BEHAVIORAL INTERACTIONS OF BREEDING BALD EAGLES (*HALIAEETUS*

LUECOCEPHALUS) AT LAKE CASCADE, IDAHO

by

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ABSTRACT

During the 2000 and 2001 breeding seasons I studied the behavioral inter- and intra-specific interactions of Bald Eagles (*Haliaeetus leucocephalus*) breeding at Lake Cascade, Idaho. In the first chapter, I describe the relationships between an increase in population density and home range and foraging habitat use by Bald eagles. In the second chapter, I describe the relationship between aggressive interactions and reproductive success, as measured by number of nestlings fledged and nestling weight.

Because home range and foraging habitat use show temporal variability, I compared breeding home ranges and foraging habitat use of Bald Eagles at Lake Cascade, Idaho in 2000 with previously obtained results from 1989 and 1990. In 2000, eight pairs nested on Lake Cascade whereas five pairs nested in 1989/90. This increase was correlated with changes in home range and foraging habitat use. The home ranges of the three new pairs included habitat that was previously used by the five pairs of eagles in 1989/90. In addition, several pairs that occupied older nest sites appeared to utilize foraging habitats farther from the main body of the reservoir, including upper reaches of tributary arms and nearby, smaller bodies of water. Pairs from recently established territories also used smaller bodies of water away from Lake Cascade. Thus, home ranges in 2000 differed in shape and foraging habitat use from those in 1989/90. The increase in the number of breeding pairs also was correlated with a decrease in home range overlap. This appears to be the first study to show how a natural population size

increase may affect home range size, overlap and shape and foraging habitat use within a bird population.

I conducted a study in 2000 and 2001 to describe the relationship between Bald Eagle inter- and intraspecific aggressive interactions and measures of reproductive success, including number of nestlings fledged and nestling mass, during the breeding season at Lake Cascade, ID. I observed activity of nine breeding pairs in both 2000 and 2001 to quantify the level of territorial aggression exhibited by nesting pairs of eagles. Interactions were classified according to the level of aggression exhibited: vocalizing, chasing, stooping, or kleptoparasitizing. I recorded a total of 124 interactions between territorial eagles and both conspecifics and heterospecifics. Eagles acted as both the aggressors and recipients of aggression in these interactions. Seven pairs of eagles produced 13 fledglings (average mass = 4.00 kg) in 2000 and four pairs produced eight fledglings (average mass = 4.15 kg) in 2001. The results of this study suggest that the level of aggression exhibited by nesting Bald Eagles may be related to the number of fledglings but not to nestling mass.

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Introduction

The relationship between home range size and population density has been examined extensively for some animal groups (especially mammals) but less is known about these relationships in birds. Changes in population density of mammals usually affect home range size and/or overlap (Saunders and McLeod 1999, Kilpatrick et al. 2001, Dahle and Swenson 2003, Kjellander et al. 2004, Benson et al. 2006, Frey and Conover 2007) but not in every case (Hoset et al. 2008). Generally there is a negative trend between population density and home range size (e.g. Kjellander et al. 2004), though the opposite also has been shown (e.g. Kilpatrick et al. 2001). Because it is impossible to experimentally reduce home range size without a concomitant change in some other ecological factor (such as food availability), experimental tests of this relationship have always manipulated population density (usually by reducing it). This necessarily results in population density being assigned as the causal factor and home range size the dependant factor. However, it is not always clear which factor is causal in nature and Abramsky and Tracy (1980) suggest that home range size may regulate population density. This is especially plausible in strongly territorial species that actively arrange themselves spatially in a population size-independent manner (Krebs 1971).

Population density may affect features other than the size of a home range. The degree of range overlap can be interpreted as the tendency of a breeding pair to share resources with neighbors. If home range size of a species is fixed due to ecological or behavioral constraints, the extent of overlap between neighboring ranges should increase with an increase in population density (Alberts 1993). However, when home range size changes in response to conspecific density, home range overlap may not be expected to change (Pons et al. 2008). Home range shape is another feature of home ranges that may vary with population size. The "compactness" (or, conversely, the "convolutedness") of a home range is a function of its edge to area ratio and, in the case of central-place foragers such as nesting birds, it is also a function of the distance from the nest (central place) to the most distant edge (which, of course, is also a function of size). This measure of home range shape is expected to vary inversely with population density because the cost of defending the perimeter of a home range (where encounters with conspecifics should be highest) is higher than defending its interior, and this cost decreases as the ratio of edge to area decreases and as population density decreases (Schoener 1983, Manteuffel and Eiblmaier 2008).

Independently of population size, home range size is influenced directly and indirectly by energy demands of animals (Mace and Harvey 1983, Peery 2000), and both may increase with brood size (Schoener 1983, Elchuck and Wiebe 2003). For example, a parent may need to increase the size of its home range to accommodate large broods or growing young. Conversely, large broods may require higher vigilance (because large broods are more conspicuous and because parents invest more in larger broods) resulting

in smaller home range size. Furthermore, increases in home range size have been reported for unsuccessful pairs (e.g., Marzluff et al. 1997). Therefore, it is important to incorporate measures of reproductive success in studies of the size of breeding bird home ranges.

Knowledge of home range size and foraging habitat use is essential to understanding population biology and managing habitats of all animals, including Bald Eagles. Information about the consequences of Bald Eagle population increase and range expansion on local movements is particularly relevant given current growth in eagle populations throughout the continental United States (US Fish and Wildlife Service 2007). Though basic descriptions of Bald Eagle home range sizes and foraging habitat use were provided by Mack et al. (1990), Gerrard et al. (1992), Hunt et al. (1992), Garrett et al. (1993), Stangl (1994), and Watson and Pierce (1998), no studies to date discuss how changes in these parameters over time may be related to a change in population density.

Bald Eagles are territorial during the breeding season (Buehler 2000), so changes in population density may result in changes in home range size, shape, and/or foraging habitat use. Bald Eagles do not maintain exclusive home ranges and some degree of range overlap often occurs (Buehler 2000). Therefore, changes in home range size, overlap, and shape and foraging habitat use may be influenced by the effects of populations size and, hence, may indicate the potential for a particular region to sustain additional population growth (Kotler et al. 2007).

