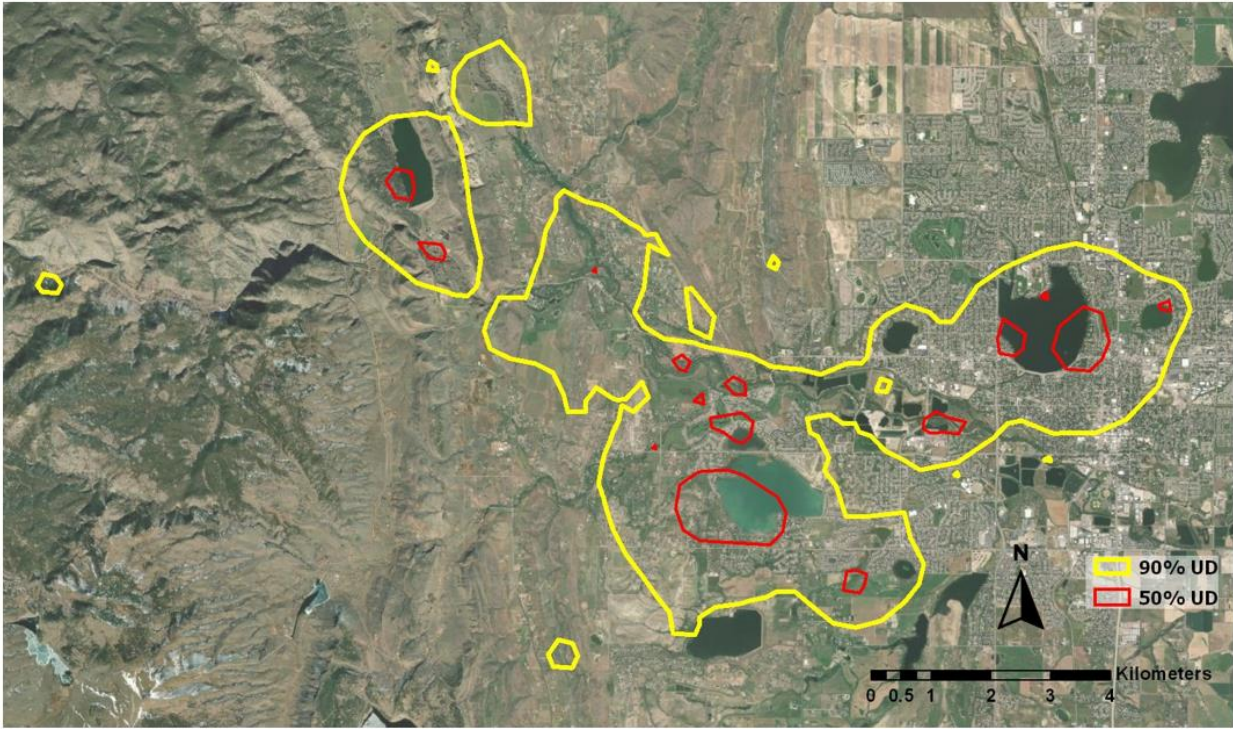


Figure 1.3: The home range (yellow) and core-use area (red) of a female Bald Eagle during the 2022 pre-nesting stage in northern Colorado, illustrating how both home range and core-use areas can consist of multiple disconnected areas.

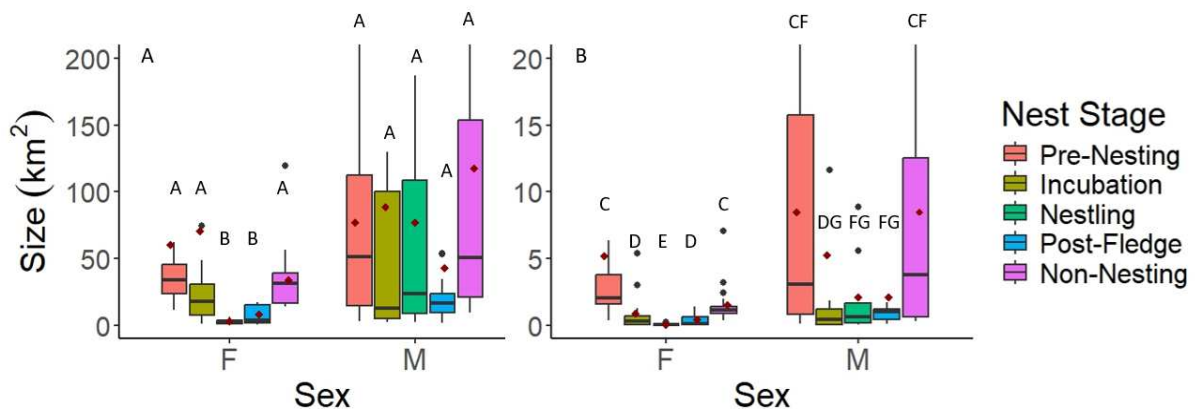


Figure 1.4: The difference in Bald Eagle home range (A) and core-use area (B) size between the different nest stages for both sexes, showing the upper quartile, lower quartile, mean (red diamond), median (black line) and outliers (black dots). The letters above the box plots represent significant differences. Nest stages with the same letters are not significantly different ($p > 0.05$). Seven of thirteen outliers could not be visualized on these axes.

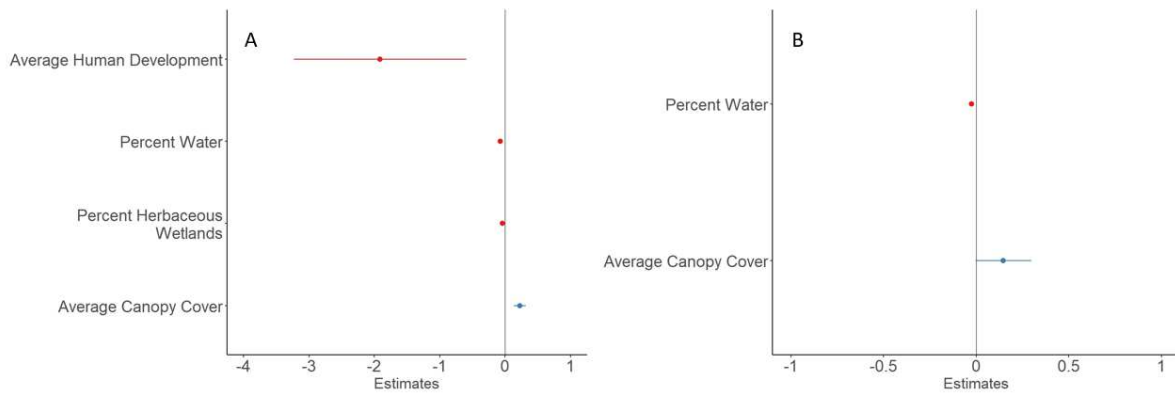


Figure 1.5: The association between Bald Eagle home range size (A) and core-use area (B) and the land cover covariates in the top (minimum $\Delta AICc$) model for both sexes and all five nest stages combined in northern Colorado during 2020 - 2024. The x axis shows the beta estimate from the linear regression model. Any covariate with a 95% confidence interval that does not cross 0 is considered a strong predictor. Covariates shown in red are associated with smaller home ranges and core-use areas and covariates shown in blue are associated with larger home ranges and core-use areas. Not shown in the figure, but in the top model for both analyses, is the interaction between sex and nest stage as well as the random effect of eagle ID.

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Chapter 2: Bald Eagle Habitat Selection in an Urbanizing Landscape

Introduction

More than half of the world's human population now lives in cities (Ramalho & Hobbs, 2012; Jiang & O'Neill, 2017), and urbanization is a leading driver of land use change (Czech et al., 1997). However, the footprint of cities extends well beyond city limits to include the conversion of natural areas into energy production (such as coal, solar, and wind), the damming and diversion of rivers, and agriculture and forestry to feed and house urban residents. Urbanization has led to fewer and more fragmented natural areas, biotic homogenization, and biodiversity loss (Czech et al., 1997; McKinney, 2006; Western, 2001). Identifying pathways for human-wildlife coexistence along the urban-rural gradient is a challenge and opportunity for conservation scientists in a world where human interactions with nature are often in places where we live and work (Western, 2001).

Although many species are unable to persist in human modified landscapes, other species, such as many species of raptors, have found ways to survive and thrive in cities and surrounding areas (Devictor et al., 2007; Hager, 2009; Rullman & Marzluff, 2014). As many as 42 different raptor species have been found in urban areas during at least one part of their annual cycle, although different raptor species have varying tolerances to urbanization (Hager, 2009; White et al., 2018). Raptors that are habitat and dietary generalists, such as Great-horned Owls (*Bubo virginianus*), Red-tailed Hawks, (*Buteo jamaicensis*), Cooper's Hawks (*Accipiter cooperii*), American Kestrels (*Falco sparverius*), Peregrine Falcons (*Falco peregrinus*), and Bald Eagles (*Haliaeetus leucocephalus*) have a higher probability of using areas with a higher density of urbanization than raptors that are considered to be more specialist such as Golden Eagles (*Aquila chrysaetos*) and Swainson's Hawks (*Buteo swainsoni*), although these two species are also occasionally found in human modified landscapes (Cade et al., 1996; Hogg & Nilon, 2015; White et al., 2018). A particularly striking success story, Peregrine Falcons were close to extinction

but have since recovered and are now commonly found nesting on skyscrapers in dense urban areas where they exploit abundant food (e.g., pigeons) and nest sites (Cade et al., 1996). While generalist raptor species have been found nesting in areas with higher density development, with the exception of Peregrine Falcons, none were found immediately adjacent to buildings and many, like Northern Harriers (*Circus hudsonius*), were only found in natural areas surrounded by development (White et al., 2018). With urbanization increasing and a growing number of raptors observed foraging and breeding in urban and surrounding areas, it is important to understand how raptors are responding to these land use changes. By examining the habitat selection of an urban adapted raptor species in a large landscape with urban, agricultural, and natural areas, we can better understand how to create policy and inform management to promote coexistence between humans and raptors.

