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NESTING BALD EAGLE POPULATION NUMBERS, DENSITY, TERRITORIAL RESOURCES, AND RELATIONSHIP TO HUMAN DEVELOPMENT IN NORTHERN COLORADO'S FRONT RANGE

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ABSTRACT: To better understand the population of the Bald Eagle (*Haliaeetus leucocephalus*) nesting along northern Colorado's Front Range, from 2016 to 2022 we studied 86 occupied nests within an area of 20,586 km^2. From 2017 to 2020, 279 juveniles fledged from 237 nesting attempts in a smaller, main nest-study area with 68 nests. The nests' success over these four years ranged from 52 to 70%, and their productivity varied from 1.1 to 1.3. The average nearest-nest distances for three discrete areas in the Front Range (5.03 to 7.26 km) are at least 2.8 to 4.0 times greater than these distances in four nesting populations in wetter regions but shorter than distances observed between nests in drier Arizona. In our study area the coverage of buildings within 400 m of Bald Eagle nests is relatively low by comparison to the coverage around randomly selected points, averaging 1344 m^2; for 63% of the nests this coverage was less than 800 m^2. We classified the 86 nest territories into eight categories that describe the dominant resource habitat and predicts the eagles' reliance on Black-tailed Prairie Dogs (*Cynomys ludovicianus*) versus fish as prey. Predation on fish was predicted to be dominant at 51% (n = 44) of the nests, predation on prairie dogs at 32% (n = 28).

Northern Colorado's Front Range urban corridor (commonly referred to as simply the Front Range) is experiencing some of the fastest human population growth in the U.S. (U.S. Census Bureau 2020), and state wildlife-management policies have changed to adapt to Bald Eagles nesting in urbanized settings (CPW 2020b). Eight of Colorado's 10 fastest growing counties are in the corridor, their growth rates from 2010 to 2020 ranging from 12.9 to 32.6% (U.S. Census Bureau 2020). Three of these counties still lack land-conservation or open-space programs (https://coloradoopenspace.org/about/), and habitat loss due to rapid human development could have a profound effect on nesting Bald Eagles.

One-third of Bald Eagle nests in south-coastal British Columbia are more urbanized and lie near residential or commercial developments (Elliot et al. 2006, Goulet et al. 2021). This population's resource-rich environment falls at the wet end of the climatic continuum. In contrast, the population nesting in Arizona represents the other extreme, as its dry ecological setting and low population density have been considered unique among Bald Eagle populations (Driscoll et al. 2006, Eakle et al. 2015, McCarty et al. 2020). Colorado's urban corridor is semiarid with weather patterns being strongly influenced by the Rocky Mountains immediately to the west (Hansen et al. 1978). The rapid development of the Front Range raises the question of how Colorado's Bald Eagle population compares with populations at each end of the rainfall extremes. Has it become more urbanized like that found in the wet climes of British Columbia? Or is it perhaps closer in character to that in drier Arizona?

Bald Eagles prefer fish as prey, even in arid to semiarid regions (Wright 1953, Stalmaster 1987, Gerrard and Bortolotti, 1988, DeLong 1990, Knight et al. 1990, Brown et al. 1991, Grubb 1995, Newsome et al. 2010), accounting for their propensity to nest near fish-containing bodies of water (Buehler 2000, Boal et al. 2009). This preference is evident in Colorado's Front Range, where about 60% of the nest territories encompass larger streams or water bodies. Although fish are a dietary preference, the Bald Eagle is an opportunistic and generalist predator whose short-term diet usually reflects the local abundance of most available prey (Buehler 2000, Thompson et al. 2005). In the Front Range, the Black-tailed Prairie Dog (*Cynomys ludovicianus*) is a valuable prey source. Its prevalence and importance as prey for the Bald Eagle vary from nest to nest. In addition to the Bald Eagle, many other raptors, including the Golden Eagle and Ferruginous Hawk (*Buteo regalis*), also depend on the Black-tailed Prairie Dog as prey, and the Burrowing Owl (*Athene cunicularia*) depends on its burrows for nesting (CPW 2020a).

In this study, we address the density, nest numbers, productivity, and success rates of the Bald Eagle population of the Front Range. We clarify the spatial relationship of nest sites with respect to human population density. We compare these aspects of the Bald Eagle's biology in this semiarid region to those in a more verdant region and in the desert Southwest. Finally, we seek to develop a baseline understanding of the Bald Eagle's resource use in a landscape of rapid human population growth and development.

METHODS

Study Area

Our study area encompasses 86 occupied nests divided into three areas of interest comprising a total area of 20,586 km^2 (Figure 1). The three study areas and their minimum bounding areas (polygonal areas around nests calculated by the convex-hull tool in ArcGIS) include (1) the main study area with 68 nests occupied during 2020, extending north from Denver to Fort Collins and from the foothills east about 60 km onto the plains (5095 km^2); (2) a subset of the main study area (the "midwestern field") containing 18 nests with a

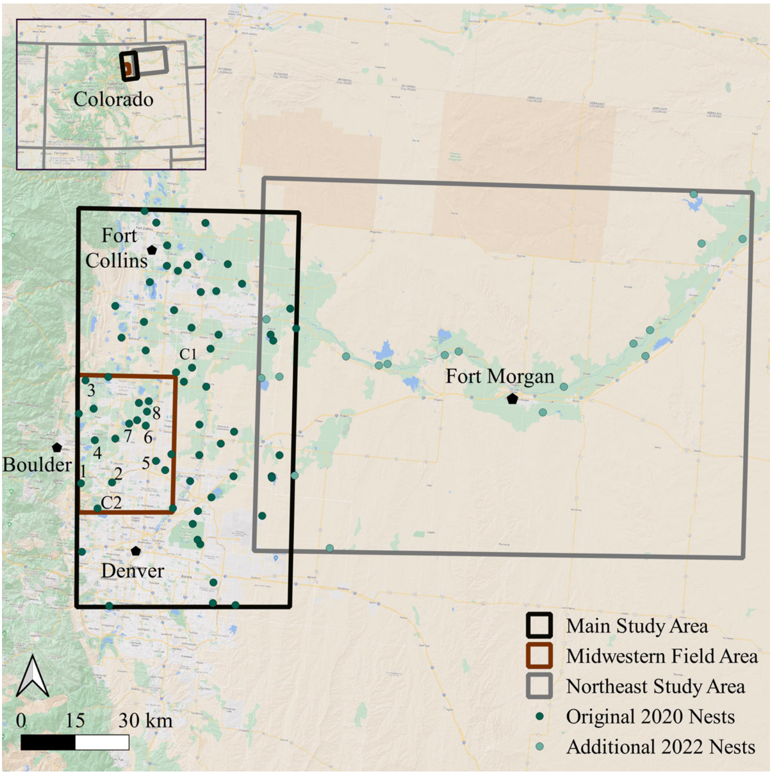


FIGURE 1. Three study areas showing (1) the main study area and its 68 occupied nest sites in 2020 (dark green points), (2) the midwestern field study area with its 8 intensively studied nests, and (3) the northeast study area with its 18 nest sites added in 2022 (light green points).

minimum bounding area of 689 km^2; and (3) the northeast study area, which includes a minimum bounding area of 6506 km^2 to the northeast and east of the main study area, added later in the study with 18 nests (Figure 1). Data from Colorado Parks and Wildlife (CPW) indicate that >120 occupied Bald Eagle nests are present in northeastern Colorado (R. Conrey pers. comm.), and many of them are located in our combined 20,586-km^2 study area.

There are >250 known occupied Bald Eagle nests in all of Colorado, most in the semiarid plains along major waterways in the Front Range (R. Conrey pers. comm.). With the steep decline in population from DDT (Grier 1982, Bowerman et al. 1995, Stinson et al. 2007), Bald Eagles were rarely noted in the Front Range from the early 1940s until the early 1980s (Henderson 1909, Boulder County Nature Association unpubl. report). The first documented nest representing recovery in our study area was established at Barr Lake in 1986 (CPW 2020b), followed by one at Standley Lake in 1993 (Colorado Bird Observatory 1993).