Bald Eagles (and other raptors) have steadily increased both reproductive success and population size following the 1973 ban on DDT (US Fish and Wildlife Service 2007). Annual Bald Eagle nest surveys in Idaho began in 1979 (Melquist 1987) for three main breeding populations of Bald Eagles in the state: near Lakes Coeur d'Alene and Pend Oreille in the panhandle; along the Henry's and South Forks of the Snake River in eastern Idaho; and along the North Fork of the Payette River and Lake Cascade in west-central Idaho. Within Idaho, nesting Bald Eagles were first documented in 1976 at Lake Cascade, a reservoir in the West Central Mountains (Melquist 1987). In 1990, there were five known breeding pairs of eagles on Lake Cascade, and by 2000, the population had increased to eight breeding pairs.

Krol and Bechard (1989a, 1989b, 1990) estimated home range size and foraging habitat use for five breeding pairs of Bald Eagles on Lake Cascade. Three of these five pairs were monitored in 1989 and the other two were monitored in 1990. Home range size and foraging habitat use were measured by visually assessing movements and behavior of unmarked territorial eagles. They defined home ranges as the sum of all observed movements by eagles and characterized them as minimum convex polygons. Krol and Bechard (1989a, 1989b, 1990) did not distinguish between defended territories and home ranges but included areas that were actively defended as well as areas where eagles foraged.

The purpose of this study was to determine how an increase in the number of nesting Bald Eagles from five territories in 1990 to eight territories in 2000 was correlated with home range sizes, amount of range overlap, home range shape, and

foraging habitat use at Lake Cascade. As population size increases home range size generally decreases (Kjellander et al. 2004, Frey and Conover 2007), home range overlap tends to increase (Hoset et al. 2008), and home range shape tends to become more compact (i.e. more circular; Pons et al. 2008). The population of Bald Eagles at Lake Cascade has increased from five breeding pairs in 1989/90 to eight breeding pairs in 2000. Therefore, I predicted that home range size in 2000 would be unchanged or smaller and extent of range overlap between adjacent pairs would be larger than in 1989/90. I predicted that use of foraging habitat on the lake and its associated tributaries would be similar between the two periods unless competition between pairs forced some to incorporate different foraging areas than those used in 1989 and 1990. If foraging areas did change, I predicted the shapes of the home ranges would be more compact. To test these predictions, in 2000 I replicated Krol's and Bechard's (1989a, 1989b, 1990) methods to estimate home range and foraging habitat use.

Methods

Study Area

Lake Cascade is a US Bureau of Reclamation reservoir on the North Fork of the Payette River in Long Valley, Valley County, Idaho (Figure 1). The reservoir is approximately 27 km long, 1.6 to 6.4 km wide, has predictable, seasonal changes in water levels, and reaches maximum storage during mid-June (US Bureau of Reclamation 2002). At full pool, Lake Cascade averages 7.5 m deep, has a surface area of 11,452 ha, and has a surface elevation of 1,524 m. The town of Cascade, with a population of

approximately 1000 (2000 US Census, US Census Bureau, Geography Division), is located on the southeast shore, and the town of Donnelly, with a population of approximately 150 (2000 US Census, US Census Bureau, Geography Division), is 1.5 km northeast of the reservoir (Figure 1).

Lake Cascade has a north-south orientation and is bordered by landscapes of variable topography. It is bounded on the west by the north-south trending forested east slope of West Mountain. Long Valley (characterized by flat shrub-grassland) extends north, south, and east of Lake Cascade but is dissected by several forested ridges. Three rivers contribute most of the inflow to Lake Cascade, and there are several small impoundments (< 20 ha) oriented north to south approximately 4.5 km east of the lake. Forests around the reservoir are dominated by Ponderosa Pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziessii*), but also include Grand Fir (*Abies grandis*) and Engelmann Spruce (*Picea engelmannii*).

Bald Eagles first began nesting at Lake Cascade in 1976 (Melquist 1987). By 2000, the Cascade eagle population had increased to 8 breeding pairs. Bald eagle nest sites are spaced relatively evenly around the perimeter of the lake. All are within 3 km of the shoreline, and adjacent occupied nests average 4.9 km apart (range: 2.8 to 7.7 km; Figure 2).

Lake Cascade supports an abundant prey base for eagles, including many potential piscine, avian, and mammalian prey species (US Bureau of Reclamation 2002). Roadside carrion is commonly available to eagles that nest on the east shore of Lake Cascade, where a state highway runs parallel to the entire length of that shoreline. This

carrion is probably more abundant early in the nesting season before Mule Deer

(*Odocoileus hemionus*) and Elk (*Cervus elphus*) migrate to higher elevations.

Home Range and Habitat Use

     I used the focal animal sampling protocol of Krol and Bechard (1989a, 1989b,

1990) to assess home range and habitat use of Bald Eagle pairs during the 2000 breeding

season. Bald Eagles were not banded or marked in any way for this study because of

funding and logistical constraints. All observations of eagle movements and behaviors

were initiated at nest trees to ensure the identity of focal individuals. I recorded data only

for those birds that I knew were the residents of a particular nest site. Home range was

defined as the area used by a pair of breeding eagles during the breeding season. This

area was not actively defended in its entirety and was not necessarily used exclusively by

one pair of eagles. The home range included the area actively defended around the nest

site (defined as the nesting territory) as well as those areas used for foraging. Because

pairs did not necessarily use the same nest or nest tree each year, I also use the term

territory in a more general sense to describe the pair and their nest site(s). All areas

within the home range were considered to be a pair's foraging area (or at least area

available for foraging). Home range overlap was the area of a pair's home range shared

with the home range of another pair.

     Observations of eagle movements and behavior began in mid-March when

courtship and egg-laying were in progress and continued until nestlings fledged

(approximately 1 August). Observations in March allowed verification of occupancy and

the presence of breeding pairs. A nest site was considered to be occupied if at least one

eagle was observed in the nest tree more than once and breeding to have occurred if an eagle laid eggs (indicated by a bird in incubating posture). Occupied territories were monitored for the duration of the breeding season. During incubation (April), I conducted observations four days per week. For the remainder of the nesting season, observations were made by one or two observers on five consecutive days per week.