Habitat selection is a common approach to evaluating space use by wildlife, and can be used to prioritize areas for conservation (Morris, 2003). Specifically, habitat selection examines what types of landscape characteristics an animal uses in relation to what types of habitats are available (Lele et al., 2013; Montgomery & Roloff, 2013; Hamilton, 2019). If an animal uses a habitat type at a higher ratio than it is available, it is assumed the animal is selecting for that habitat, and if an animal uses a habitat type at a lower ratio than it is available, then it is presumed to be avoiding that habitat (Hamilton, 2019). These models assume that animals select for habitats that increase their fitness and chances of survival, given that they have a knowledge of the landscape and the ability to traverse across it at will (Lele et al., 2013; Montgomery & Roloff, 2013; Hamilton, 2019). Animals select for areas that provide food, shelter, and an ability to reproduce (Montgomery & Roloff, 2013; Hamilton, 2019). By using habitat selection models, we can better understand how raptors use space in urban environments.

Bald Eagles are an iconic species in North America that were once in crisis and remain a conservation and management priority (Grier, 1982; Watts & Byrd, 2022). In the 1970s, Bald Eagles were close to extinction after exposure to the pesticide DDT caused their eggshells to become too thin and

crack under the weight of an incubating adult (Grier, 1982). This species made a remarkable recovery after the pesticide was banned, and in 2020, there were over 316,700 eagles in the contiguous U.S. (U.S. Fish and Wildlife Service, 2020). Historically, Bald Eagles were found in areas with little development and an abundance of water, such as along rivers, lakes, and seashores (Anthony et al., 1982; Fraser et al., 1985; Buehler et al., 1991). However, as their numbers continue to grow they are increasingly found in semi-arid urban and suburban areas, which often have little water outside of artificial water sources such as man-made ponds and reservoirs (Hunt et al., 1992; Hunt et al., 2002; Schirato & Parson, 2006). Surprisingly, Bald Eagles have even been observed at high densities in urban areas, and along the Front Range of Colorado the number of Bald Eagle nest sites has been increasing rapidly (Colorado Parks and Wildlife Statewide Raptor Nest Database), with some nests in close proximity to areas with human disturbance (Millsap et al., 2004). This is unexpected because previous studies showed that eagles prefer to nest in areas that have lower levels of human development than the surrounding areas (Andrew & Mosher, 1982; Wood et al., 1989; Bove et al., 2024). Bald Eagles tend to build nests in the largest tree in an area and prefer open, uneven canopy cover in areas with trees of varying heights with open patches (Andrew & Mosher, 1982). They select nest sites along uneven shorelines near rivers, open water, swamps, or marshes (Harris et al., 1987; Saalfeld & Conway, 2010; Mundahl et al., 2013).

Much less is known about habitat selection by territorial Bald Eagles beyond the nest site (Buehler et al., 2022). Yet, understanding what characteristics of the landscape are preferred for foraging is important for sustaining critical food resources (Smith et al., 2017). Most Bald Eagle home ranges consist of multiple disconnected core-use areas that can be a few kilometers away from their nest (Smith et al., 2017, Chapter 1). Eagles forage in different areas throughout the year depending on season, likely due to differences in weather and food availability (Watts et al., 2015; Schmuecker et al., 2020). In some parts of their range, reservoirs and lakes freeze over in the winter, limiting their ability to acquire fish and affecting habitat selection. While eagles are dietary generalists, fish is a main

component of their diet, followed by waterfowl and small mammals such as prairie dogs (*Cynomys* spp.), rabbits (Leporidae), and squirrels (Sciuridae; Stalmaster & Plettner, 1992; Newsome et al., 2015; Bove et al., 2024). Access to waterfowl and small mammals may also be seasonal. Waterfowl abundance varies as they migrate and move based on water availability (Crissey, 1955) while some small mammals hibernate, are less active during times of inclement weather, or have different emergence dates depending on snow cover and temperature (Harlow et al., 1986; Fagerstone, 1988). While eagles frequently select for areas that support fish, and forage along shorelines (Thompson et al., 2005), other types of habitats that support other prey, such as prairie dogs colonies, may be selected for as well in the absence of suitable water (Boal et al., 2006). During the breeding season, breeding Bald Eagles stay close to their nests and are territorial (Grier, 1982; Chapter 1). Outside of the breeding season, in some parts of their range, eagles stay in their territory but are less territorial and range farther from their nests (Chapter 1). In other parts of their range, eagles may migrate to a completely different region (Wheat et al., 2017; Buehler et al., 2022).

There is some evidence that non-breeding eagles avoid foraging in areas with year round human occupancy (Thompson et al., 2005). However, Bald Eagles do not avoid all forms of human development. In areas with little water, dams and decommissioned sand and gravel mines can create new sources of water that support fish and are used by eagles the same way as natural water (Hunt et al., 2002). Eagles have also been known to congregate at landfills for protection, as landfills are often shielded from the wind and warmer than the surrounding landscape (Elliott et al., 2006). Eagles may be attracted to certain types of agriculture, such as dairy farms, since afterbirth from cows can provide a good food resource (Duvall et al., 2023). Overall, Bald Eagles appear to respond to human development in complex ways (Hunt et al., 1992; Hunt et al., 2002; Thompson & McGarigal, 2002; Schirato & Parson, 2006). Understanding habitat selection beyond nest sites and winter foraging areas is important to conserve and manage the full suite of resources needed for Bald Eagles to thrive in our cities and towns.

The objective of this study was to examine habitat selection of breeding Bald Eagles in a rapidly urbanizing and semi-arid landscape. Specifically, we examined which land use and land cover characteristics eagles select for or against, including human development intensity (Theobald et al., 2020), distance to water, agriculture, herbaceous wetlands, grasslands, and canopy cover (National Land Cover Database 2021, Colorado Department of Transportation 2012). We hypothesized that habitat selection would differ between sexes and across the various nest stages of the annual cycle, given that males and females have different home ranges sizes that vary throughout the year (Gerrad et al., 1979; Grier, 1982, Chapter 1) and that resource availability varies between the breeding and non-breeding seasons as prey abundance and location changes seasonally (Harlow et al., 1986; Fagerstone, 1988). We hypothesized that Bald Eagles would select for areas closer to water, with less development, increased canopy cover, and for herbaceous wetlands as these areas are associated with nest site selection (Andrew & Mosher, 1982; Mundahl et al., 2013; Bove et al., 2024). We predicted eagles would select against increased agriculture and grasslands, as these areas do not provide good cover or foraging habitat, beyond prairie dog colonies in our study region, and have not previously been associated with nest site selection (Berry et al., 1998; Grande et al., 2018).

Methods

Study Site

This study took place in northern Colorado (U.S.A.) in the following counties: Adams, Arapahoe, Boulder, Broomfield, Denver, Douglas, Jefferson, Larimer, and Weld (Figure 2.1). This region has a semi-arid climate, includes both public and private lands, and is characterized by urban centers, rural towns, forest, grassland, and farmland. Population densities vary from 32.03 ppl/km² in Weld County to 1804.76 ppl/km² in Denver County. Colorado experienced a 14.8% human population increase between 2010 and 2019 (US Census Bureau, 2020). Four of the five fastest growing counties in 2022 in Colorado were part of the study area: Weld, Douglas, Adams, and Larimer Counties (Colorado Department of

Local Affairs, 2023). The most rural county in the study area, Weld, is also the fastest growing county in Colorado.

Nest Monitoring

The first documented Bald Eagle nest in the study area was found in 1986, and by 2024 there were over 130 known active nests (Colorado Parks and Wildlife (CPW) Statewide Raptor Nest Database). In 1986, the Bird Conservancy of the Rockies' volunteer program, Bald Eagle Watch, began monitoring nests in the study area. Starting in 2020, CPW research staff assisted Bird Conservancy of the Rockies in collecting these data. Additional data were collected by city, county, and CPW staff and volunteers. This larger project is still ongoing, but only data collected between 2020 and 2024 were used for analysis here. Starting in mid-January, prior to the start of incubation, we visited all nests in the study area at least twice/month. We continued to monitor nests until they failed or until successful completion (mid-June to mid-July). Successful nest completion was defined as at least one fledged young. When feasible, we monitored a subset of the nests until the young had dispersed. Nest observations, made at a distance and often using a vehicle as a blind to avoid changing bird behavior, were used to assess nest stage and identify which nests could be targeted for trapping.

Telemetry

To collect data to inform habitat selection models, we captured Bald Eagles and fitted GPS/GSM (Global Positioning System/Global System for Mobile Communications) transmitters manufactured by Cellular Tracking Technologies (Figure S2.1). See Chapter 1 for detailed methods on how birds were selected, and when and how capture occurred. The transmitters collected data on location, time, activity, and accuracy via satellite and relayed the data via cell towers daily. The data collection interval varied from 4 sec during flight to 6 hours while stationary, based on the voltage of the solar-powered battery, which was influenced by feather coverage and the angle of the sun. However, the most common data collection interval was 30 sec during flight and 15 min while stationary. Location data

were only collected during daytime hours (dawn to dusk) as eagles are usually sedentary at night. See Chapter 1 for detailed information on how we calculated home ranges and divided the annual cycle of the Bald Eagle into the following five nest stages: pre-nesting, incubation, nestling, post-fledge, and non-nesting. In cases where the nest failed during incubation, we did not calculate nestling or post-fledge home ranges, nor did we calculate post-fledge home ranges if the nest failed during the nestling stage. In these cases, the non-nesting period was extended. Similarly, if a territorial eagle did not lay eggs, we only calculated home ranges for the pre-nesting and non-nesting stages, ending the pre-nesting stage on the average date when incubation began for eagles with nesting attempts in the study area that year.