Average precipitation values for the main study area and the northeast study area are 414 and 404 mm, respectively, with a total combined average of 409 mm.

Mapping and Defining Nest Territories

We define a nest territory as essentially equivalent to a core-use area (Burt 1943, Kaufmann 1962, Ewer 1968, Samuel et al. 1985), comprising the nest, known perches, and a significant proportion of the pair's foraging habitat. A core-use area comprises over half the area an animal uses and may be much smaller than its entire home range (area of year-round or multi-year usage) (Samuel et al. 1985). Because a Bald Eagle's core-use area is commonly calculated on the basis of the wider home range—well beyond visual tracking—it is commonly based on telemetry. However, the equivalence of core-use areas for nesting eagles can be reliably determined by careful field studies that integrate locations of perches and defense against other eagles. We define a perch as any fixed location on which an eagle has been observed. Nest-territory size for eight nests in the midwestern field area averaged 3.7 km^2 and ranged from 2.4 to 4.8 km^2 (Table 1). Then we calculated the nest territory as the area encompassed by a line tightly fit around all mapped perches and within 2 km of the nest, near the maximum distance a territorial Bald Eagle defends against other Bald Eagles in our study area (Bove unpubl. data).

Nest Locations and Productivity

We obtained data on Bald Eagle nest locations and productivity in the main study area from 2017 to 2020 from the Bald Eagle Watch program of the Bird Conservancy of the Rockies. Nest observations typically began in January or early February and continued to nest failure or when young fledged. Visiting nest sites at least twice monthly, the program's trained volunteers verified the location, condition, and status of each nest. New nests located by volunteers, CPW staff, wildlife researchers, and the public were verified by Bird Conservancy of the Rockies staff and volunteers and assigned for observation by the Bald Eagle Watch coordinator. Volunteers entered data online, and the coordinator checked them periodically to verify

Table 1 Territory Sizes and Numbers of Perches Used by Eight Pairs of Bald Eagles Nesting in Colorado's Front Range

Nest	Map number[a]	Territory size (km^2)	Total perches (*N*)	Perches >2 km from nest (*N*)	Study hours
MALA	1	4.2	11	0	93
STEA	2	4.8	157	3	2013
LYON	3	2.9	144	2	912
WHRO	4	2.6	30	2	192
DACO	5	2.4	14	2	45
SULL2	6	4.8	99	13	1812
BOCR	7	3.3	66	9	1051
BCIC	8	4.3	97	3	1020
Mean ± SD		3.7 ± 0.97			

[a]See Figure 1.

that data-entry guidelines were followed and to detect errors. The program's senior coordinator independently inspected each nest before monitoring and intermittently through the nesting season to ensure that volunteers' data were consistent and representative. Data were downloaded at the end of each nesting season and edited to remove errors, duplicates, omissions, and inconsistencies, prior to analysis.

The Bald Eagle Watch program considers a nest to be "successful" if at least one young has fledged or survived to at least eight weeks of age (Steenhof and Newton 2007). An "occupied" nest is defined as one that a Bald Eagle pair used during a given year. A "nesting attempt" is an observation of a bird in an incubating position at an occupied nest, or a nest with eggs or young. We calculated mean apparent nest success by dividing the number of successful nests by the total number of occupied nests in which nesting was attempted. We calculated the productivity of nesting attempts by dividing the number of fledglings by the total number of nesting attempts.

Definitions related to nest activity and productivity used in some other studies differ slightly, affecting comparisons. Researchers in Louisiana (Smith 2014, Seymour 2018), Chesapeake Bay (B. Watts pers. comm.), and northern Colorado and southeastern Wyoming (Kralovec et al. 1992) also followed the convention Bald Eagle Watch used in determining nest success.

Field Methods

In addition to the productivity monitoring by the Bald Eagle Watch program, staff and volunteers with Front Range Nesting Bald Eagle Studies observed other activities. During each timed session, typically 90 minutes to two hours long, they recorded data at 3-minute intervals on up to six Bald Eagles. Data recorded include perch location, behavior, flight type (hunting, soaring, perch change, flight distance relative to territorial boundary, or high-speed gliding), flight direction, interactions with other species, and the type and distance to nest of any prey acquired. We transferred field data to a standardized digital datasheet and reviewed it for quality control.

Nearest-Nest Distances

For all occupied nests in the three study areas we measured the distance to the next nearest nest by using QGIS 3.24 (www.qgis.org). We compared our results to those from five other areas: (1) 24,185 km^2 of riverine habitat in central Arizona with 48 occupied nests (Arizona Game and Fish Department unpubl. data), (2) 3745 km^2 in southern Louisiana with 195 occupied nests in 2017/2018 (Seymour 2018, M.A. Seymour pers. comm.), (3) 80 km^2 along the lower Susquehanna River in Chesapeake Bay with 34 occupied nests (Watts and Paxton 2019), (4) 700 km^2 in central Florida south of Kissimmee with 112 occupied nests in 2021 (https://cbop.audubon.org/conservation/about-eaglewatch-program), and (5) 4800 km^2 in the Upper Mississippi River National Wildlife and Fish Refuge with 53 active nests (Mundahl et al. 2013).

We calculated average precipitation for the main and northeast study areas from the Global Summary of the Year dataset by NOAA (Lawrimore et al. 2016). Specific stations used for each of the study areas can be found in Appendix 1 at www.westernfieldornithologists.org/bove_et_al_Bald_Eagle_appendices.pdf.

Data Analysis

Our analysis of resource selection in the main study area was based on GIS files containing all 68 locations of nests attempted in 2020 and coverage of buildings in our entire study area in 2021 (https://www.ecopiatech.com). We considered this file with coverage of each building to be the best and most recent proxy for human development in the study area. With this, we calculated the total area occupied by buildings within 0.25 km around each nest within the main study area. We then compared the results to the coverage of buildings within 0.25 km of 1000 randomly generated points also within the main study area, provided that the coverage of buildings within a 30-m square including the point did not exceed 25%.

Prey and Resource Habitat Analysis

Two types of prey dominate the diet of territorial Bald Eagles in our study area—fish and prairie dogs. Therefore we defined four resource habitats—quarry ponds, water bodies, rivers, and prairie dog colonies—and mapped them within each of the 86 nest territories. For this analysis, we defined the area of each nest territory as 4.5 km^2, which is near the maximum size of eight well-studied territories in the midwestern field area (Table 1). Because the Bald Eagles nesting in these territories spend a high proportion of their time in them year round, and acquire ample prey within these territories, we infer that 4.5 km^2 is a reasonable approximation of the area sustaining a territorial eagle in this region. At five nests studied intensively during the period of post-fledging dependence, the proportion of prey taken within 0.8 km of the nest (i.e., within 2.0 km^2) averaged 34.4% and ranged from 18.1 to 53.1% (Table 2). This radius is thus well within the 1.2-km radius corresponding to an area of 4.5 km^2.

Table 2 Prey Brought to Seven Bald Eagle Nests in Colorado's Front Range

	Nest						
	BOCR (7)	BCIC (8)	SULL2 (6)	LYON (3)	STEA (2)	STAND2 (C2)	WILD (C1)
Years monitored	2019–2021	2019–2022	2019–2021	2018–2022	2016–2022	2020–2021	2021–2022
Hours monitored	747	612	775	506	1702	52	68
Number of prey items	58	68	133	95	150	54	85
Undetermined (%)	39.7	35.3	54.1	23.2	33.3	17.5	6
Prairie dog (%)	10.3	11.8	28.6	45.3	35.3	27.8	33.5
Undifferentiated mammal (%)	12.1	16.2	8.3	11.6	16.7	5.6	4.7
Rabbit (%)	1.7	1.5	3	1.1	2.7	11.1	5.9
Rodent (%)	0	0	0	2.1	1.3	0	0
Squirrel (%)	0	0	0	0	0	0	0
Fish (%)	34.5	32.4	4.5	15.8	9.3	24.1	47.6
Reptile (%)	1.7	0	0.8	0	0	0	1.2
Bird (%)	0	2.9	0.8	1.1	1.4	14	1.2
Source of prey <800m of nest (%)	34.5	30.9	18.1	53.1	35.3	ND [a]	ND [a]

[a]Not determined; prey brought to nest recorded by nest camera.