I ordered observations of pairs by randomly selecting pairs without replacement until all pairs had been sampled. After the last pair in each sequence had been selected, the method was repeated through the end of the breeding season. This method ensured that the same level of effort was used to monitor each breeding pair. Observations generally began at 07:00 MST, weather permitting, and continued until approximately 21:00. As the season progressed, and some eagles spent long periods (> 2 hr) away from the nest, observation periods were shortened to be sufficient to observe at least one of the breeding pair within the home range. Thus, observation periods were not always uniform in length. However, average time spent at each nest site remained approximately equal (Table 1).

For the purpose of this study, I define foraging as an attempt to procure food (for example, capture live prey, find carrion, kleptoparasitize). This is a conservative definition and differs from that of Krol and Bechard (1989a, 1989b, and 1990), which included perched, alert birds near water bodies. However, perched birds are not necessarily hunting. They may be resting, sunning, or guarding and defending the territory or nest. Consequently, I recorded all of these behaviors as perching, because it is difficult to distinguish among them and they are not mutually exclusive.

Observations of eagle movements and behaviors were made using binoculars and spotting scopes. Following the protocol of Krol and Bechard (1989a, 1989b, 1990), when only one observer was available, the objective was to keep the focal bird in view and to maintain sight of the nest if possible. When two observers were present (only during the nestling stage), the stationary observer monitored the focal pair from a fixed position from which the nest and as much of the foraging area as possible were visible. From a boat or truck, the mobile observer began observations either at the fixed observer's point or another location that offered the widest view of foraging areas. The mobile observer's objective was to keep the target bird in view at all times by following the bird as movements occurred. Every effort was made to minimize the impact of observers on eagle behavior, namely by restricting movements when near nest or perch sites and maintaining a minimum 0.5 km following and observation distance. Observers communicated by hand-held radios to improve their ability to maintain visual contact when birds changed locations.

Locations of eagles and the types and duration of activities were recorded continuously throughout each observation period. We categorized activities as flying (flapping, soaring, or gliding), foraging (active attempts to acquire a food item), sitting/brooding, nest maintenance, feeding (adult feeding nestling), eating (adult eating), drinking/washing, preening, perching, and aggressive interactions. We quantified activities in "eagle minutes" such that the activities of each bird of a pair were quantified separately and combined for a total number of hours per pair.

Gender was assigned to individuals based on size only when a pair was seen perching within 1 m of each other (Buehler 2000). Consequently, many observations were of eagles of unknown gender, and home range sizes and foraging habitat use were based on combined observations of both genders.

All perch locations were plotted on USGS 7.5 min topographic maps and I calculated point to point distances after movements occurred. I used prominent topographic features and other obvious features of the landscape (for example, roads and bridges) to determine the locations of moving eagles in the few instances when observers were unable to follow them.

Data Analysis

To assess the effects of the number of nesting pairs on home ranges, I compared home range area, overlap with adjacent home ranges, and shape (calculated as edge to area ratio and distance from the nest site to the farthest edge) for five nest sites occupied in 1989 or 1990 with the same five nest sites in 2000. Because the five sites were used during each of the two periods (and, hence, are not independent), the associated home ranges during the two periods were considered to be matched pairs. I also performed unmatched tests including all eight sites from 2000, and only report the results when they differ qualitatively from matched pairs analyses. Home ranges were based on observations of both flying and perched eagles. Although it was not explicitly included in Krol and Bechard's (1989a, 1989b, 1990) analyses, I was able to determine the amount of overlap in ranges in 1989 and 1990 from descriptions and figures of home ranges. I plotted perch locations and flight paths in the GIS program ArcView GIS (version 3.2;

Environmental Systems Research Institute, Inc.) and formed home ranges (i.e. minimum convex polygons) based on the outermost locations. Using ArcView GIS, I provide a measure of home range size, overlap, distance from nest to farthest edge, and edge to area ratio for each pair and for each year, including pairs with non-overlapping home ranges (zero overlap) to allow comparisons of the nest sites occupied in both years.

Measures of home range were not distributed normally within the two periods, so I used the nonparametric Wilcoxon matched-pairs signed-rank test (for matched pairs analyses) and Wilcoxon rank sums tests (for unmatched analyses; JMP® 8.0 statistical software; SAS Institute Inc., Cary, NC) to test for differences in these values between the two periods.

Finally, I compared productivity between periods (t-test) and compared productivity with home range size for both periods (linear regressions). I define productivity as the number of young counted approximately 60 d after hatching (80% of fledging age, approximately the time of banding; Steenhof 1987), because I could not account for some young after fledging dates had passed. I measured productivity at all nests in 2000 by obtaining counts of nestlings during and after banding operations. Banding at each nest occurred when nestlings were 40 to 65 d post-hatch.

Results

During 1989 and 1990, 967 hr of observation were conducted at five nest sites (Table 1; $\overline{X}$ = 193.4 h, $S_{\overline{X}}$ = 31.8; Krol and Bechard 1989a, 1989b, 1990).

Observations during the 2000 season totaled 465 hr at eight nest sites (Table 1; $\overline{X} = 58.1$ h, $S_{\overline{X}} = 9.9$). We used an average of 63 perching and 79 flying locations to define home ranges in 2000 (locations were not necessarily independent). Mean home range size for five pairs in 1989/90 was 29.70 km^2 (Table 1; $S_{\overline{X}} = 6.63$, range = 14.58 to 54.15) and 24.92 km^2 (Table 1; $S_{\overline{X}} = 2.98$, range = 11.22 to 36.77) for all eight pairs in 2000. Mean home range size in 2000 for the five territories occupied in 1989/90 was 23.89 km^2 (Table 1; $S_{\overline{X}} = 4.13$, range = 11.22 to 36.77). With one exception, the smallest home ranges in 1989/90 and 2000 were in the northern part of the lake, and larger ranges were in the southern portion (Figure 2). There was an overall trend toward smaller home ranges in 2000 (Figure 2), but the difference was not significant (Wilcoxon matched-pairs signed-rank test, $Z = -0.405$, df = 4, $p = 0.686$).