Covariates

We analyzed habitat selection during each of the five nest stages and for both sexes, evaluating the effects of human development intensity (Theobald et al., 2020) and four different National Land Cover Database (NLCD) 2021 land cover types: herbaceous wetlands, canopy cover, agriculture, and grasslands, as well as distance to water (calculated using ArcGISPro 2.0.0 from NLCD 2021 and Colorado Department of Transportation 2012 layers; Table S2.1). Sex and nest stage were determined via field collection. Sex was determined by weight, culmen, tarsometatarsus, and hallux claw length of the eagle at time of capture (Bortolotti, 1984). We used the Human Development Index (Theobald et al., 2020) as a proxy for the extent of human modification in the study area (see Chapter 1 for more information on this index). The Human Development Index assigns reservoirs a value near 1 (most developed and a score akin to downtown Denver). Yet, we expect that eagles view reservoirs as similar to natural water bodies, particularly in this semi-arid region (Hunt et al., 2002). Thus, we re-assigned reservoirs a value of 0, but made no other changes to this index. We used the 2021 NLCD open water classification and the Colorado Department of Transportation (CDOT) 2012 rivers and streams layer to identify areas with water. Because a spatial layer for cottonwood trees, the preferred nesting substrate for Bald Eagles in our region, is not available, we used herbaceous wetlands (2021 NLCD emergent herbaceous wetlands)

as a proxy for this land cover type. We also evaluated overall canopy cover (NLCD 2021 U.S. Forest Service Tree Canopy Cover) as a covariate because of the presumed value of trees for nesting and perching. Finally, we used the 2021 NLCD pasture/hay and cultivated crops classifications to identify agricultural areas, and we used the 2021 NLCD grassland/herbaceous classifications to denote grassland. We did not have access to accurate prairie dog layers for each year of the study (their shape, size, extent and occupancy can change annually), so we were not able to incorporate this potentially important prey species (Bove et al., 2024) into our models.

Modeling Habitat Selection

All statistical modeling was performed in Program R (R Core Team 2023; V 4.3.2). Before calculating habitat selection, we thinned the GPS points to one point per hour to avoid violating the assumption of no temporal autocorrelation. Eagles in our study typically had top speeds of 100 - 150 km/h and are capable of crossing the diameter of their home range in under an hour. We checked for correlations among the covariates and chose the better performing covariate of any pair with a correlation coefficient greater than 0.70 to incorporate into our models. Using the lme4 (V 1.135.1) package (Bates et al., 2015), we ran a logistic regression model to examine the ratio of used sites to available sites at two different scales: within the individual eagles' home ranges and within the study area. We considered every covariate of interest (Table S2.1), and any covariate with a p-value < 0.05 was considered statistically significant. We ran separate logistic regressions for the five different nest stages and both sexes. For both scales we used a ratio of five available points for every used point, as after five points the results stabilized. An available point was considered to be any point within the individual's home range for the first analysis and any point within the study area for the second analysis. For both scales we used eagle ID as well as year as random effects. We also included an interaction between water and human development, as we hypothesized eagles would select for water but against human development; however, in our study region, water is often surrounded by human development. We

investigated a quadratic effect of human development, because we hypothesized that eagle response to human development would be nonlinear, with eagles tolerating a low to moderate level of development. When doing the logistic regression, we scaled all continuous variables using the function “scale (covariate)” in the lme4 package to standardize the data.

Results

We fitted 24 Bald Eagles with a GPS/GSM transmitter (n = 13 male; 11 female). A total of 135 home ranges were calculated across all eagles and nest stages (see Chapter 1). Telemetry data were collected for a mean duration of 438 days/eagle, with a range of 42 - 1371 days. Data collection ended prior to the conclusion of the study for 18 eagles due to the death of the eagle (n=6), loss of territory (n=5), removal of transmitter by the eagle (n=4), GPS malfunction (n=2), and 3G sunset (n=1). In total, after thinning the data, 180,348 GPS locations were used (Table S2.2) in both habitat selection analyses (within home range and within study area).

We found little variation in Bald Eagle habitat selection for natural land cover types among nest stages (Figure 2.2). Throughout all nest stages and at both scales (home range and study area), eagles selected for herbaceous wetlands and proximity to water (Figure 2.3). They selected for grasslands during all nest stages except for non-nesting. Eagles avoided high canopy cover, although their avoidance of high canopy cover was weak during the pre-nesting stage at the study area scale. Additionally, eagles selected for agriculture during the incubation stage but avoided this land use during the other four stages at both scales.

Habitat selection varied by sex for more land cover characteristics at the within home range scale than for the within study area scale (Figure 2.4). At the within home range scale, females selected against grasslands and agriculture and (weakly) for increased canopy cover, while males selected for grassland and agriculture and against increased canopy cover. At the within study area scale, grasslands

were the only landscape characteristic where males and females differed, with females selecting against grasslands and males selecting for grassland cover. At both scales, males and females strongly selected for herbaceous wetlands and proximity to water.

Bald Eagles' selection for human development was more complex compared to other landscape features. For both sexes and at both spatial scales, their probability of using developed areas was nonlinear and increased with proximity to water (Figures 2.3, 2.5, S2.2). Eagles had the highest probability of using developed areas directly adjacent to water, and beyond 1000 m from water, eagles had a very low probability of using even undeveloped areas. At no point did eagles have a high probability of using highly developed areas. At the home range scale, their selection for development varied by nest stage (Figure 2.3). During the incubation and nestling stages, eagles had the highest probability of use for low to moderate development levels near water, while during the post-fledge stage, the probability of use decreased sharply as development levels increased. During the pre-nesting and non-nesting stages, eagles selected for lower development levels compared to other stages, but were more likely to use developed areas overall. Their selection for development did not change significantly between nest stages at the scale of the study area (Figure S2.2). Overall, eagles were generally more likely to use developed areas at the study area scale than they were within their home ranges. Male and female eagles responded differently to human development depending on distance to water and spatial scale (Figure 2.5). At the within home range scale, the response of male eagles was similar to that seen for both sexes combined during the post-fledge nest stage (Fig 2.3C): as development increased, the probability of use decreased across all distances from water. Within the home range for females and within the study area for both sexes, eagles had the highest probability of use for moderate levels of development when near water. At both spatial scales, females had a higher probability of using developed areas than males.

Discussion

Urbanization and climate change are altering the abundance and distribution of species globally (Czech et al., 1997; Western, 2001). In some cases, this has led to movement of animal populations into what appear to be new ecological niches (González-Oreja, 2011; Møller et al., 2015). For example, historically, Bald Eagles were typically found in regions with abundant water and minimal human development (Anthony et al., 1982; Fraser et al., 1985; Buehler et al., 1991). Recently, however, they have been observed breeding in arid and semi-arid areas with increasing human activity (Hunt et al., 1992; Schirato & Parson, 2006, Chapter 1). This study investigated Bald Eagle habitat selection in the northern Front Range of Colorado, a semi-arid region experiencing both rising eagle and human populations and rapid development. Our findings indicate that Bald Eagles' habitat preferences are influenced by factors such as spatial scale, nest stage, sex, herbaceous wetlands, and proximity to water. Bald Eagles were more likely to use developed areas within the broader study area compared to their home ranges, especially if they were female. Within their home range, eagles were less likely to use developed areas during the pre-nesting, post-fledge and non-nesting stages. Across all nest stages, eagles used areas with low to moderate levels of development near water while avoiding highly developed areas.

Bald Eagle habitat selection showed similar patterns at the home range and study site scale when considering land cover such as grass, agriculture, herbaceous wetlands, canopy cover and proximity to water. However, the likelihood of Bald Eagles using developed areas varied across scales. Overall, the relationship between development and eagle use was non-linear, with eagles showing the highest probability of using areas with low to moderate development close to water. Within their home range, eagles were less likely to use developed areas compared to the overall study area. Yet, the most highly developed areas within the study site were absent from the eagles' home ranges and therefore not reflected in the home range analysis. This suggests that while eagles will use areas with moderate

development within their home range, they tend to avoid areas with the highest levels of development altogether. However, at the scale of the study area, the least developed areas are also areas that are otherwise not suitable habitats for eagles, because they are far from water and mainly agricultural or else heavily forested, mountainous regions with little opportunity for foraging or nesting. This finding aligns with previous research indicating that eagles prefer less densely developed areas that are oftentimes surrounded by more intensive development (Andrew & Mosher, 1982; Mundahl et al., 2013; Bove et al., 2024). Our findings are also consistent with the well-documented association between Bald Eagles and water, and their tolerance of human activity to access prime fishing and waterfowl locations (Anthony et al., 1982; McGarigal et al., 1991; Chapter 1).

Females had a higher probability of using developed areas compared with males, both within home ranges and at the scale of the study area. This difference may be attributed to the different roles of each sex during the breeding season. Males spend less time incubating and attending to the nest compared to females and have greater freedom to leave and travel farther from the nest (Gerrard et al., 1979; Wallin, 1982; Buehler et al., 2022). This allows males to have larger home ranges during the breeding season (Gerrard et al., 1992, Chapter 1), providing them with more options for foraging locations. Eagle pairs typically show high nest site fidelity, often using the same nest site for many years (e.g., > 30 years in our study area; Stalmaster, 1987; Buehler et al., 2022). A pair of eagles may have initially chosen a nest site based on its proximity to water or other favorable environmental characteristics before it became developed, but continue to use it despite new development being built in the surrounding area. In the study area, there are a few examples of nest abandonment after new development encroached on the nest site; however, more research is needed to determine the exact cause of abandonment, and there are also many cases of nesting pairs being seemingly unaffected by new development in the immediate area. Encroachment has been limited in some cases due to Colorado Parks and Wildlife recommendations for minimizing disturbance near raptor nest sites (Colorado Parks

and Wildlife, 2020) Newly established nest sites are more likely to be abandoned than well-established nest sites with the encroachment of human development (U.S. Fish & Wildlife Service, 2024). Since females have limited ability to leave the nest during the breeding season, they may not be able to avoid areas with development, if development has encroached on a long-used nest site.