We obtained digital maps of quarry ponds and gravel pits from the Colorado Division of Water Resources (https://maps.dnrgis.state.co.us/dwr/Index.html?viewer=mapviewer). This source did not include some quarry ponds evident in 2021 and 2022 Google Earth imagery so we hand-digitized them and merged the results into a single coverage. Many of the mapped quarry ponds originated from gravel mining beginning during the 1950s and 1960s (Wilburn and Langer 2000). Subsequent to mining, the pits filled with groundwater, and many now host an abundance of fish. Water bodies include lakes, ponds, and reservoirs other than ponds left over from gravel mining. We obtained digital maps of water bodies and streams from the U.S. Geological Survey's National Hydrography Dataset (https://apps.nationalmap.gov/downloader/), again hand-digitizing from 2021 and 2022 Google Earth satellite images water features missing in that source. We included in our analysis all water bodies of >0.02 km^2.

To evaluate fishing habitat for Bald Eagles, we categorized each stream by five types based loosely on stream order, discharge (https://dwr.state.co.us/Tools/Stations?Stations=All), sinuosity (rated as per Horacio 2014), and the abundance of associated quarry ponds. Stream types 3–5 are defined as "rivers" in our study and have the greatest potential to provide fishing for Bald Eagles. Sinuosity is correlated with the number of deeper pools at stream bends that fish tend to prefer (Sullivan et al. 1987). We categorized lakes and reservoirs as fed principally by canals or ditches or as supplied at least in part by creeks.

Prairie dog colonies within the 86 nest territories were hand digitized in 2021 and 2022 by means of Google Earth satellite imagery. We outlined the colonies by following the outer boundary of all the burrows, regardless of the prairie dogs' activity or inactivity. We validated the mapping by field-checking 16 of the 237 apparent colonies that were easily surveyed from nearby roads. Out of the 153 hectares of field-verified colony sites, only 14 hectares or 9% were false positives in which the satellite imagery closely resembled a prairie dog town but was an area with ant hills or similar features. Colonies were active, with prairie dogs observed, in the remaining 91% of the area that was field verified.

We were able to quantify the prey taken at only seven nests (Table 2), so were unable to devise a statistically significant model relating extent of the four foraging habitats to the quantity of prey actually taken. Still, we reasoned that a multiple linear regression should associate this extent with the relative abundance of these two main prey types in each nest territory. Therefore, to provide a basis for categorizing the territories by likely predominant prey, we used the ratio of recorded prairie dog prey to fish prey as the dependent variable in a linear model for all 86 nests based upon the percentage of their territory covered by prairie dog colonies, quarry ponds, rivers, and water bodies. The results ($R^2 = 0.55$, df = 2, $F = 0.627$, $p = 0.69$) indicate that the data did not have the best fit, as expected with a small sample size, but a reasonable amount of the prey ratio variability could still be explained with our habitat variables. Regression plots of the independent variables are displayed in Figure 2.

Using the results of this analysis, we categorized each nest territory on the basis of the predicted relative use of prairie dogs versus fish as prey for each

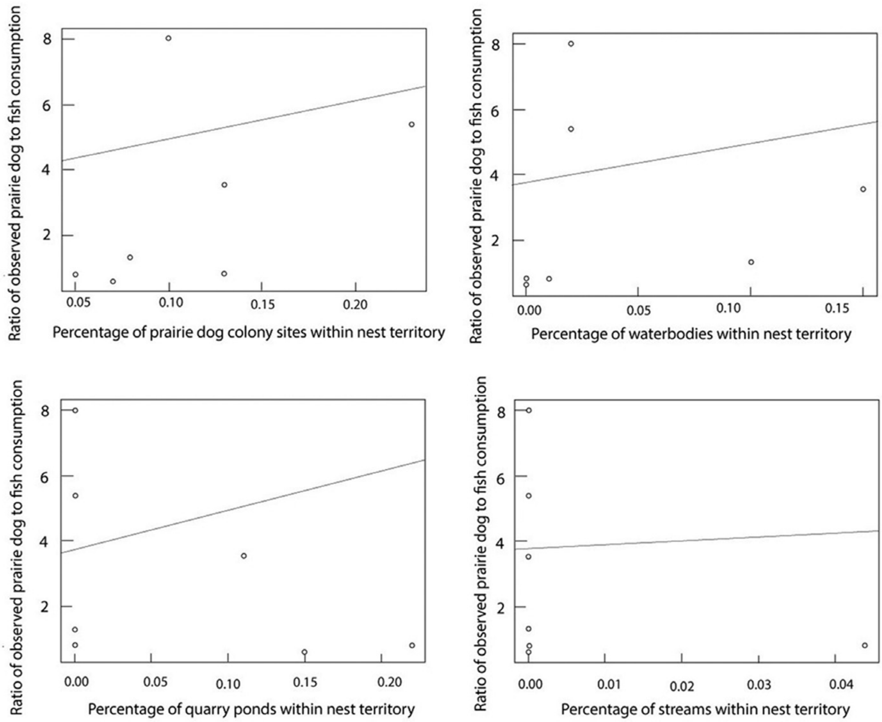


FIGURE 2. Plots of the observed ratio of prairie dog to fish consumption by the percentage of four source habitats within the seven territories where prey consumption was quantified. Lines represent results of multiple linear regression. Evaluation of the model's normality by the Shapiro–Wilk test yielded $p = 0.95$, implying the data are distributed normally. Evaluation of homoscedasticity by the Breuch–Pagan test yielded $p = 0.1971$, so we cannot reject the hypothesis of homoscedasticity. Evaluation of independence of errors by the Durbin–Watson test yielded a value of 1.35, indicating a level of positive correlation, but not a particularly strong one. Evaluation of multicollinearity with a correlation matrix yielded acceptable results with the strongest value of correlation of –0.56.

nest according to the percent of the territory covered by the four foraging habitats. Since our regression was not meant to be a true predictive model, we reasoned that the model should still be sufficient to classify each nest according to its dominant prey resources. We classified territories as "prairie dog" if the weight of this input variable was >1.5× the combined weights of the water resources in the model. Similarly, we classified territories as "fish" if the converse was true. The y-intercept ($b = 3.76$) of this model was artificially high because of its small sample size, skewing some nests' results toward prairie dog predation where this may not have been an accurate classification. For this reason, we classified some nests as "resource-limited" if the absolute value of the weights of the four variables in the model added up to less than

15% of the absolute value of the weights plus the *y*-intercept. Any remaining nests that did not fit these criteria were categorized as "mixed," an imprecise classification for which predicted prairie dog predation still outweighed fish by a ratio between 2 and 5. Of these territories, those with a dominant source of fish were classified as "mixed/water body" or "mixed/quarry pond," depending on the main source of fish. Territories where the dominant fish source could not be distinguished we classified simply as "mixed."

RESULTS

Nest Productivity

From 2017 to 2020 Bald Eagles attempted nesting at 237 nests in our study area. The annual apparent nest success ranged from 52 to 70%, averaging 62% (Table 3). We observed 279 juveniles that either fledged or remained in the nest for at least 8 weeks. The productivity rate varied from 1.1 to 1.3 per nest per year, averaging 1.1. Twenty-eight percent of successful nests produced one young, 53% produced two, and the remaining 19% produced three young (Table 3).