Mean home range overlap was 3.18 km^2 in 1989/90 (Table 1; $S_{\overline{X}} = 0.70$, range = 0.94 to 5.07) and 1.16 km^2 for all pairs in 2000 (Table 1; $S_{\overline{X}} = 0.33$, range = 0.00 to 2.03). Mean range overlap was 1.32 km^2 in 2000 among territories also occupied in 1989-90 (Table 1; $S_{\overline{X}} = 0.42$, range = 0.00 to 2.03). Ranges overlapped significantly less in 2000 than in 1989/90 (Wilcoxon matched-pairs signed-rank test, $Z = -2.023$, df = 4, $p = 0.043$; Fig. 2).

Home ranges became slightly more "compact" in 2000 than they were in 1989/90 (Table 1). The distance from the nest to the most distant edge of the home range tended to decrease between periods, though differences were not significant (Table 1; Wilcoxon

matched-pairs signed-rank test, $Z = -5.500$, df $=4$, $p = 0.188$). However, when all nests

from 2000 were included in the analysis (i.e. not matched pairs), the difference between

periods became significant (Table 1; Wilcoxon rank sums test, $Z = 2.269$, df $=4$, $p =$

0.023). There was also a trend toward a decrease in the edge to area ratio of home ranges

between the two periods (Table 1; Wilcoxon matched-pairs signed-rank test, $Z = -6.500$,

df $=4$, $p = 0.125$). Again, when all nests from 2000 were included in the analysis, the

difference between periods became highly significant (Table 1; Wilcoxon rank sums test,

$Z = 2.712$, $p = 0.007$).

Because both eagles of a breeding pair were simultaneously out of view on

average 52.2% of observation hours (range $= 41.6$ to 63.4), the following percentage data

were calculated from observation hours during which at least one adult was present.

Nesting Bald Eagle pairs spent the larger portions of observation periods on perches ($\overline{X}$

$= 32.47$ h or 60.7% of observation time) or sitting on eggs or brooding young ($\overline{X} =$

14.24 h or 26.6%). Eagles that fledged young spent a mean of 16.87 h sitting or brooding

(or 25.1%). During incubation and early nestling phases (most of April and May), the

eagles spent most of their time sitting or brooding on the nest ($\overline{X} = 15.4$ h or 59.1%).

During the late nestling phase (June and July), they spent most of their time perching ($\overline{X}$

$= 34.3$ h or 86.0%). All other activities of successful breeding pairs are summarized in

Appendix A.

In 1989/90, home ranges of Bald Eagles at Lake Cascade included most open

water portions of the lake, and did not include tributaries and nearby smaller

impoundments (with the exception of a pair using the downstream portion of the North Fork Payette River; Figure 2). All pairs continued to use the main reservoir in 2000 (Figure 2), but five pairs also used foraging areas away from the main body of the lake. Eagles from the northern and eastern territories included tributaries and nearby smaller impoundments in their foraging areas and another pair flew to the North Fork of the Payette River below the dam south of Lake Cascade to forage. It was difficult to follow eagles that used these areas; I was, however, able to confirm foraging at locations away from Lake Cascade by observations of eagles returning from these areas with what appeared to be fresh prey.

In 2000 I documented 26 foraging attempts that accounted for approximately 0.1% of the time spent observing eagles when at least one adult was in view ($\overline{X}$ = 0.06 h, range 0-0.18). Foraging attempts averaged 0.74 min. Most of the foraging attempts I observed were by males, took place over open water, and resulted in captures of fish (species unknown).

There was no reduction in brood size between banding and the end of observations in August. Mean productivity at Lake Cascade (number of young fledged per occupied nest site) was slightly lower in 2000 (Table 1; 1.3 fledglings, $S_{\overline{X}}$ = 0.4) than in 1989/90 (1.6 fledglings, $S_{\overline{X}}$ = 0.6), but the difference was not significant (t = 0.570, df = 12, p = 0.579). Home range size was not correlated with productivity in either period (linear regression, in 1989/90: F = 1.267, df = 4, p = 0.343; in 2000: F = 0.004, df = 7, p = 0.953).

Discussion

<u>Home Range Size</u>

Home range sizes of Bald Eagles at Lake Cascade were variable, but fell within the range (5 to 40 km^2) reported in other Bald Eagle studies in western North America (Haywood and Ohmart 1983, Gerrard et al. 1992, Harmata and Oakleaf 1992, Garrett et al. 1993, Watson and Pierce 1998, Buehler 2000). Contrary to my prediction, home range sizes in 2000 were similar to those in 1989/90, suggesting that eagles at Lake Cascade either could not or did not need to decrease home range size following a population increase. Instead, eagles appeared to use alternative strategies to avoid a potential increase in competition from more nesting pairs, including utilizing different foraging areas and using more "compact" home ranges.

Foraging areas at Lake Cascade were typical of those throughout the species' range (Buehler 2000). Eagles incorporated large open water areas, rivers and small lakes, and a diverse prey base within the areas they hunted. Watson (2002) describes differences in home range size based on home range habitat types, and both availability of foraging habitat and availability of prey often affect home range size (Peery 2000); however, data from this study show that eagles may accommodate population growth by changing the shape of their ranges instead of the size. I observed changes in home range shape as eagles incorporated previously unused habitats in their foraging activities. In this study area, eagles did not use tributaries to the reservoir during the 1989 and 1990

breeding seasons, but in 2000, four pairs incorporated tributaries into their home ranges and two ranges included small impoundments.

The changes in home range overlap and shape and foraging habitat use I observed may have been a response to decrease competition for foraging sites associated with higher eagle breeding pair densities in 2000. As the number of nesting pairs increased, eagles may have used tributaries and smaller impoundments to avoid intraspecific competition. Nesting eagles at Besnard Lake, Saskatchewan, Canada, also used smaller lakes away from the larger body of water when additional breeding pairs of eagles joined the population (Gerrard et al. 1992).

My ability to determine an eagle's location and habitat use was influenced by a number of factors, including stage of the nesting cycle, observer access to areas away from Lake Cascade, weather, topography, and limitations inherent in the methods used to track eagle movements.

Factors other than those imposed by methods also limited my ability to observe foraging behavior. First, opportunities to observe attempts to capture prey were minimized, since Bald Eagles often capture relatively large prey infrequently (Buehler 2000). Second, eagles often foraged earlier in the day than I was able to observe them (due to low light conditions), and third, low visibility (usually due to fog) often prevented viewing of distant nest sites early in the morning.