The probability of using developed areas differed by nest stage within the home range. Bald Eagles had a higher probability of using areas with low levels of development during the pre-nesting, non-nesting, and post-fledge stages compared to the incubation and nestling stages, during which they were most likely to use areas with moderate levels of development. Bald Eagles do not migrate during the non-breeding season in this study area; however, they have larger home ranges and are less territorial during this period (Grier, 1982; Gerrard et al., 1992; Chapter 1). This increased freedom from the nest allows them to move farther to access foraging locations in less developed areas. During the post-fledge stage, eagles are still tied to the nest and have a small home range (Wallin, 1982; Chapter 1); however, one member of the breeding pair may take a hiatus from their territory allowing them greater freedom in choice of habitat type. During parts of the annual cycle when eagles can leave the nest for extended periods, they tend to use less developed areas more frequently.

With the exception of agriculture and development, habitat selection was similar among nest stages at both spatial scales. Within both the home range and study area, eagles selected for agriculture only during the incubation nest stage. When given the choice, animals will select for habitats that increase fitness and survival (Hamilton, 2019); however, eagles have limited ability to leave their nest during incubation. In addition, traditional food sources, like fish and small mammals, may be less available as reservoirs and other water bodies are often frozen and small mammals are less active during the first part of incubation (Harlow et al., 1986; Fagerstone, 1988), which occurs from late January to early March in our region. During this time period, Colorado also hosts many non-breeding

eagles, which likely increases competition for limited resources. These limitations may drive eagles to use less ideal foraging areas.

Bald Eagles selected for grasslands, herbaceous wetlands, lower canopy cover, and proximity to water. This selection for grasslands was surprising, as we predicted eagles would select against grasslands due the limited foraging opportunities they provide (with the exception of prairie dog towns, which were not examined in this study due to a lack of available data on their locations and size). However, grasslands may support higher densities of prey than previously assumed, making grasslands higher quality habitat than hypothesized. A detailed spatial layer of prairie dog and other mammalian populations would be needed to investigate further. Bald Eagle selection for herbaceous wetlands is not surprising, as this land cover is associated with higher quality habitat, often containing cottonwood trees which are good for perching and nesting (Chapter 1). Bald Eagle selection for lower canopy cover is also consistent with literature that shows eagles prefer areas with open canopy cover and varying canopy height, as it provides better visibility and is easier to navigate (McEwan & Hirth, 1979; Anthony & Isaacs, 1989; Wood et al., 1989). Their selection for proximity to water is also expected, as it is well documented that Bald Eagles are associated with water, which provides good foraging opportunities (Andrew & Mosher, 1982; Harris et al., 1987; Mundahl et al., 2013). These same landscape characteristics, with the exception of grasslands, which did not have a correlation with home range size, were associated with smaller home ranges (Chapter 1, Jaffee, 1980; Andrew & Mosher, 1982; Harris et al., 1987; Watson, 2002; Millsap et al., 2004; Saalfeld & Conway, 2010; Mundahl et al., 2013) and presumably, higher quality habitat (Rolando, 2002; Smith et al., 2017).

This study offers valuable insights into Bald Eagle habitat selection in a semi-arid, urbanizing landscape. However, there were some limitations to our approach and several promising avenues for future research. Our analysis classified development intensity using a single index; however, eagles may

respond differently to various types of development. For example, urban open spaces such as city parks, and neighborhoods with planted trees and artificial water bodies may increase prey availability and attract eagles (Rosenfield et al., 2018), while developed areas with extensive impervious surfaces and minimal vegetation might be avoided by eagles (Ciminelli, 2006). To better understand these preferences, comprehensive and high resolution spatial layers for each type of development (e.g., residential, commercial, transportation, energy) at the scale of the study area need to be compiled and analyzed. Also, parsing out the relative importance of each type of development in influencing habitat selection will only be possible if these development types are not strongly correlated. This study focused only on the overall amount of development. Examining the contiguity of developed spaces may provide valuable insight, as Bald Eagles may avoid large continuous developed areas while utilizing smaller fragmented patches consisting of the same level of overall development. Additionally, this study concentrated on development itself rather than potential disturbances to eagle behavior caused by human activity. While eagles are known to be relatively resilient to anthropogenic noise, visual disturbances could have a greater impact on behavior and habitat selection (Grubb & King, 1991; Brown et al., 1999). In Alaska, for instance, eagles spent less time preening and tending to their nests when people were within 100 m compared to 500 m (Steidl & Anthony, 2000). Eagles also exhibit varying flushing rates depending on location, activity of the eagle, and type of human activity (Stalmaster & Newman, 1978; Knight & Knight, 1984; Mcgarigal et al., 1991; Anthony et al., 1995; Stalmaster & Kaiser, 1997; Thompson et al., 2005). Future research evaluating eagle responses to human activity in rapidly urbanizing environments could help complement and explain our findings on the associations among land use and cover and Bald Eagle habitat selection. Further, as the Bald Eagle population increases in our study area, competition for optimal habitats may be forcing some eagles to select less ideal locations (Fretwell & Lucas, 1969; Morris, 2003). An important priority for future research is to explore Bald Eagle source-sink dynamics in urbanizing landscapes. Although Bald Eagle numbers and nest

success rates are high in Colorado and throughout their range (U.S. Fish and Wildlife Service, 2020; Conrey et al., 2024), the fate of immature eagles is less known and it is unclear whether newly breeding eagles immigrated to the area or were born locally.

Conservation Implications

The population of Bald Eagles in the northern Front Range Colorado is increasing (CPW Statewide Raptor Nest Database). However, access to their preferred habitats may be decreasing or limited, and without effective conservation measures, this positive trend could be jeopardized. Bald Eagles are well known to be associated with water (Hunt et al., 2002; Thompson et al., 2005), and as this region is semi-arid, access to the limited water that is available is vital. As Colorado's human population continues to increase, the lands adjacent to water are becoming increasingly developed. Although eagles can tolerate some development, this study showed that they tend to avoid heavily developed areas. Herbaceous wetlands, which are characterized by cottonwood trees in Colorado, are also important habitat for Bald Eagles in this region (Chapter 1). In particular eagles prefer large, mature cottonwoods (Fayette et al., 2000), which are limited in supply and at risk of removal or senescence in urban settings, though they are currently increasing along a major river (South Platte) in the study area, where a significant number of territories are found (Christensen et al., 2023; Hanberry et al., 2024). This study demonstrates that Bald Eagles can coexist with humans in urban settings. However, they tend to select areas near water and low to moderate levels of development. Conservation strategies for Bald Eagles in urbanizing regions should prioritize protecting habitats close to water that are characterized by herbaceous wetlands and open canopy, and should minimize the intensity of development in these landscapes.

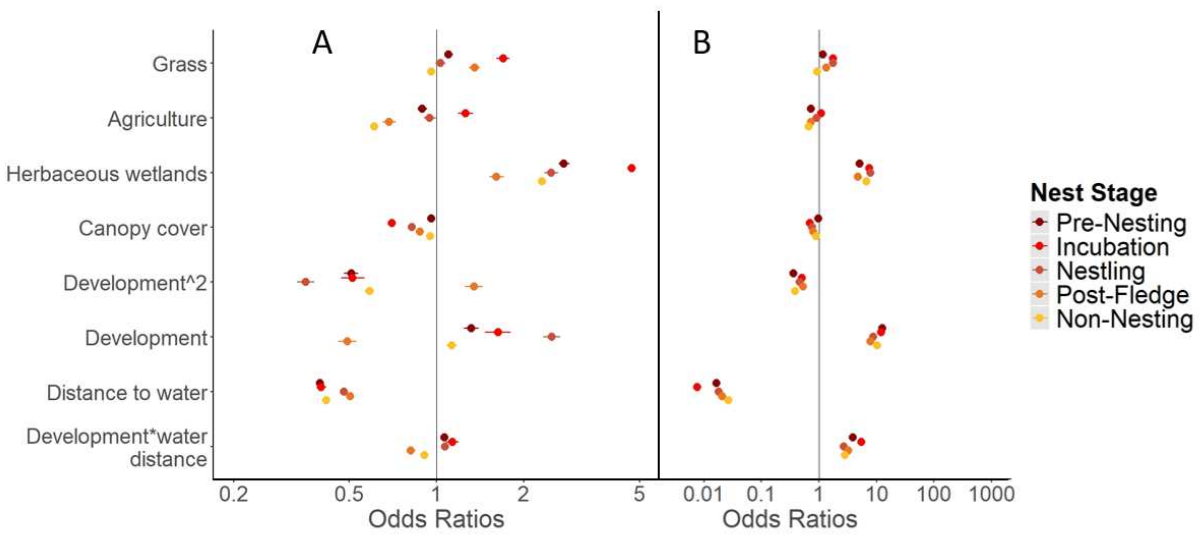


Figure 2.2: The odds ratio showing the selection for landscape characteristics of Bald Eagles (sexes combined) in northern Colorado during 2020 - 2024 for each nest stage within the home range (A) and within the study area (B). Any point on the left side of the black line indicates that eagles select against that landscape characteristic during that nest stage, and points on the right side of the vertical line indicate landscape characteristics that eagles select for. Any point where the standard error bars crossed 0 were neither selected for nor against.