Table 3 Nest Productivity and Success Rates for 68 Bald Eagle Nests in Northern Colorado's Front Range Compared to Those Elsewhere

Location and year	Average annual precipitation (mm)	Nest attempts (*n*)	Success rate (%)	Productivity ratio	Source
Colorado (2017–2020)	404	237	62	1.1	This study
2017		40	70	1.3	
2018		58	52	1.1	
2019		71	62	1.2	
2020		68	65	1.2	
Arizona (2017–2020)	345	253	55		McCarty et al. (2020)
2017		60	51	0.9	
2018		63	64	1.0	
2019		67	55	0.9	
2020		63	51	0.8	
Northern Colorado/ Wyoming	366				
1981–1989		78	63	1.2	Kralovec et al. (1992)
Louisiana	1527				
2005–2008		1261			Smith (2014)
2018		264	95	1.3	Seymour (2018)
British Columbia	1158				
2004–2009		648			Goulet et al. (2021)
Chesapeake Bay	1130				
2018		34	86	1.6	Watts and Paxton (2019)
Upper Mississippi	828				
2009		53	62	0.9	Mundahl et al. (2013)
Iowa	864				
2021		264	74	1.0	Shepherd (2021)

Nearest-Nest Distance

In 2020, the average distance to the next nearest nest of the 68 active nests in the main study area was 5.32 ± 2.89 km with a median of 4.97 km (Figure 3). In the midwestern field area this distance averaged 5.02 ± 2.05 km with a median of 4.65 km. In the northeast study area it averaged 7.26 ± 4.54 km with a median of 5.89 km (Figure 3). Figure 3 also compares the nearest-nest distances of 86 occupied nests in our semiarid study to those in four more verdant areas and to nests in Arizona's desert. In the areas with higher precipitation, these distances ranged from 1.17 to 1.81 km, whereas in Arizona it was 7.86 km.

Resource-Selection Analysis

Within our main study area, the mean coverage of buildings within a 400-m (0.25 mile) radius of the nest was 1344 ± 2424 m^2, whereas the mean

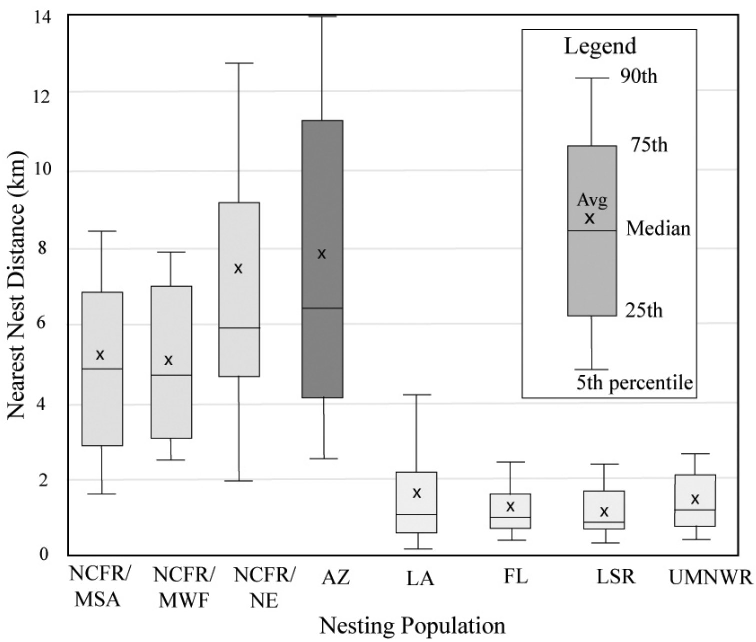


Figure 3. Distances to next nearest nest for 86 Bald Eagle nests in three subsets of our Colorado study area (NCFR/MSA, main study area, $n = 68$; NCFR/MWF, midwestern field, $n = 18$; NCFR/NE, northeastern area, $n = 25$; see Figure 1) in comparison to that in semiarid Arizona (AZ) in 2020 ($n = 48$, Arizona Game and Fish Department unpubl. data), and in four more verdant areas of the United States (LA, southern Louisiana, 2017–2018, Seymour 2018, M.A. Seymour pers. comm.; FL, central Florida, 2021, n =112, https://cbop.audubon.org/conservation/about-eaglewatch-program; LSR, lower Susquehanna River in Chesapeake Bay, Maryland, 2018, $n = 34$, Watts and Paxton 2019; UMNWR, Upper Mississippi River National Wildlife and Fish Refuge, Minnesota/Wisconsin/Illinois/Iowa, 2013, $n = 53$, Mundahl et al. 2013).

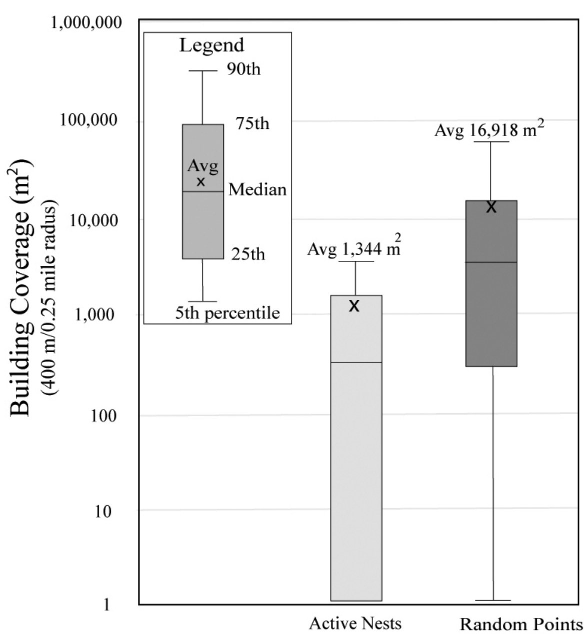
coverage of buildings around the 1000 randomly generated points was nearly 13 times greater, 16,918 ± 29,905 m^2 (Figure 4). Of the 68 occupied nests, 63% had building coverages within 400 m of less than 800 m^2, which approximates the combined area of three to four medium-sized residential homes (Figure 5). Around only 12% of the occupied nests did the coverage of buildings within 400 m exceed 1 standard deviation of the mean or 3767 m^2 (Figure 6).

Prey Resource and Habitat Analysis

Four Principal Resources and Habitats. Quarry ponds were present in 23% of the 86 nest territories (n = 20) and are located along Type 2 through 5 streams (Figure 8), primarily at distances less than 35 to 50 km from the mountain front. The average areal proportion of quarry ponds within the nest territories was 2.6 ± 6.2% (Appendix 2 at www.westernfieldornithologists.org/bove_et_al_Bald_Eagle_appendices).

Water bodies ranged in size from 0.02 to 7 km^2, and the total proportion of water bodies within the 86 nest territories averaged 7.2% with a median of 0.7 ± 12.5% (Appendix 2). Of the 86 territories, 41 consisted of >1% water.