Foraging behavior was difficult to observe for all pairs in 2000 due in large part to limitations of the methods used to locate and follow eagles. Following Bald Eagles by foot, vehicle, and boat presents obvious difficulties. I consider this to be a major

weakness in the data, and would not recommend using the estimates of home ranges to compare across studies using different methodologies. However, the methods used were necessary and expected in my effort to make valid comparisons with data collected by Krol and Bechard (1989a, 1989b, 1990), who also were limited in their ability to follow birds throughout the season. My inability to follow birds may have influenced my interpretation of the consequences of increases in population size on nesting eagles, because eagles in 2000 used habitats and foraging areas that were more difficult to access than in 1989/90. However, I believe that I have accurately, but conservatively, described the qualitative (if not the quantitative) nature of those changes.

Habitat Use

In 2000, Bald Eagles at Lake Cascade continued to nest along the main body of the reservoir. The open terrestrial habitats (grasslands and shrub-forest mosaics) along the shores and upland areas adjacent to the lake create good nesting conditions for several reasons. Open habitats provide eagles a commanding view of surrounding areas, allowing detection of potential predators and competitors. Other raptor species (for example, Red-tailed Hawks [*Buteo jamaicensis*]; Perkins et al. 1996) are known predators of Bald Eagle nestlings, and Ospreys (*Pandion haliaetus*) are potential competitors for nest sites and prey. In open habitats, individuals of these other species are more likely to see and avoid resident eagles before entering the territory, preventing costly aggressive encounters. Open nesting habitat is also an advantage during territory establishment: when eagles arrive at their territory in the spring (after the reservoir begins

to clear of ice), they can advertise their residency over greater distances and prevent territorial disputes (Newton 1979).

In contrast, topography along rivers tended to be steep and irregular, reducing line-of-sight distances. In some cases, however, these habitats may offer some advantages to eagles. On a regulated-water-flow river system in Montana, Mack et al. (1990) demonstrated that Bald Eagles foraging along rivers had higher capture rates than those foraging at lakes. Hunt et al. (1992) also observed Bald Eagles breeding along stretches of the Pit River and its associated impoundments in California regulated in much the same way as Lake Cascade and the North Fork Payette River. Two radio-tagged adult Bald Eagles on the Pit River system foraged along river reaches within their territories more frequently than on adjacent reservoirs. If competition increased on Lake Cascade, eagles may have compensated by foraging in nearby tributaries and small impoundments. At lower densities (and lower competition?) in 1989/90, the potential costs of utilizing tributaries and small impoundments (which were always out of view of nest sites) and leaving nests and young unattended may have been too high to outweigh possible benefits of higher prey capture rates, or simply may have been unnecessary.

Home Range Shape

The home ranges of Bald Eagles in 2000 tended to be more "compact" than in 1990. Edge to area ratios were smaller in 2000 than 1989/90, though results from matched pairs tests were not statistically significant. These results followed predictions associated with an increase in population size and are consistent with research on highly territorial Dartford Warblers (*Sylvia undata*; Pons et al. 2008). Pons et al. (2008) found

that as the population density of Dartford Warblers increased, territory roundness (measured as a function of the perimeter and area of the territory) increased. The distance from the nest to the farthest edge of home ranges also tended to be shorter for breeding Bald Eagles at Lake Cascade, though again, matched pairs tests were not statistically significant. Both of these factors could be a response by breeding pairs to minimize costs by accommodating more neighbors while minimizing intrusions into neighboring home ranges. Given the fact that home range overlap increased between the two periods, it's possible that territorial eagles will accept some degree of home range overlap, but they may try to minimize contact with neighbors by utilizing more compact ranges.

Food habits

I did not quantify prey taken by Bald Eagles during foraging bouts or brought to the nest, but observations during nest climbs gave a subjective impression of prey species taken by eagles in 2000. Northern Pikeminnows (*Ptychocheilus oregonensis*) and Western Grebes (*Aechmophorus occidentalis*) accounted for most of the prey items we observed in nests with some use of American Coots (*Fulica americana*), ducklings (*Bucephala* sp. and *Anas* sp.), Largescale Suckers (*Catostomus macrocheilus*), and Columbian Ground Squirrel (*Spermophilus columbianus*). Krol and Bechard (1989a, 1989b, 1990) conducted more extensive observations and described Yellow Perch (*Perca flavescens*) as a major component of eagle diets at Lake Cascade. The difference in prey composition is likely the result of a dramatic decline in perch populations and an equally impressive increase in pikeminnows at the reservoir from 1990 to 2000 (Millar 2003).

Northern Pikeminnows have been implicated in the decline in Yellow Perch; however, there is no evidence that overall prey availability changed during the shift, but it remains a possibility given differences in the two fish species' foraging and breeding habits. Although I did not measure prey availability during my study, changes in foraging habitat use observed from 1990 to 2000 may be explained by a decline in prey availability in the reservoir during that period. Prey availability may change with predator density and composition (Relyea 2003). Predator density (and, potentially, competition) has increased on the main body of the reservoir since 1990, due to increases in both eagle and Osprey populations (W Melquist, pers comm); thus, a decrease in prey availability may have compelled eagles to forage along tributaries.

Bald Eagles have high levels of fidelity to their nest sites (Buehler 2000), which may increase the likelihood that they stay on the reservoir to nest. Although tributaries and secondary impoundments may decrease eagle competition for prey at Lake Cascade, they are also much farther (>1000m) from nest sites than the lake itself. Thus, eagles expended more energy flying to and from these sites and carrying prey to nests. Time and energy constraints may be the reason that eagles spent little time at these alternate sites in the past. Although foraging opportunities may be better at these sites, the fact that eagles are not nesting there suggests that nesting habitat may be more available or more optimal at Lake Cascade.