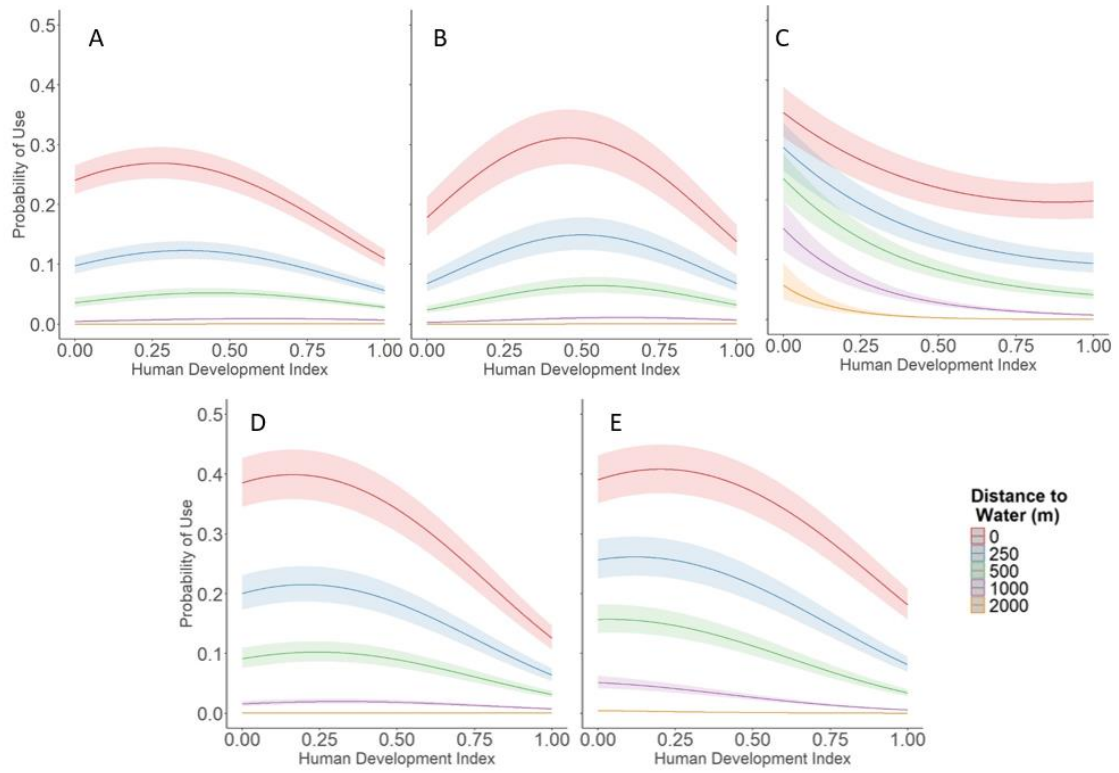


Figure 2.3: The relationship between development intensity (x-axis) and Bald Eagle (sexes combined) probability of use (y-axis) as a function of distances from water (colored lines) for incubation (A), nestling (B), post-fledge (C), non-nesting (D), and pre-nesting (E) periods at the scale of the home range in northern Colorado (2020-2024). Shaded areas denote 95% confidence intervals.

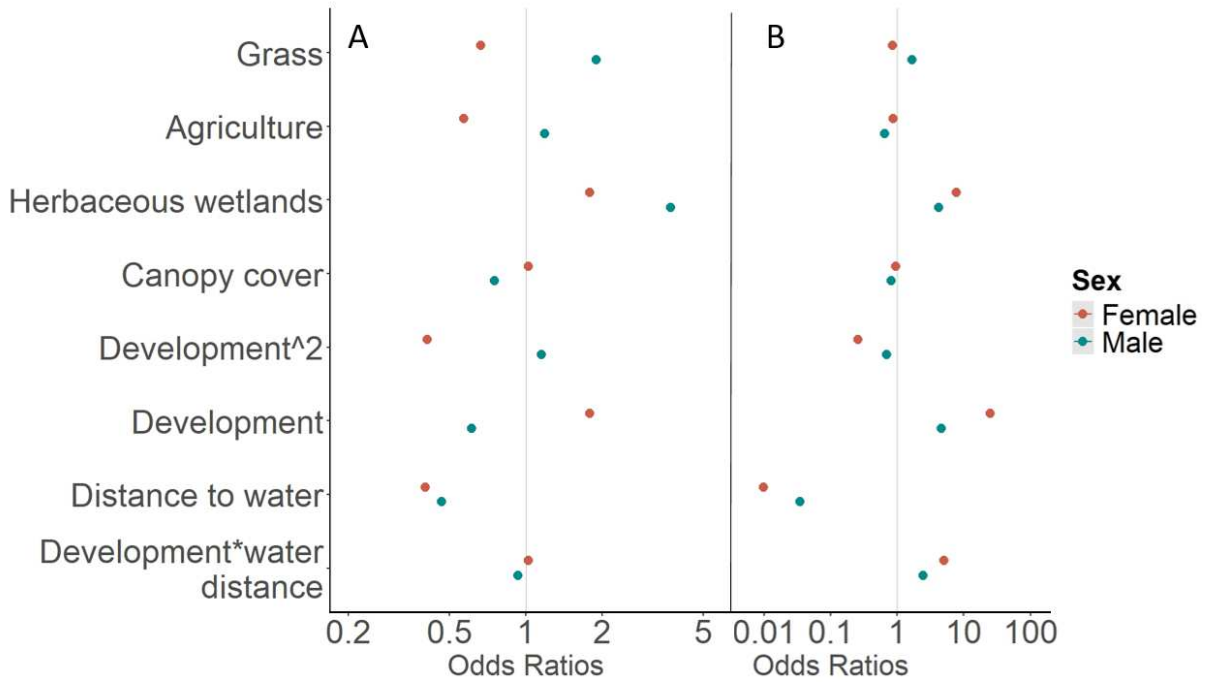


Figure 2.4: The odds ratio showing the selection for landscape characteristics of Bald Eagles in northern Colorado during 2020 - 2024 for each sex within the home range (A) and within the study area (B). Any point on the left side of the grey line indicates that eagles select against that landscape characteristic, and points on the right side of the grey line indicate landscape characteristics that eagles select for. Any point where the standard error bars crossed 0 were neither selected for nor against.

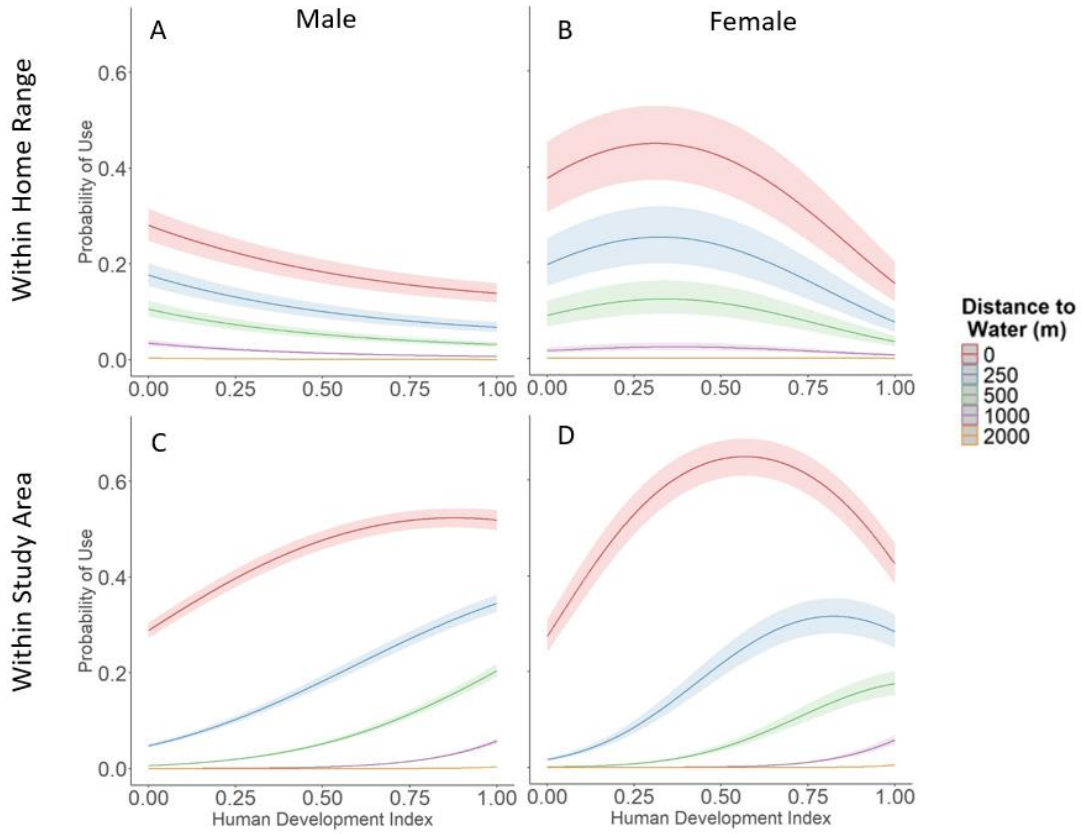


Figure 2.5: Probability of use (y-axis) in relation to development intensity (x-axis) at different distances from water (colored lines) for male Bald Eagles within the home range (A), females within the home range (B), males within the study area (C), and females within the study area (D) in northern Colorado (2020-2024). The shaded areas are the 95% confidence intervals.