Of the 86 territories, 25% (n = 22) are bisected by rivers (streams of types 3, 4, or 5). Since the widths of these rivers are so similar, and each passes near the center of each territory, we assigned a uniform areal proportion of 4.4%



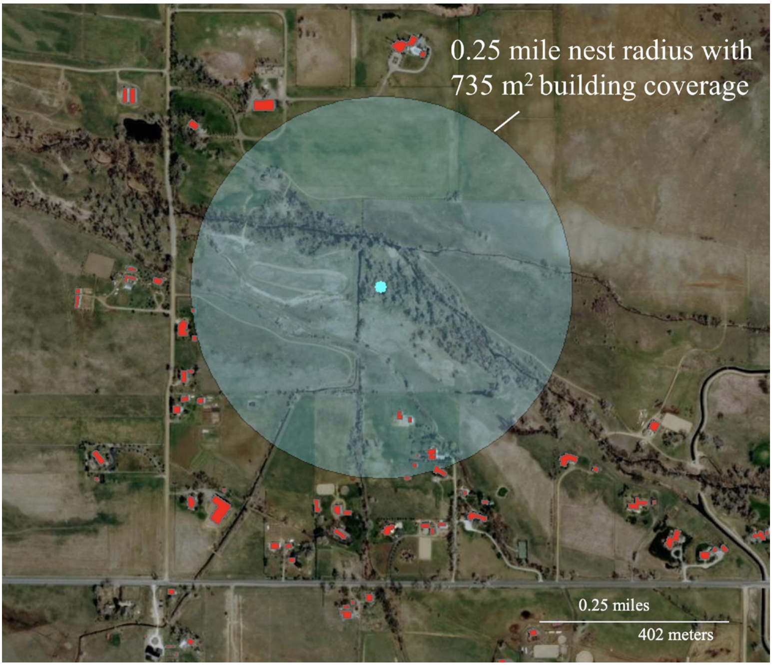


FIGURE 5. Example showing a coverage of buildings measured at 735 m^2 within the 400-m (0.25 mile) buffer around an actual Bald Eagle nest. Red polygons outline buildings from which the coverage was calculated.

to all 22 territories bisected by rivers. The mean areal proportion of rivers within the 86 territories was 1.1% (Appendix 2).

Within these 86 territories, coverage of prairie dog colonies averaged 6.6 ± 11.1% with a median of 3.2%. Coverage of prairie dog colonies exceeded 1% in 65% of the territories (n = 56) (Appendix 2).

Five Stream Types and Water Bodies in Relation to Fish Predation. Bald Eagles were observed fishing along streams of types 3, 4, and 5 but not along those of types 1 and 2. Of the 86 territories defined as 4.5 km^2, 26 contained only small streams of types 1 or 2, and 33 contained no stream even as large as Type 1. Streams of types 3 or 4 passed through two and four of the territories, respectively. The South Platte River—Type 5—passes through 17 of the 86 territories (Figure 7). Quarry ponds were absent in 13 of the 17 nest territories along the South Platte River where it extends beyond ~35 to 50 km east of the mountain front (Figure 7). The soil's gravel content and therefore quarry ponds diminish markedly beyond a prominent transition from gravel to sand-dominated alluvium about 47 km from the mountain front along the South Platte River, referred to as "the Delta" in Figure 7 (Cappa et al. 2000). Quarry ponds are absent farther east.

Lakes and reservoirs fed by canals or ditches were present within 22% of the 86 nest territories (n = 19). The extent of these water bodies aver-

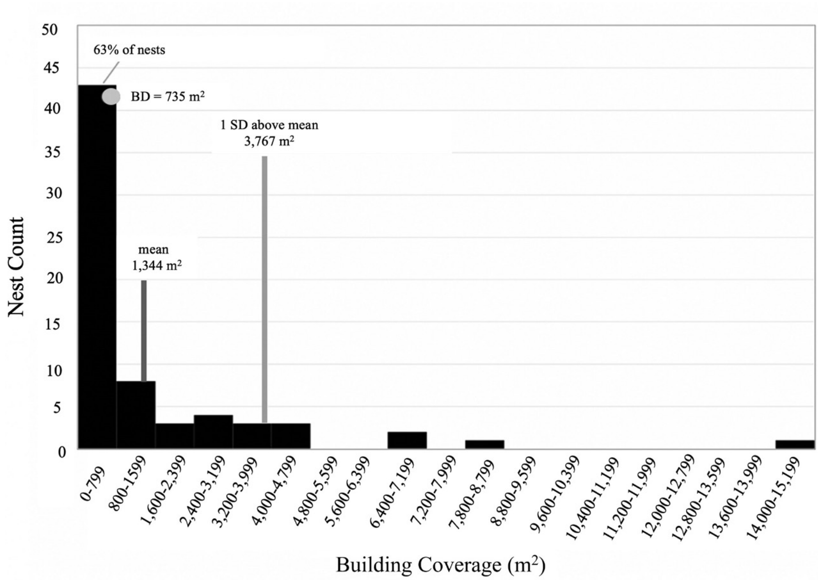


FIGURE 6. Numbers of Bald Eagle nests in the main study area by coverage of buildings within 400 m (0.25 mile) of the nests in the main study area.

aged 2.56 ± 2.01 km^2 and ranged from 0.15 to 6.98 km^2. None of these 19 territories was located along a clearly defined stream of types 1 through 5. In contrast, only 8% of the 86 nests (*n* = 7) contain lakes and reservoirs and also lie within Type 1 stream drainages. Water bodies within these seven territories averaged 2.52 ± 4.0 km^2 and ranged in size from 0.06 to 10.72 km^2. All water bodies mapped for the resource analysis provided potential fishing for nesting Bald Eagles (Appendix 3 at www.westernfieldornithologists.org/bove_et_al_Bald_Eagle_appendices).

Nest Territories and Relation to Prey Resources. Prey brought to the seven nests where it was studied varied with local habitat (Table 2). At the two of these nests located near quarry ponds—with 15 to 22% quarry ponds in the territories—fish represented a larger percentage of the prey (32–35%) (Table 2). By contrast, in the two territories with the lowest water-body coverage (2%), the prey comprised 40–56% mammals and only 5–9% fish (Table 2). Prairie dogs were the dominant mammalian prey, constituting at least 10–45% and an average of 27.5 ± 12.6% of the prey brought to each nest (Table 2).

Classification of 86 Nest Territories by Linear Regression Analysis

On the basis of the linear model, prey consumption at 12% (*n* = 10) of the 86 nest territories was dominated by prairie dogs (Figure 8, Appendix 2). At these nests, the mean predicted ratio of prairie dogs to all fish provided at these nests was 7.18 (Figure 9, Appendix 2). The coverage of prairie dog colonies in these 10 nest territories averaged 29.5 ± 19.4% with a median of 20%.

Prey consumption at 51% of the 86 nest territories (*n* = 44) was dominated by fish. These may be categorized further by the habitat likely supplying the

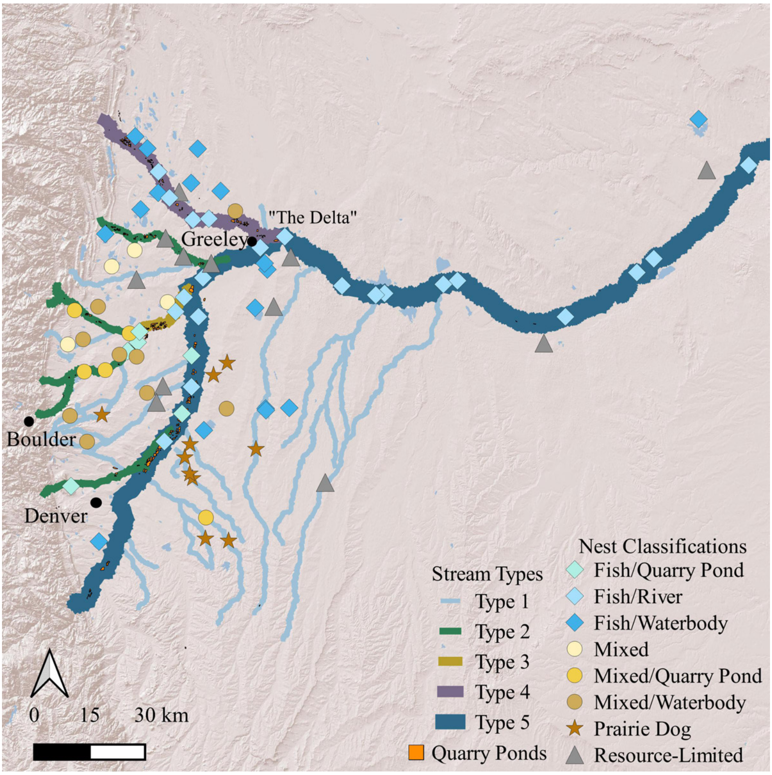


FIGURE 7. Categorization of streams in the study area and of Bald Eagle nests according to a linear regression based on the principal habitat for prey in the territory.

fish: quarry pond (*n* = 6), river (*n* = 21), or other water body (*n* = 17; Figure 8, Appendix 2). The mean predicted ratio of prairie dogs to fish provided at these nests was 0.17 (Figure 9). Water bodies covered an average of 29.5% of the 17 territories classified as "fish/water body." Quarry ponds covered an average of 19.5% of the six territories classified as "fish/quarry." Four of these six territories contained prairie dog colonies whose coverage of the eagle territory ranged from 4 to 8%. Thirteen of the territories classified as "fish/river" also had coverage of prairie dog colonies ranging from 2 to 15%.