Increased use of tributaries and secondary impoundments is likely responsible for the fact that home range overlap among neighboring pairs decreased in 2000. As pairs moved away from Lake Cascade, they were less likely to share the home ranges of

neighbors. If increases in Bald Eagle population size in fact did lead to the observed changes in foraging habitat use and range overlap, Lake Cascade is arguably approaching its Bald Eagle carrying capacity. Though calculating carrying capacity is difficult in the best circumstances, behavioral cues may be useful in understanding whether or not a population is approaching carrying capacity (Kotler et al. 2007, Morris and Mukherjee 2007). Populations approaching or exceeding carrying capacity often experience decreases in survivorship and/or reductions in breeding success (Morris and Mukherjee 2007). While productivity did not differ between periods during this study, in 2001 I witnessed two unsuccessful attempts by Bald Eagles to establish new territories (in addition to the eight from 2000) on Lake Cascade. These two pairs built nests and defended sites but did not successfully rear nestlings (it was unclear whether they laid eggs). If Bald Eagles are at or near carrying capacity at Lake Cascade, proper management and protection of currently unoccupied habitats away from the lake will be needed to accommodate expanding populations of this recovering species.

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Table 1. Summary of variables associated with home ranges of Bald Eagles breeding at Lake Cascade, Idaho, during 1989/90 and 2000. Data from 2000 are presented using two sets of nests: five nests that were used in 1989/90 and all eight nests that were occupied in 2000 (all measures presented as $\overline{X} \pm S_{\overline{X}}$).

Variable	1989/90	2000 (5 pairs)	2000 (all 8 pairs)
observation effort (hr)	193.4 ± 31.8	48.9 ± 14.2	58.1 ± 9.9
productivity (# fledged/occupied nest)	1.6 ± 0.6	0.6 ± 0.3	1.3 ± 0.4
home range size (km^2)	29.70 ± 6.63	23.89 ± 4.13	24.92 ± 2.98
home range overlap (km^2)	3.18 ± 0.70	1.32 ± 0.42	1.16 ± 0.33
edge:area ratio	0.86 ± 0.09	0.55 ± 0.06	0.52 ± 0.04
nest to edge distance (km)	7.14 ± 0.77	4.64 ± 0.56	4.27 ± 0.42

Figure 1. Location of Lake Cascade, Idaho.

streams
minor roads
major roads

Donnelly

Lake Cascade

Cascade

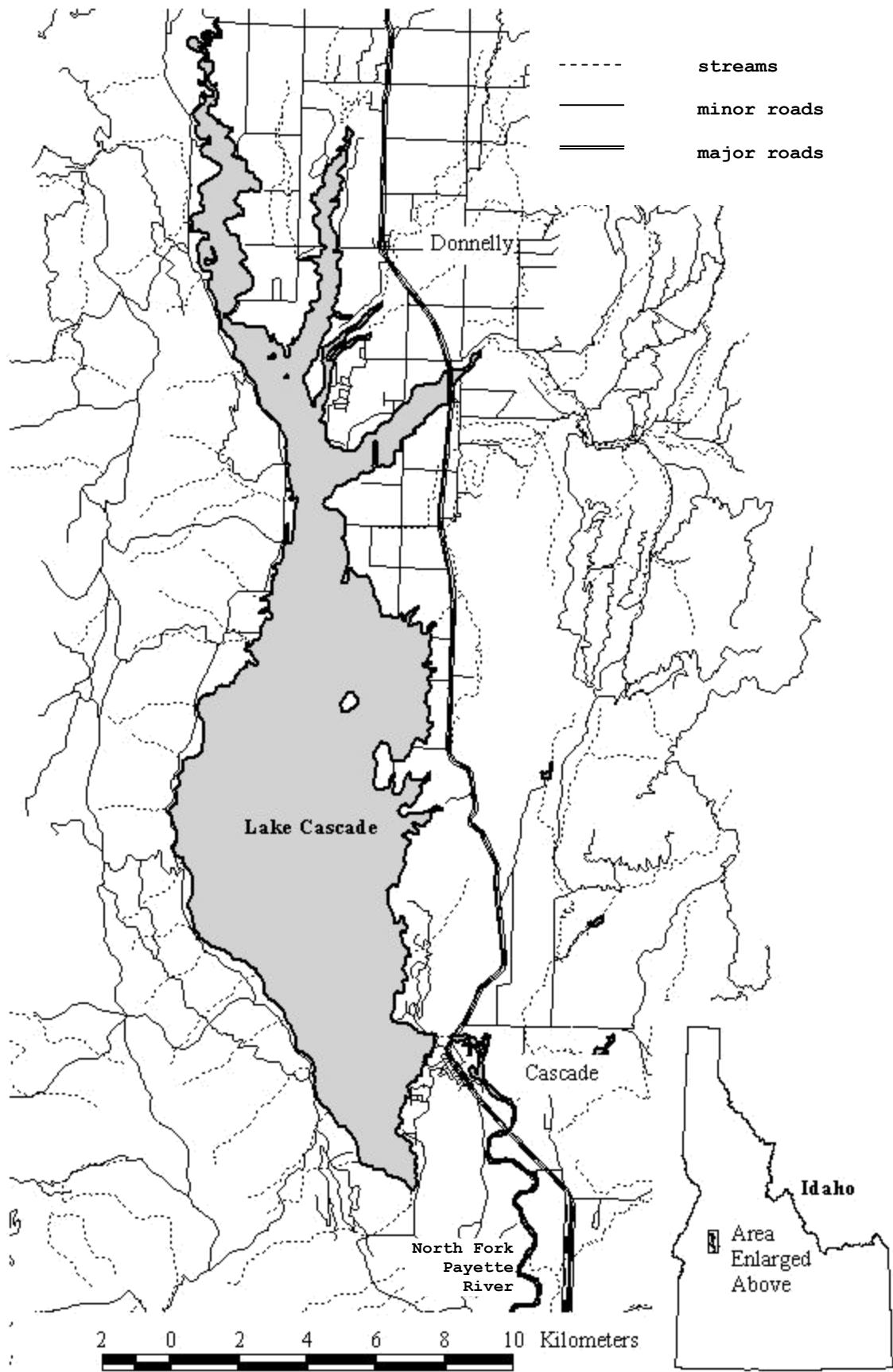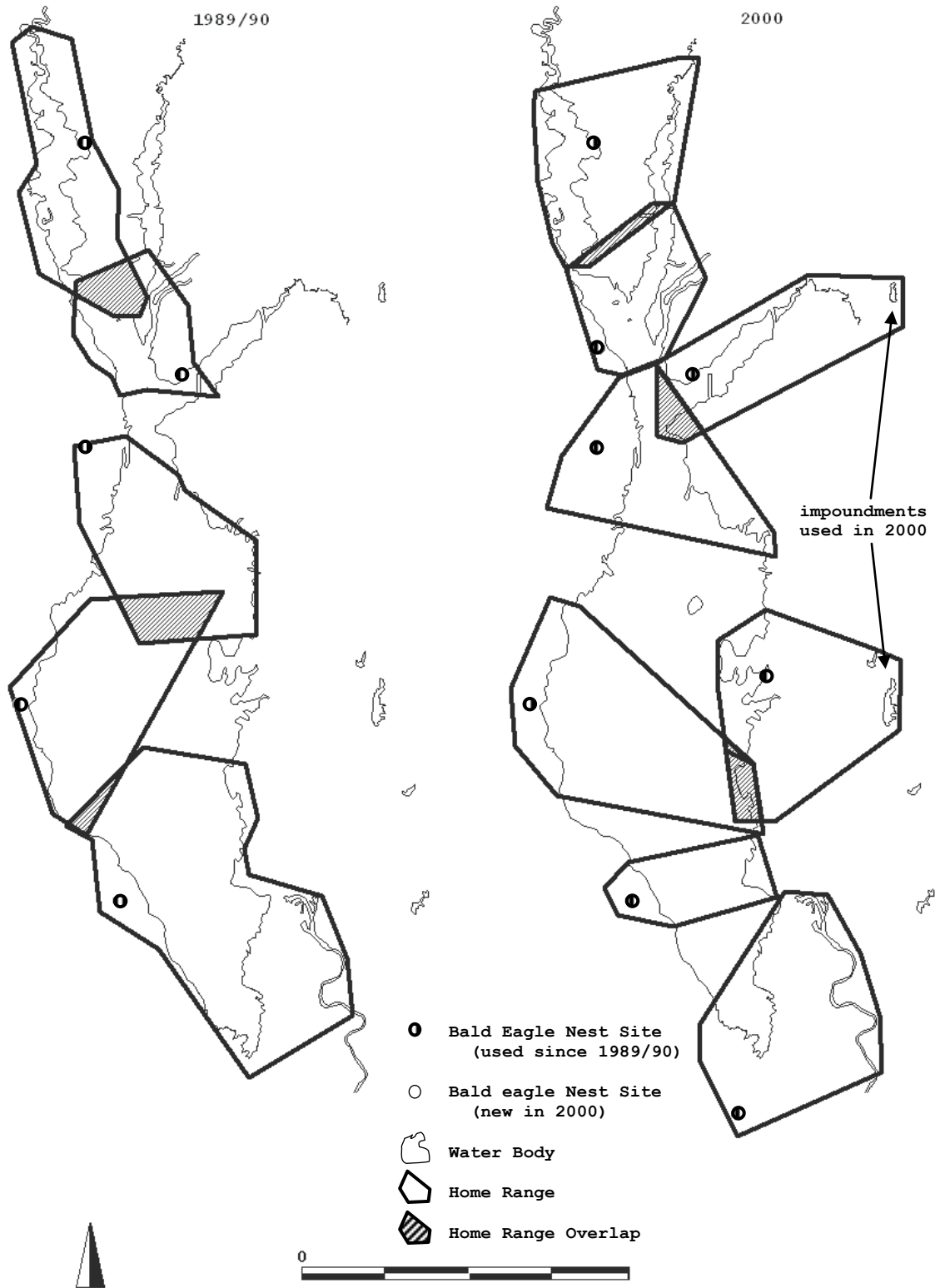North Fork
Payette
River