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Appendix

Table S1.1: The mean, standard deviation, range, and sample size of home range sizes (90% UD) for Bald Eagles along the Front Range of Colorado from 2020 to 2024 for each sex and nest stage, and across sexes and all nesting stages. All area measurements are shown in km².

| Nest Stage Sex | Pre-Nesting | | | | | Incubation | | | | | Nestling | | | | |
|-------------------|-------------|--------|-------|--------|----|-------------|--------|-------|--------|----|----------|--------|------|--------|-----|
| | Mean | SD | Min | Max | N | Mean | SD | Min | Max | N | Mean | SD | Min | Max | N |
| Male | 77.16 | 79.95 | 2.7 | 241.6 | 14 | 88.69 | 158.43 | 2.59 | 487.88 | 14 | 77.03 | 111.6 | 2.59 | 340.84 | 10 |
| Female | 60.43 | 108.59 | 11.08 | 449.53 | 15 | 70.31 | 183.48 | 1.2 | 703.99 | 14 | 2.86 | 2.14 | 0.58 | 6.49 | 7 |
| Combined | 68.51 | 94.53 | 2.7 | 449.53 | 29 | 79.5 | 168.47 | 1.2 | 703.99 | 28 | 46.49 | 91.78 | 0.58 | 340.84 | 17 |
| Nest Stage Sex | Post-Fledge | | | | | Non-Nesting | | | | | Combined | | | | |
| | Mean | SD | Min | Max | N | Mean | SD | Min | Max | N | Mean | SD | Min | Max | N |
| Male | 43.89 | 98.67 | 1.54 | 421.38 | 17 | 117.31 | 177.04 | 9.57 | 708.21 | 15 | 79.8 | 129.73 | 1.54 | 708.21 | 70 |
| Female | 8.32 | 7.32 | 0.62 | 16.88 | 11 | 34.08 | 24.98 | 13.99 | 119.44 | 18 | 40.24 | 101.11 | 0.58 | 703.99 | 65 |
| Combined | 29.49 | 78.03 | 0.62 | 421.38 | 28 | 71.91 | 125.76 | 9.56 | 708.21 | 33 | 60.75 | 118.08 | 0.58 | 708.21 | 135 |

Table S1.2: The mean, standard deviation, range, and sample size of core-use area sizes (50% UD) for Bald Eagles along the Front Range of Colorado from 2020 to 2024 for each sex and nest stage, and across sexes and all nesting stages. All area measurements are shown in km².

| Nest Stage Sex | Pre-Nesting | | | | | Incubation | | | | | Nestling | | | | |
|-------------------|-------------|-------|------|-------|----|-------------|-------|------|-------|----|----------|-------|------|-------|-----|
| | Mean | SD | Min | Max | N | Mean | SD | Min | Max | N | Mean | SD | Min | Max | N |
| Male | 8.48 | 11.91 | 0.11 | 38.69 | 14 | 5.26 | 15.08 | 0.03 | 56.59 | 14 | 5.44 | 10.92 | 0.03 | 35.41 | 10 |
| Female | 5.19 | 10.67 | 0.34 | 43.28 | 15 | 0.85 | 1.53 | 0.01 | 5.34 | 14 | 0.06 | 0.09 | 0.01 | 0.26 | 7 |
| Combined | 6.78 | 11.21 | 0.11 | 43.28 | 29 | 3.06 | 10.75 | 0.01 | 56.59 | 28 | 3.22 | 8.63 | 0.01 | 35.41 | 17 |
| Nest Stage Sex | Post-Fledge | | | | | Non-Nesting | | | | | Combined | | | | |
| | Mean | SD | Min | Max | N | Mean | SD | Min | Max | N | Mean | SD | Min | Max | N |
| Male | 2.09 | 5.25 | 0.12 | 22.36 | 17 | 8.51 | 11.42 | 0.3 | 37.87 | 15 | 5.86 | 11.16 | 0.03 | 56.59 | 70 |
| Female | 0.42 | 0.49 | 0.02 | 1.39 | 11 | 1.55 | 1.54 | 0.38 | 7.04 | 18 | 1.89 | 5.44 | 0.01 | 43.28 | 65 |
| Combined | 1.43 | 4.13 | 0.02 | 22.36 | 28 | 4.71 | 8.41 | 0.3 | 37.87 | 33 | 3.95 | 9.07 | 0.01 | 56.59 | 135 |

Table S1.3: Full list of models analyzed for Bald Eagle home range (90% UD) showing covariates used in each model, the number of parameters (K), $\Delta AICc$, and model weight. All models included an intercept as well as eagle ID as a random effect. See Table 1 for description of each covariate. Can = canopy cover, Dev = human development index, Herb = herbaceous wetlands.

| Model | K | $\Delta AICc$ | Weight |
|--|---|---------------|----------|
| Can+Dev+Herb+Water+Season+Sex+Season*Sex | 9 | 0 | 0.857853 |
| Can+Herb+Water+Season+Sex+Season*Sex | 8 | 3.906425 | 0.121659 |
| Can+Dev+Water+Season+Sex+Season*Sex | 8 | 7.850279 | 0.016933 |
| Can+Water+Season+Sex+Season*Sex | 6 | 12.82151 | 0.00141 |
| Dev+Herb+Water+Season+Sex+Season*Sex | 7 | 14.24009 | 0.000694 |
| Can+Dev+Herb+Water+Season | 6 | 14.24503 | 0.000692 |
| Herb+Water+Season+Sex+Season*Sex | 6 | 16.48247 | 0.000226 |
| Can+Dev+Herb+Water+Season+Sex | 8 | 16.51052 | 0.000223 |
| Can+Herb+Water+Season | 6 | 16.54337 | 0.000219 |
| Can+Herb+Water+Season+Sex | 6 | 18.71243 | 7.41E-05 |
| Dev+Water+Season+Sex+Season*Sex | 7 | 22.7616 | 9.79E-06 |
| Water+Season+Sex | 5 | 24.527 | 4.05E-06 |
| Water+Season+Sex+Season*Sex | 6 | 28.77887 | 4.83E-07 |
| Dev+Herb+Water+Season | 6 | 29.7314 | 3.00E-07 |
| Herb+Water+Season | 5 | 30.09123 | 2.51E-07 |
| Can+Herb+Water | 5 | 30.38586 | 2.16E-07 |
| Herb+Water+Season+Sex | 6 | 30.86947 | 1.70E-07 |
| Can+Dev+Water+Season | 6 | 30.89995 | 1.67E-07 |
| Can+Dev+Herb+Water | 6 | 31.13938 | 1.48E-07 |
| Can+Dev+Water+Season+Sex | 7 | 31.21378 | 1.43E-07 |
| Can+Dev+Water+Sex | 6 | 32.6113 | 7.11E-08 |
| Can+Herb+Water+Sex | 6 | 33.39136 | 4.81E-08 |
| Can+Water+Season | 5 | 35.94142 | 1.35E-08 |
| Can+Water+Season+Sex | 6 | 36.78363 | 8.83E-09 |
| Herb+Water | 4 | 41.95298 | 6.66E-10 |
| Dev+Herb+Wate | 5 | 42.63437 | 4.74E-10 |
| Herb+Water+Sex | 5 | 43.30653 | 3.38E-10 |
| Can+Dev+Herb+Season+Sex+Season*Sex | 8 | 43.55887 | 2.98E-10 |
| Dev+Herb+Water+Sex | 6 | 44.17093 | 2.20E-10 |
| Can+Dev+Season+Sex+Season*Sex | 7 | 47.58157 | 3.99E-11 |
| Can+Herb+Season+Sex+Season*Sex | 7 | 48.33123 | 2.74E-11 |
| Dev+Water+Season+Sex | 6 | 48.49073 | 2.53E-11 |
| Dev+Water+Season | 5 | 49.82365 | 1.30E-11 |
| Water+Season+Sex | 5 | 49.91072 | 1.25E-11 |
| Can+Dev+Herb+Season | 6 | 50.09972 | 1.13E-11 |
| Water+Season | 4 | 50.73501 | 8.25E-12 |
| Can+Season+Sex+Season*Sex | 6 | 52.41259 | 3.57E-12 |

| | | | |
|--------------------------------|---|----------|----------|
| Can+Dev+Herb+Season+Sex | 7 | 52.43501 | 3.53E-12 |
| Dev+Herb+Season+Sex+Season*Sex | 7 | 52.85832 | 2.85E-12 |
| Can+Herb+Season | 5 | 53.09838 | 2.53E-12 |
| Can+Herb+Season+Sex | 6 | 55.18505 | 8.92E-13 |
| Dev+Season+Sex+Season*Sex | 6 | 55.55081 | 7.43E-13 |
| Herb+Season+Sex+Season*Sex | 6 | 57.35479 | 3.01E-13 |
| Can+Dev+Water | 5 | 57.76686 | 2.45E-13 |
| Dev+Herb+Season | 5 | 59.28088 | 1.15E-13 |
| Can+Dev+Water+Sex | 6 | 59.50316 | 1.03E-13 |
| Can+Water | 4 | 60.00652 | 8.00E-14 |
| Season+Sex+Season*Sex | 5 | 60.60524 | 5.93E-14 |
| Dev+Herb+Season+Sex | 6 | 61.29596 | 4.20E-14 |
| Herb+Season | 4 | 61.42966 | 3.93E-14 |
| Can+Water+Sex | 5 | 61.56621 | 3.67E-14 |
| Can+Dev+Season | 5 | 63.61122 | 1.32E-14 |
| Herb+Season+Sex | 5 | 63.61956 | 1.31E-14 |
| Can+Season | 4 | 64.80257 | 7.27E-15 |
| Herb+Water+Season+Sex | 6 | 65.88573 | 4.23E-15 |
| Can+Dev+Herb | 5 | 66.4231 | 3.23E-15 |
| Can+Season+Sex | 5 | 67.09223 | 2.31E-15 |
| Can+Dev+Herb+Sex+Season*Sex | 7 | 68.50634 | 1.14E-15 |
| Dev+Season | 4 | 71.80987 | 2.19E-16 |
| Season | 3 | 73.16729 | 1.11E-16 |
| Dev+Season+Sex | 5 | 73.27499 | 1.05E-16 |
| Season+Sex | 4 | 74.74105 | 5.05E-17 |
| Water+Sex | 4 | 75.13719 | 4.15E-17 |
| Water | 3 | 75.31256 | 3.80E-17 |
| Dev+Herb | 4 | 75.66691 | 3.18E-17 |
| Dev+Water+Sex | 5 | 76.22128 | 2.41E-17 |
| Can+Herb | 4 | 76.35877 | 2.25E-17 |
| Dev+Water | 4 | 76.49218 | 2.11E-17 |
| Can+Herb+Sex | 5 | 77.57923 | 1.22E-17 |
| Dev+Herb+Sex | 5 | 77.70785 | 1.15E-17 |
| Herb | 3 | 84.05573 | 4.80E-19 |
| Herb+Sex | 4 | 86.19665 | 1.64E-19 |
| Can+Dev | 4 | 90.62305 | 1.80E-20 |
| Can+Dev+Sex | 5 | 92.80424 | 6.04E-21 |
| Can | 3 | 97.04842 | 7.24E-22 |
| Dev | 3 | 97.94694 | 4.62E-22 |
| Can+Sex | 4 | 99.14029 | 2.54E-22 |
| Dev+Sex | 4 | 99.52886 | 2.09E-22 |
| Sex | 3 | 106.9305 | 5.17E-24 |