At 21% of the 86 nests (*n* = 18) the predicted ratio of prairie dog to fish predation ranged from 2.3 to 5.0, and we categorized their prey use as mixed (Figure 9). Nine of the 18 "mixed" nests were classified as "mixed/water body," five were classified as "mixed/quarry pond," and four were classified simply as "mixed" (Figure 8, Appendix 2). Coverage of prairie dog colonies averaged 2.9% in these territories and varied from 1.5 to 13.4%.

In the remaining 16% of the nest territories (*n* = 14), the four resource variables were responsible for just 7% of the linear model's predicted prairie-dog-to-fish ratio, so we classified these territories as "resource-limited"

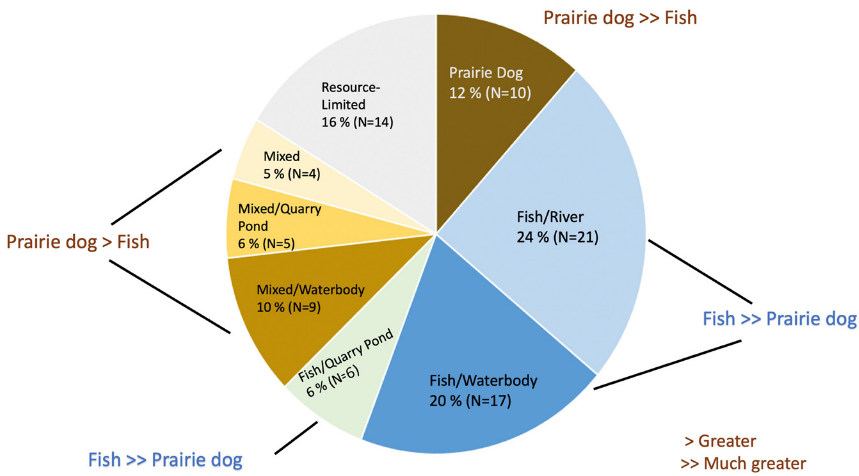


FIGURE 8. Numbers and percentages of 86 Bald Eagle nest territories in northern Colorado's Front Range by the eight categories defined by a linear regression model associating predominant prey and source habitats. The categories are grouped by the predicted relationship between the two predominant types of prey, fish and prairie dogs.

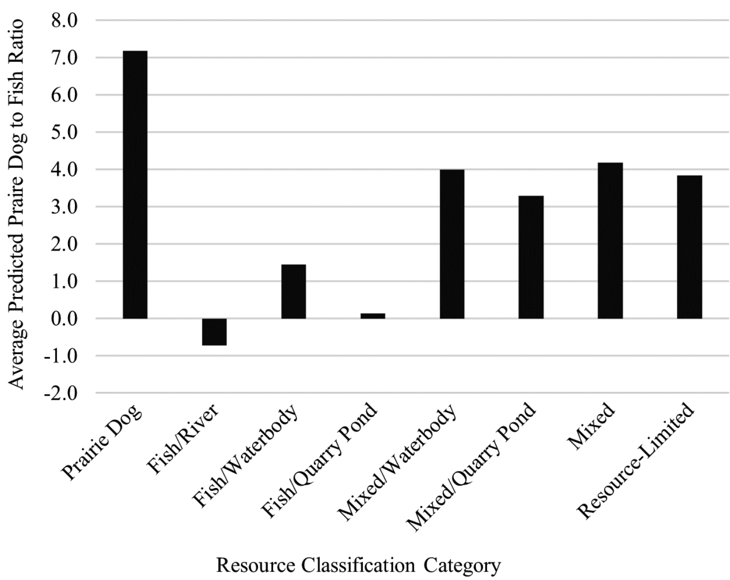


FIGURE 9. Average ratios of prairie dogs to fish taken in eight categories of Bald Eagle territories according to a linear regression model associating predominant prey and source habitats.

(Figure 8, Appendix 2). Quarry ponds and rivers were absent in these 14 territories (Appendix 2), and their coverage of water bodies averaged only 1.1 ± 1.4% with a median of 0.7%. These territories' coverage of prairie dog colonies averaged 1.5 ± 0.2% with a median of 0.1%.

DISCUSSION

Nest Productivity

Nest productivity in our main Colorado study area was similar to that in several wetter regions of North America, as well as to productivity reported from previous studies in northern Colorado and Wyoming (Table 3). However, the average success rate in the main study area was notably lower than in these wetter regions, including British Columbia, Iowa, Chesapeake Bay, and Louisiana, where success rates ranged from 68 to 95% (Table 3). Success rates in our main study area were more similar to the rates found in Arizona and northern Colorado and Wyoming from 1981 to 1989, where average annual precipitation was closer to that in our Colorado study area (Table 3).

Heavy snowfall is common in the main study area with totals averaging 35 cm monthly from February through March (https://psl.noaa.gov/boulder/bouldersnow.html). Fragile old-growth plains cottonwoods (*Populus deltoides monilifera*) are the Bald Eagle's primary nest substrate in our study area, and while the massive nests and nestlings are vulnerable to heavy late spring snows, they are perhaps even more vulnerable to the punishing windstorms. Lying on the lee side of the Rocky Mountains, the study area is subject to frequent windstorms sweeping downslope (Mercer et al. 2008). From the Boulder foothills east 20 km (https://psl.noaa.gov/boulder/wind.html), wind gusts during 332 storms over 51 years averaged 130 km/hr and ranged from 72 to 241 km/hr. Notably, 27% of these storms occurred from mid-February to the end of June, when Bald Eagle nests contain eggs or nestlings. During 2018, severe windstorms in late March and April resulted in the failure of five of 18 nests in the smaller 1000-km^2 midwestern field area. Four of these five failures resulted from the downing of the entire nest tree or collapse of the nest. Along the foothills of northern Colorado and in southeastern Wyoming, Kralovec et al. (1992) also noted that the most important factor causing failure of Bald Eagle nests was destruction of nest trees by heavy winds; a minimum of 11 nests with at least 10 eggs or young were lost between 1983 and 1989.

In Arizona, factors contributing to nest failures include heavy spring winds blowing nests or entire nest trees down, major floods during early spring, excessive heat later in the nesting season, and early May snowstorms at higher elevations (K. Jacobson pers. comm.). The higher nest-success rates in the regions with higher precipitation and less severe winters could be due to weather more equable than in eastern Colorado and Arizona. Also, raptors may be less likely to forage during inclement weather, which could affect both the female's body condition prior to egg laying or provisioning of nestlings, ultimately leading to lower success rates (Sergio 2003). Steidl et al. (1997) concluded that a decrease in reproductive success after severe winters may be associated with diminished availability of prey. For example, from December 2022 through February 2023 mean temperatures in the midwestern field area were the coldest over the past century, and monthly snowfall averaged 30 cm (Stephen Jones pers. comm.). Still waters were mostly frozen through that period, restricting eagles' fishing, and prairie dogs spent less time above ground than in previous winters (Bove unpubl. data). Under such extreme winter conditions, males may have been unable to deliver enough prey to keep females on or around nests. Thus females might have been obliged to forage over distances greater than normal, expending more energy, which may have contributed to failure to lay or the loss of eggs. In 2023 five of seven of the most intensively studied nests in the midwestern field study area failed—in three nests no eggs were laid (Bove unpubl. data). These failures may have been due not to the direct effects of cold but to a reduction in prey.