Idaho

Area
Enlarged
Above

2   0   2   4   6   8   10 Kilometers

Figure 2. Home ranges and home range overlap of Bald Eagles nesting at Lake Cascade,

Idaho, in 1989/90 and 2000.

1989/90

2000

impoundments
used in 2000

O Bald Eagle Nest Site
(used since 1989/90)

○ Bald eagle Nest Site
(new in 2000)

Water Body

Home Range

Home Range Overlap

0

RELATIONSHIP BETWEEN AGGRESSION AND REPRODUCTIVE SUCCESS OF

TERRITORIAL BALD EAGLES AT LAKE CASCADE, IDAHO

Introduction

Aggressive behaviors, such as territorial defense, defense of mates and young, and aggression that results in material rewards (e.g., foraging and kleptoparasitism), can contribute to an animal's survival and reproductive success and, consequently, its fitness. Individuals in high quality territories are likely to experience higher reproductive output than those in poorer territories. Similarly, adults that lose few young to predators experience increased fitness. Defending a mate from aggression may increase fitness, particularly if it is a high quality mate or mates are scarce (e.g., Back et al. 2002). Mate defense in birds (a group that commonly maintains pair bonds across breeding seasons) also may increase direct fitness in subsequent years, since familiarity with a mate is positively related to nest success (Ens et al. 1996). Each of these cases (territorial, offspring, or mate defense) would produce a positive relationship between aggressive behaviors and reproductive success.

Alternatively, there are also situations in which a negative relationship between aggression and reproductive success would be predicted. For instance, highly aggressive individuals may be a direct threat to a mate or offspring. On the other hand, individuals exhibiting low levels of aggression may be more nurturing parents (although this has not directly been assessed in nature, it is nevertheless a logical possibility that should be tested in the future). Peters et al. (2002) experimentally increased testosterone levels in

male Superb Fairy-wrens (*Malurus cyaneus*) and found it reduced paternal care. In other species there is evidence that reduced aggression after egg-laying improves nesting success. For example, contrary to expectation, male White-crowned Sparrows (*Zonotrichia leucophrys*) did not increase aggression (as one might expect) following testosterone implantation during the incubation phase, suggesting a mechanism for reducing aggression, even in the presence of elevated testosterone (Meddle et al. 2002). Vleck and Brown (1999) demonstrated that testosterone levels (and aggression) in two species of *Aphelocoma* jays differed depending on the species' reproductive strategies (monogamous pairs on territories versus large social breeding groups).

Relationships between levels of aggression and reproductive success have not been clarified. Brood size potentially could affect parental aggression. With a larger brood, there is a greater threat to reproductive success if the parent is not aggressive. Large broods require more food and are more attractive to potential predators. Alternatively, both aggression and reproductive success could be related to a third factor, such as age or past reproductive experience. Older, more experienced birds generally experience higher reproductive success (Ens et al. 1996), thus birds with previous experience in a nesting area may be more aggressive in its defense. Hyman et al. (2004) found that Song Sparrow (*Melospiza melodia*) aggression was positively related to experience in the nesting area.