Table S1.4: Full list of models analyzed for Bald Eagle core-use areas (50% UD) showing covariates used in each model, the number of parameters (K), $\Delta AICc$, and model weight. All models included an intercept as well as eagle ID as a random effect. See Table 1 for description of each covariate. Can = canopy cover, Dev = human development index, Herb = herbaceous wetlands.

| Model | K | $\Delta AICc$ | Weight |
|-------------------------------------|---|---------------|----------|
| Can+Water+Season+Sex+Season*Sex | 7 | 0 | 0.382494 |
| Water+Season+Sex+Season*Sex | 6 | 0.88312 | 0.245956 |
| Can+Dev+Season+Sex+Season*Sex | 7 | 2.185232 | 0.128265 |
| Can+Dev+Water+Season+Sex+Season*Sex | 8 | 2.301247 | 0.121036 |
| Dev+Water+Season+Sex+Season*Sex | 7 | 3.314523 | 0.072926 |
| Dev+Season+Sex+Season*Sex | 6 | 4.803454 | 0.034639 |
| Can+Season+Sex+Season*Sex | 6 | 8.367158 | 0.005831 |
| Can+Water+Season+Sex | 6 | 10.60515 | 0.001904 |
| Season+Sex+Season*Sex | 5 | 11.18862 | 0.001422 |
| Can+Water+Season | 5 | 11.49182 | 0.001222 |
| Can+Dev+Season+Sex | 6 | 12.11347 | 0.000896 |
| Can+Dev+Season+Sex | 6 | 12.12422 | 0.000891 |
| Can+Dev+Water+Season+Sex | 7 | 12.81252 | 0.000632 |
| Water+Season+Sex | 5 | 13.43526 | 0.000463 |
| Can+Dev+Water+Season | 6 | 13.48667 | 0.000451 |
| Water+Season | 4 | 14.56258 | 0.000263 |
| Can+Season | 4 | 15.66611 | 0.000152 |
| Dev+Water+Season+Sex | 6 | 15.75385 | 0.000145 |
| Can+Season+Sex | 5 | 16.29889 | 0.000111 |
| Dev+Season+Sex | 5 | 16.47174 | 0.000101 |
| Dev+Season | 4 | 16.78812 | 8.65E-05 |
| Dev+Water | 4 | 16.8034 | 8.59E-05 |
| Season | 3 | 20.33275 | 1.47E-05 |
| Season+Sex | 4 | 20.53492 | 1.33E-05 |
| Can+Dev | 4 | 62.47803 | 1.04E-14 |
| Can+Dev+Sex | 5 | 63.20909 | 7.19E-15 |
| Can+Water | 4 | 63.57545 | 5.99E-15 |
| Can+Water+Sex | 5 | 63.72535 | 5.56E-15 |
| Can+Dev+Water | 5 | 64.41695 | 3.93E-15 |
| Can+Dev+Water+Sex | 6 | 64.90423 | 3.08E-15 |
| Water+Sex | 4 | 66.58464 | 1.33E-15 |
| Water | 3 | 66.7484 | 1.23E-15 |
| Dev | 3 | 66.77875 | 1.21E-15 |
| Dev+Sex | 4 | 67.13168 | 1.01E-15 |
| Can | 3 | 67.61771 | 7.94E-16 |
| Dev+Water | 4 | 68.10377 | 6.22E-16 |
| Dev+Water+Sex | 5 | 68.12244 | 6.17E-16 |

| | | | |
|-----|---|----------|----------|
| Can | 3 | 68.86181 | 4.26E-16 |
| Sex | 3 | 72.26098 | 7.79E-17 |

Table S2.1: The covariates (name, metric, and source) used to evaluate habitat selection in Bald Eagles along the Front Range of Colorado between 2020 and 2024. All covariates were continuous. CDOT = Colorado Department of Transportation.

| Variable | Metric | Source |
|-------------------------|-----------------|---|
| Human Development Index | Scale index 0-1 | Dave Theobald et al., 2020 |
| Herbaceous Wetlands | % cover | National Land Cover Database (NLCD) 2021 |
| Canopy Cover | % cover | National Land Cover Database (NLCD) 2021 |
| Agriculture | % cover | National Land Cover Database (NLCD) 2021 |
| Grassland | % cover | National Land Cover Database (NLCD) 2021 |
| Water | % cover | National Land Cover Database (NLCD) 2021, CDOT 2012 |

Table S2.2: The total number of home ranges and used telemetry locations for each nest stage for both scales (within home range and within study area). A ratio of five available locations for every one used location was used for Bald Eagles in Colorado’s northern Front Range between 2020 and 2024. A total of 70 home ranges and 467,058 points were used for males. A total of 65 home ranges and 615,030 points were used for females.

| Nest Stage | Total # of Home Ranges | Total # Used Points |
|-------------|------------------------|---------------------|
| Pre-nesting | 29 | 39292 |
| Incubation | 27 | 16680 |
| Nestling | 17 | 26454 |
| Post-fledge | 28 | 22094 |
| Non-nesting | 33 | 75828 |
| Total | 135 | 180348 |

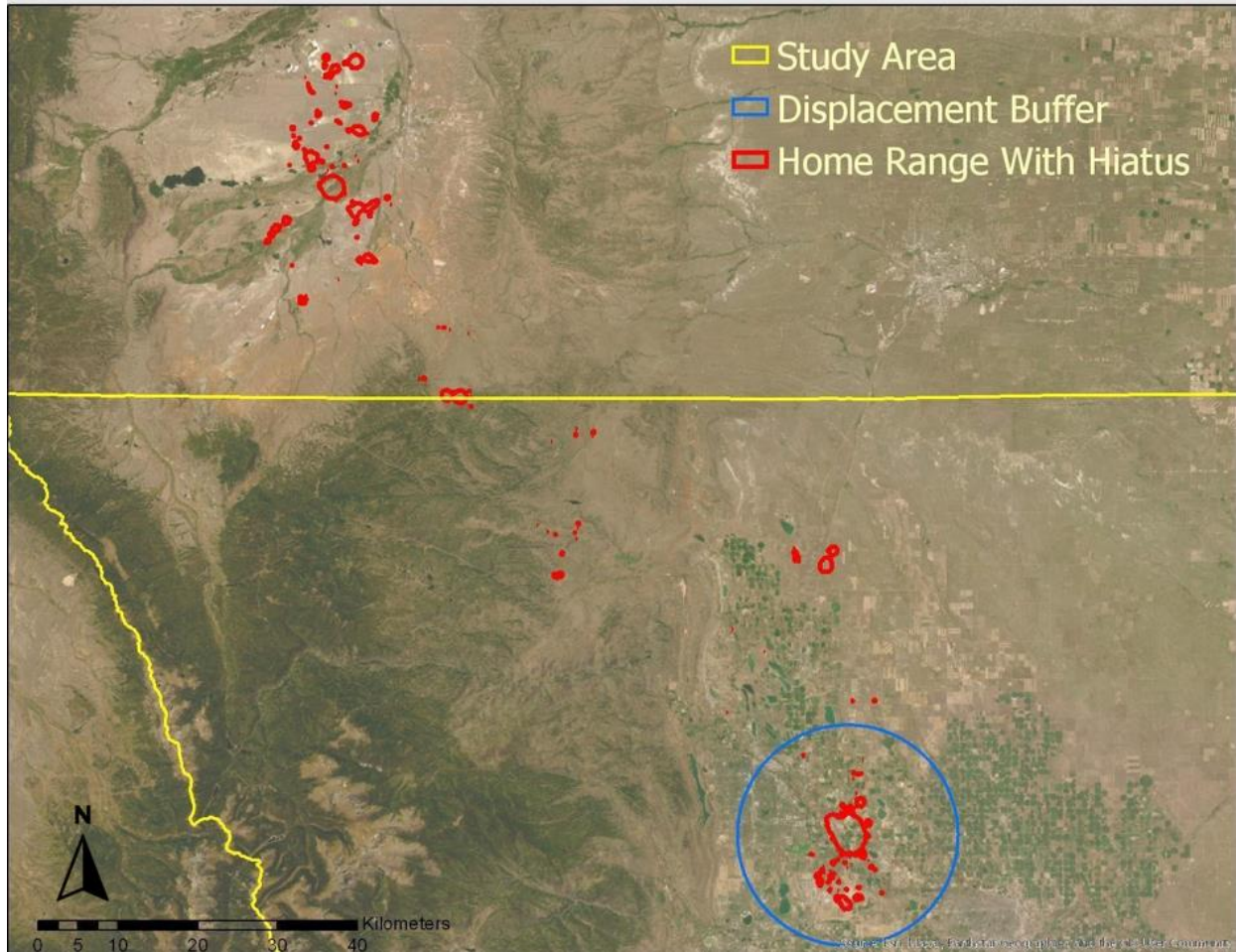


Figure S1.1: Example of the displacement function used to remove the hiatus period from the home range for one male Bald Eagle. The final home range included only the red outlined region inside the blue displacement buffer.