It is also probable that more prey are available in areas that receive more precipitation annually. More prey and thus less competition for food likely result in greater provisioning of food for young, also contributing to greater success rates. This may also explain the trend toward higher success rates in regions more verdant than our study area.

Nearest-Nest Distance

The average distance to the next nearest nest in all three of our Colorado study areas is at least 2.8 to 4.0 times greater than in four other areas with significantly higher annual precipitation (Louisiana, central Florida, Chesapeake, and upper Mississippi). The distribution of nearest-nest distances in our northeast study area (mean 7.26 km) is similar to that among 48 nests in Arizona's arid setting (mean 7.86 km; Figure 3). The distributions of nearest-nest distances in our main (mean 5.32 km) and midwestern field (mean 5.02 km) study areas are also similar (Figure 1).

Studies of raptors have concluded that within suitable habitat, densities of breeding birds are naturally limited by either food or nest sites, owing to competition for these critical resources (Martin 1987, Ratcliffe 1993, Hunt 1998, Newton 1998, 2017, Watson 2010). Analyses of nearest-nest distances have revealed that densities are related to food supply or a specific prey source available in a nesting area (Newton 2017). Fish as well as suitable nest substrates are in shorter supply in our Colorado study area than in habitats in wetter climates. This likely explains the wider spacing of nests in Colorado and Arizona. In Colorado, and likely at higher elevations in Arizona, the availability of fish becomes even further restricted during the winter. Although Bald Eagles reportedly prefer fish (Wright 1953, Stalmaster 1987, Gerrard and Bortolotti 1988, DeLong 1990, Knight et al. 1990, Newsome et al. 2010), their diet commonly reflects available prey at the local habitat level (Buehler 2000, Thompson et al. 2005, Elliott et al. 2006). This foraging strategy enables the Bald Eagle to exploit a diversity of other prey including birds, mammals, and reptiles (McEwan and Hirth 1980, Hunt et al. 1992, Markham and Watts 2008). While fish may be limited in Colorado, especially in winter, territorial Bald Eagles in our study area can rely on mammals, particularly prairie dogs. Waterfowl can be a seasonally important prey source during the winter at larger lakes and reservoirs (e.g., Table 2).

Although analyses of nearest-nest distances reveal critical information regarding nest density and resource availability for nesting populations, the differences among our three study areas emphasize the importance of comparing data from similar habitats. For example, in our main study area streams of all types are widely distributed along the mountain front. The network of drainages, floodplains, and irrigation ditches in the main study area is associated with a supply of suitable nest trees, water bodies, and associated wetlands. In contrast, the northeast study area, away from the mountain front, has only widely spaced Type 1 streams and a single Type 5 river. As a result, potential nest trees are fewer, as are other water-related resource habitats in this overall drier area. Most nests in the drier and less vegetated northeast study area are in the riverine habitat along the South Platte River (Figure 7). Nearest-nest distances in the northeast study tend to be greater than in the main study area, and some nests are very widely scattered, as in the drier Arizona nesting habitat where most nests are also along larger rivers.

Resource-Selection Analysis

The resource-selection analysis demonstrated that the coverage of buildings within a 0.4-km radius of Bald Eagle nests in our study area is significantly lower than within the same radius of random points. Around only 12% of nests in our main study area did building densities exceed one standard deviation of the average. Eagles nesting in areas where buildings are so dense may represent to a reduced sensitivity to human disturbance. As we discuss below, these results may inform management around nests in more densely built-up areas.

Prey and Resource-Habitat Analysis

Our model-based classification of territories by habitat and dominant prey provides a contextual tool for understanding the relationships between these resources. For example, in the 10 territories classified as "prairie dog," the eagles' diet is likely to be dominated by prairie dogs, but three of these territories contained between 1 and 2.5% of a water source, implying that there the diet was likely augmented with fish. All 10 territories classified as "prairie dog" lie east of the region containing quarry ponds and streams of types 2 through 4 (Figure 7). We defined territories in which the nest is at least 1.9 km from a stream of Type 2 or greater as "upland" (Figure 7). These upland territories lie along low-discharge Type 1 tributaries or poorly defined drainages, which lack alluvial gravel, quarry ponds, and the wetlands that are commonly accompany them (Appendix 3). The abundance of the Black-tailed Prairie Dog in our study area and its prevalence in the diet are uncommon across the Bald Eagle's range; compilations of diet studies have found that mammals are relatively minor or unimportant as prey in most Bald Eagle populations (Wright 1953, Stalmaster 1987, Gerrard and Bortolotti 1988, Jensen 1988, Mabie et al. 1995). A few exceptions, however, have been noted in the literature; examples include the Texas Panhandle in grasslands away from permanent water bodies, where the Black-tailed Prairie Dog is seasonally important (Boal et al. 2009), or San Juan Island, Washington, where rabbits are in unusual supply (Retfalvi 1970). Although consumption of fish is predicted to dominate over consumption of prairie dogs in 51% of the 86 nest territories, the fish source mapped in nearly half of these territories is primarily bodies of still water and quarry ponds, which often freeze in the winter. Thus the Bald Eagles nesting in our study area derive a particular benefit from the abundance of prairie dogs, especially during the winter.

We predicted that in nesting territories grouped within the three fish-dominated categories, the eagles should feed overwhelmingly on fish, as average prairie-dog-to-fish ratios were extremely low. All 17 nest territories classified as “fish/water body” contain larger water bodies, and all but two of these are fed entirely by ditches or canals and are in what we defined as upland areas (see above; Figure 7). Six of these “fish/water body” territories contain prairie dog colonies, which likely augment the fish-dominated diet. Although most fish captured in the 21 territories classified as “fish/river” are likely from streams of types 3, 4, and 5, seven of the “fish/river” nest territories also are covered by 3 to 20% quarry ponds. Most of the “fish/river” nests are located along the South Platte River (Type 5), whereas the remaining six nests are located along Type 3 and 4 streams. Unlike water bodies and quarry ponds that can freeze during the winter, fish remain available along streams of types 3, 4, and 5. Of the 21 “fish/river” nests, 13 consisted of 2–15% prairie dog colonies (Appendix 2), further enriching these territories with this key mammalian prey source. Four of the six “fish/quarry pond” territories also contained prairie dog colonies. All six of the “fish/quarry pond” territories encompass Type 2 and Type 5 streams, although fishing is largely restricted to Type 5 in these territories.

The 18 nest territories categorized as “mixed” did not have a particularly dominant fish source but included enough combined prairie dog and fish sources to be considered more viable than the “resource-limited” nests.

The “resource-limited” nests have fewer identified sources of fish and prairie dogs than do the other territories we studied. Data from five nests in the midwestern study area at which we studied post-fledging dependence intensively demonstrated that adults’ territorial attendance—the time at least one territorial adult was in the territory—varied from 50 to 95% year round. Limited data for adults’ territorial attendance at three “resource-limited” nests suggests this rate was lower at these nests than at the five other nests, where the classification confirmed that fish and prairie dogs were more abundant (Figure 10). From September through February—outside the nesting season when eggs or young are present—adults’ territorial attendance at three “resource-limited” territories averaged 50.4 ± 8.1%, whereas at the five nests in other categories it averaged 71.7 ± 11.4% (Figure 10). These preliminary findings are consistent with the inference that territorial Bald Eagles spend more time outside of their territories when prey resources are more limited.

We suggest that continuing studies of nesting Bald Eagles in northern Colorado’s Front Range be focused on expanding our knowledge of these “resource-limited” nests (1) to clarify the extent to which the eagles use resources outside of the nest territory, (2) to provide additional data on the adults’ territorial attendance and time outside the territory, and (3) to compile nest-inception dates to determine if the numbers of “resource-limited” nests have increased over time, as the carrying capacity of more favorable resource habitats is reached.

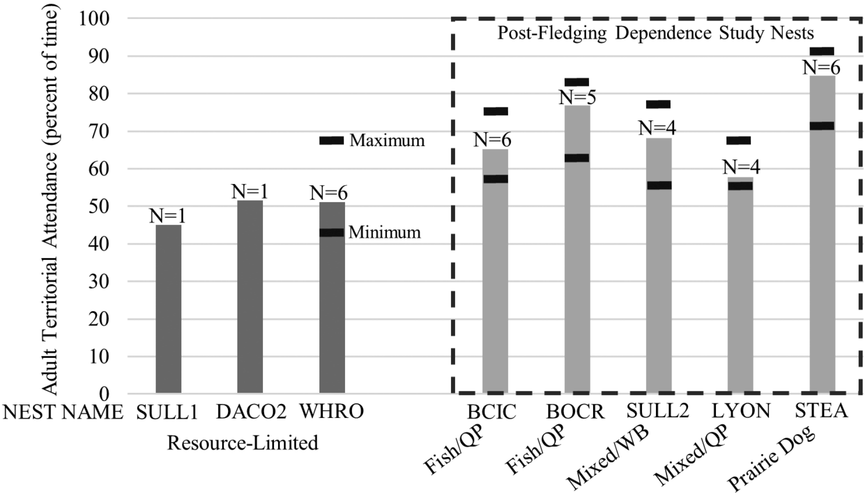


Figure 10. Adult Bald Eagles' average rate of attendance in their territory from September through February at five nests with ample prey resources (fish or prairie dogs) compared with that at three "resource-limited" nests. All data from midwestern field study area along northern Colorado's Front Range from 2016 through 2021. Sample sizes refer to number of years of study. Territories are categorized by a linear regression model associating predominant prey and source habitats (see Figure 7) QP, quarry pond; WB, water body.

CONSERVATION CONSIDERATIONS

State wildlife managers at Colorado Parks and Wildlife have expressed concerns about "densely [human] developed areas [in the Front Range corridor] that also contain a high concentration of Bald Eagles" (https://coloradooutdoorsmag.com/2021/07/14/studying-bald-eagles-along-colorados-densely-populated-front-range/). This appears to have led to a new definition applicable to management of Bald Eagle nests located in "highly developed areas" (CPW 2020b). Colorado Parks and Wildlife defines nests in "highly developed" areas as those situated "where the existing density [of buildings] exceeds 10 or more daily occupied facilities" within 400 m of the nest." Instead of the previous recommendation of "no surface occupancy" aimed at protecting all Bald Eagle nests with a buffer of 400 m year round or 800 m seasonally (CPW 2008), a new buffer of 200 m now applies to nest territories deemed "highly developed" (CPW 2020b). This new buffer for nest territories considered urbanized or human tolerant is based on the U.S. Fish and Wildlife's management guidelines, which have long-recommended a buffer of radius 200 m around Bald Eagle nests (USFWS 2007).

The recommendation for a 200-m buffer can be traced to studies of the effects of timber clearcutting around Bald Eagle nests in dense northern boreal forests (Manville 2018). The supporting basis for extending it to "highly developed areas" in Colorado Parks and Wildlife's 2020 raptor guidelines is not explained. In the absence of these supporting references, we are led to several questions pertinent to Bald Eagle management in the northern Colorado's Front Range: (1) Is the 200-m criterion from dense boreal forests applicable to the open habitat and behavioral attributes of Bald Eagles in northern Colorado's Front Range? (2) If any reduction in Colorado Parks and Wildlife's 0.4-km perennial or 0.8-km seasonal radius of "no surface occupancy" is warranted for urban-nesting Bald Eagles, how should "highly developed area" be defined? (3) Do buffers of 200 or 400 m protect critical resources including prey sources that sustain nesting territories? (4) Are these buffers aimed only at protection against disturbances of the nest, primarily during productive periods of the season? (5) How can critical foraging and habitat areas outside the 800-m buffer—which can be of particular importance to resource-limited territorial pairs—be protected?

With respect to the first question: our data demonstrate that the ecology of the Bald Eagle population in the dry, open terrain of northern Colorado's Front Range differs considerably from that of populations in wetter, densely forested regions. Yet, a 200-m buffer based on studies in such forests is currently being applied to nests in Colorado's drier open terrain. We recommend that the current definition and threshold for nests in "highly developed areas" be reevaluated, and if any reduction of the buffers from the previous 800-m seasonal or 400-m perennial standards is applied, that it be based on studies that quantify the density of buildings or human population with respect to the Bald Eagle population. We found no evidence for a statistically "high concentration of Bald Eagle nests" in densely developed areas in northern Colorado's Front Range. We further recommend that a coverage of buildings within 400 m of the nest being >1 standard deviation of the regional mean or another statistical threshold be applied if a Bald Eagle territory is to be defined as "urban."

CONCLUSIONS

In this study, we compared nest numbers, nearest-nest distances, productivity, and success rates of the Bald Eagle population in northern Colorado's semiarid Front Range to those in more verdant and resource-rich areas, as well as to one in the desert Southwest. We found that in Colorado nests are more widely spaced than in wetter climatic regions, at a density more like that in Arizona.

We found no indication of a high concentration of nesting territories in areas with dense human development, as often reported in the Colorado media (https://www.rmpbs.org/blogs/news/colorados-bald-eagle-population-is-booming-in-urban-areas-the-state-is-trying-to-figure-out-why/; https://coloradooutdoorsmag.com/2021/07/14/studying-bald-eagles-along-colorados-densely-populated-front-range/).

Finally, we developed a baseline for understanding territorial Bald Eagles' resource use based on prey sources in nesting territories. Unsurprisingly, over half of the nesting territories studied are dominated by fish predation. However, the abundance of the Black-tailed Prairie Dog and its prevalence in the diet of many of its territorial Bald Eagles are uncommon elsewhere. We inferred that the eagles' consumption of prairie dogs exceeded that of fish in nearly one-third of the 86 territories we studied. In these same territories, the average areal coverage of prairie dog colonies was 15%. In nearly half of the territories where fish are the principal prey, the primary source habitat often freezes over the winter. Thus the abundance of prairie dogs in our study area benefits the Bald Eagle population especially during the winter.

As the spacing of Bald Eagle nests likely corresponds with the abundance of prey and other resources, so does territory size reflect the abundance of these resources and the extent to which territorial eagles need to defend them. Few avian species in northern Colorado's Front Range require a territory as large as do nesting Bald Eagles. Yet, the region is experiencing some of the fastest human population growth in the U.S. While land-management policies and guidelines typically focus on minimizing disturbance of nests, the loss of habitat and critical prey resources—particularly prairie dogs—as a result of development must be more seriously considered. Although the prairie dog is valued by some for its ecological role as a keystone species (Kotliar et al. 2006), human activities conflict with it frequently. Human land use and the rapid pace of development in northern Colorado's Front Range continues to destroy prairie dog colonies and associated raptor habitat. In addition, plague and poisoning periodically eradicate entire colonies or portions of colonies, followed by varying degrees of recovery over a period of years (Sidle et al. 2012).

Open-space programs and land conservation can help to protect critical habitat required to sustain key resources such as the Black-tailed Prairie Dog, fish, and the dwindling number of mature cottonwoods suitable for nesting (Bove 2022). However, the distinctive aspects of the Bald Eagle population nesting in northern Colorado's Front Range need to be understood. Not only is the supply of resources there more limited than in more verdant regions, but the competition for these resources in this rapidly developing environment could impair these Bald Eagles' reproduction and undermine their large territories.

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