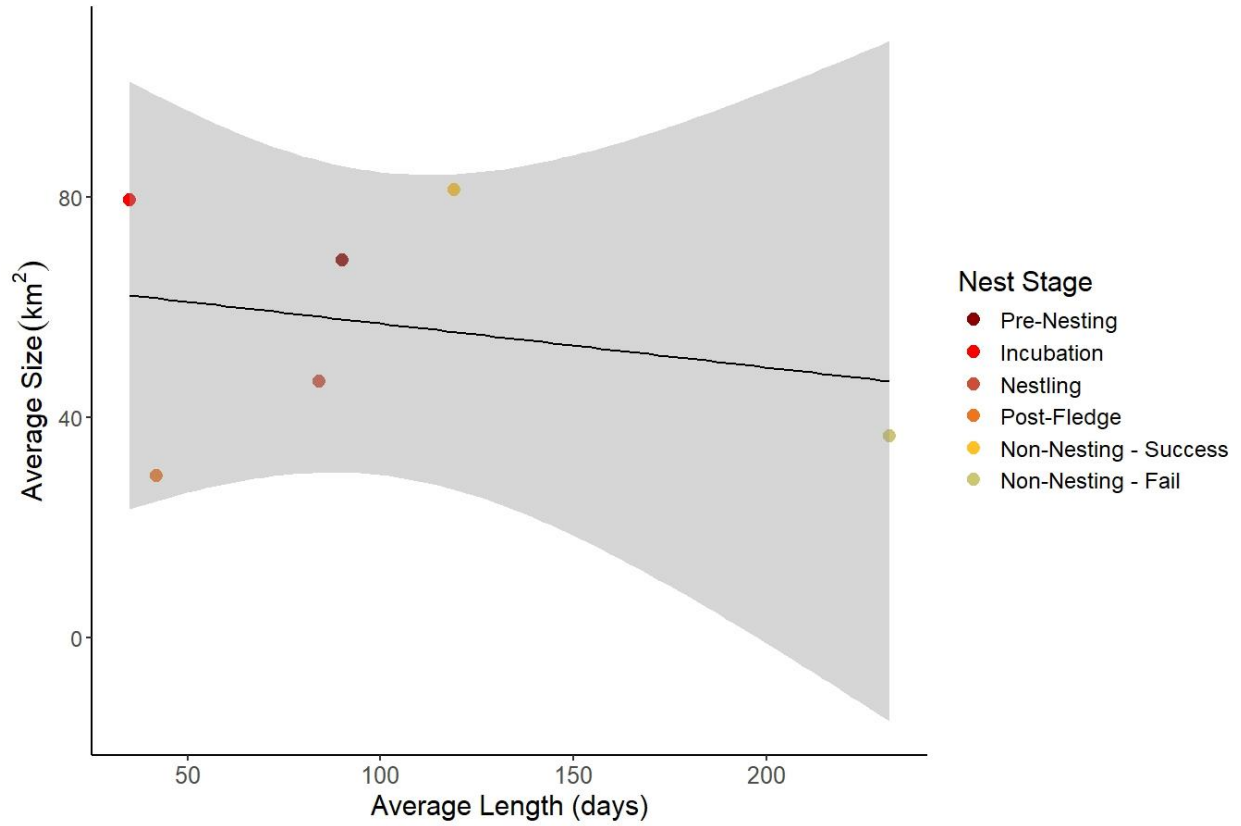


Figure S1.2: Average home range size (km²) plotted against average duration of the nesting stage (days). The non-nesting phase is categorized into failed and successful nests, with failed nests exhibiting a significantly longer duration. Standard error is represented in grey. No significant correlation was observed between nesting stage length and home range size.

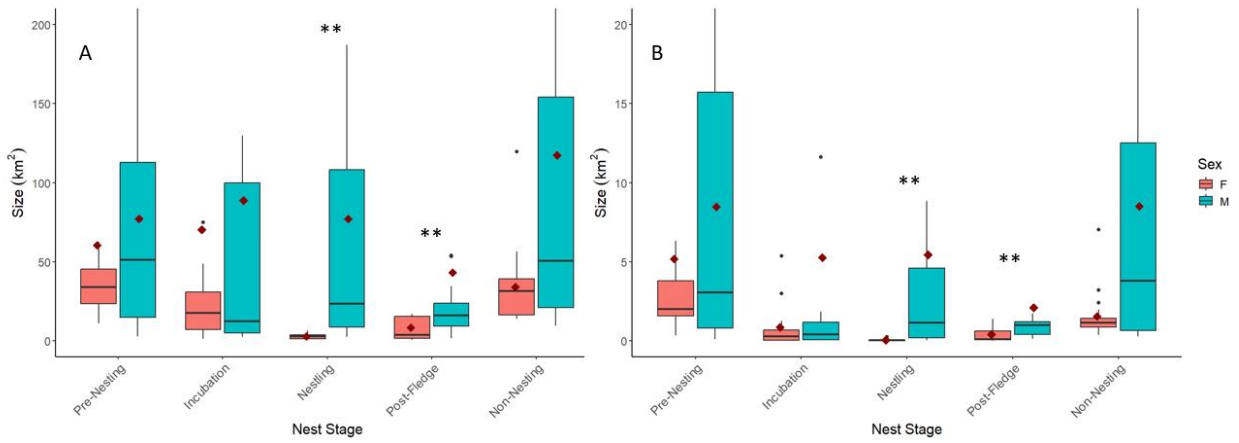


Figure S1.3: The difference in Bald Eagle home range size (A) and core-use area (B) between the sexes for each nest stage in northern Colorado during 2020 - 2024, showing the upper quartile, lower quartile, mean (red diamond), median (black line), and outliers (black dots). Asterisks (**) represent statistically significant differences ($p < 0.05$) between male and female home range sizes and core-use areas. Seven of the eleven outliers could not be visualized on these axes.



Figure S2.1: An adult Bald Eagle with a transmitter affixed to its back via a backpack harness. Photo credit M. Middleton.

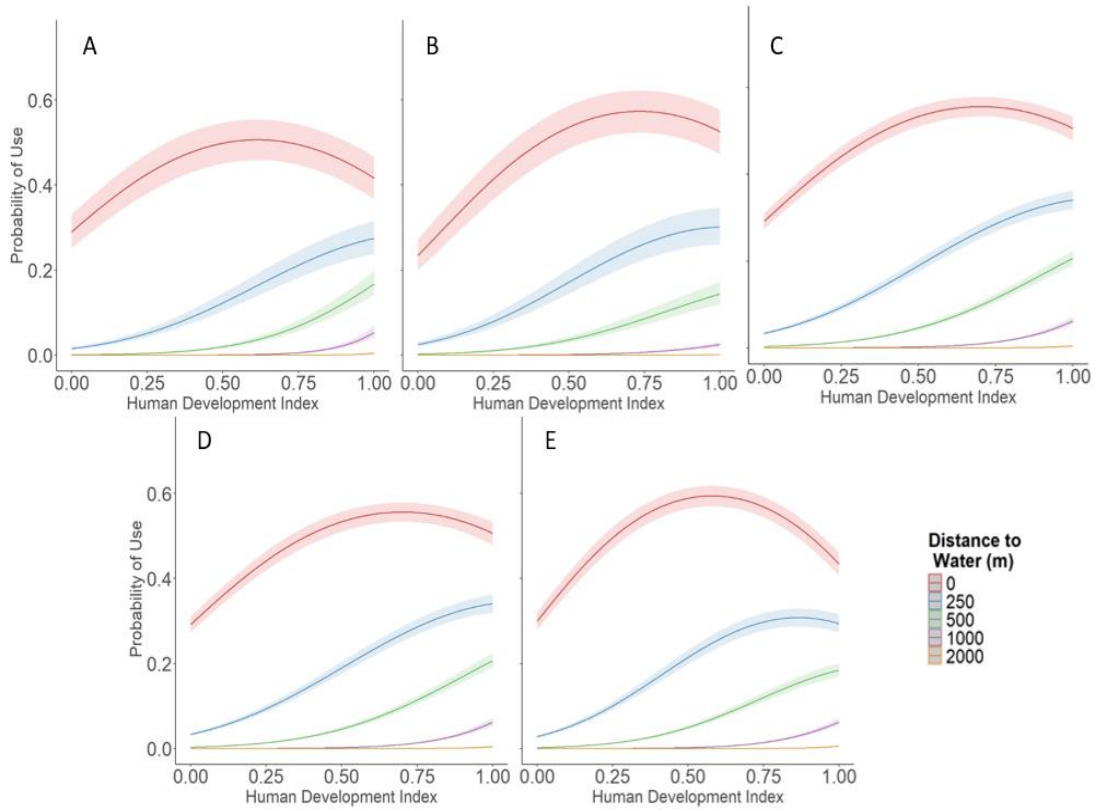


Figure S2.2: The relationship between development intensity (x-axis) and Bald Eagle (sexes combined) probability of use (y-axis) in northern Colorado (2020-2024) as a function of distances from water (different colored lines) for incubation (A), nestling (B), post-fledge (C), non-nesting (D), and pre-nesting (E) periods at the scale of the study area. Shaded areas denote 95% confidence intervals.