There have been no previous attempts to describe relationships between aggression, *per se*, and reproductive success in falconiform raptors (though see Watson and Watson [1987] for a discussion of the effect of one type of aggressive behavior on

productivity). Aggressive interactions between territorial Bald Eagles are conspicuous

behaviors during the breeding season (Buehler 2000). Unfortunately, these behaviors

typically are described only anecdotally, and most reports of aggression in Bald Eagles

(*Haliaeetus leucocephalus*) describe intraspecific interactions at wintering areas where

eagles congregate in large numbers at locally abundant food sources (Fischer 1985,

Hansen 1986, Jorde and Lingle 1988, Knight and Skagen 1988, Bennetts and McClelland

1997). Mahaffy and Frenzel (1987) described aggressive interactions between territorial

Bald Eagles and proposed a technique for designating areas actively defended by Bald

Eagles. Whereas several studies have defined the "rules" of aggressive encounters and

circumstances that lead to them (Hansen 1986, Knight and Skagen 1988, Bennetts and

McClelland 1997), none has addressed the relationship between these interactions and

breeding success.

Bald Eagles often nest and feed in close proximity to Ospreys (*Pandion haliaetus*)

and opportunities for aggression are common. Though Ospreys have been the aggressors

(not the recipients) in most interactions (Burr 1912, Prévost 1979, Jamieson and Seymour

1983), these encounters between Bald Eagles and Ospreys often carry disproportionately

negative consequences for Ospreys (Ogden 1975, Gerrard et al. 1976). Osprey

aggression toward eagles may stem from the propensity of Bald Eagles' to pirate (i.e.

kleptoparasitize) fish from Ospreys (Ogden 1975), but threats of predation by eagles also

may trigger such antagonism. Bald Eagles may eat Osprey eggs (Grubb and Shields

1977), and Flemming and Bancroft (1990) and Liston (1996) have described incidences

of possible and actual predation of Osprey nestlings by Bald Eagles. MacDonald and

Seymour (1994) documented the only reported case of a Bald Eagle killing and eating an adult Osprey.

The objectives of this study were to 1) quantify and describe aggressive interactions of breeding Bald Eagles with conspecifics and other avian species, and 2) explore the costs and benefits of Bald Eagle aggression using productivity and nestling weight as indicators of reproductive success. This study explicitly describes relationships between aggression and reproductive success and does not attempt to assert that change in one factor is the direct cause or effect of change in the other. We predict that bald eagle reproductive success will be correlated with aggression for the Bald Eagle breeding population at Lake Cascade, Idaho.

Methods

<u>Study Area</u>

Lake Cascade is a reservoir on the North Fork of the Payette River in Long Valley, Valley County, Idaho (Figure 3). The reservoir is approximately 27 km long, 1.6 to 6.4 km wide, has predictable, seasonal changes in water levels, and reaches maximum storage during mid-June (US Bureau of Reclamation 2002). At full pool, the reservoir averages 7.5 m deep, has a surface area of 11 452 ha, and has a surface elevation of 1524 m.

Bald Eagles first began nesting at Lake Cascade in 1976 (Melquist 1987). By 2001, the Lake Cascade eagle population had increased to 10 territorial pairs, nine of which were included in this study. Nest sites are spaced relatively evenly around the

perimeter of the lake and along the North Fork Payette River. All are within 3 km of the
shoreline, and, on average, adjacent nests are 4.9 km apart (range: 2.8 – 7.7 km; Fig. 3).

Lake Cascade also supports a large population of breeding Ospreys. During the
1978-1980 breeding seasons, the number of occupied Osprey nest sites (i.e. the number
of breeding pairs) ranged from 23-28 (Van Daele and Van Daele 1982). Since that time
the number of breeding Ospreys at Lake Cascade has increased substantially to an
estimated 90 pairs (US Bureau of Reclamation 2002), although no comprehensive survey
has been conducted recently. Other bird species known to be aggressive toward nesting
eagles and occurring on Lake Cascade include Red-tailed Hawks (*Buteo jamaicensis*),
American Crows (*Corvus brachyrhynchos*), and Common Ravens (*Corvus corax*) (US
Bureau of Reclamation 2002).

Field Observations of Aggressive Behaviors

We used a focal animal sampling protocol to observe behavioral interactions at
Lake Cascade during the 2000 and 2001 breeding seasons. Because of funding and
logistical constraints, we did not band or mark adult Bald Eagles for this study. Instead,
we focused on birds that were associated with specific nest sites and recorded data only
for those birds that we knew were residents of a particular territory. All observations
began at the nest site and, therefore, all observations were associated with a bird of
known identity.

Observations of nesting territories began in mid-March when courtship and egg-
laying were in progress, and continued until nestlings fledged (approximately 1 August).
Observations in March allowed verification of occupancy and the presence of breeding

pairs (as determined by birds in incubation postures). Occupied territories were monitored for the duration of the breeding season. During incubation (April), we conducted observations four days per week. For the remainder of the nesting season, observations were made by one or two observers on five consecutive days per week.

I ordered observations of pairs by randomly selecting pairs without replacement until all pairs had been sampled. After the last pair in each sequence had been selected, the method was repeated through the end of the breeding season. This method ensured that the same level of effort was used to monitor each breeding pair. Observations generally began at 07:00 MST, weather permitting, and continued until approximately 21:00. As the season progressed, and some eagles spent long periods (> 2 hr) away from the nest, observation periods were shortened to be sufficient to observe at least one of the breeding pair within the home range. Thus, observation periods were not always uniform in length. However, average time spent at each nest site remained approximately equal.

Observations of eagle movements and behaviors were made using binoculars and spotting scopes. When only one observer was available, the objective was to keep the focal bird in view and to maintain sight of the nest if possible. When two observers were present (only during the nestling stage), the stationary observer monitored the focal pair from a fixed position from which the nest and as much of the foraging area as possible were visible. From a boat or truck, the mobile observer began observations either at the fixed observer's point or another location that offered the widest view of foraging areas. The mobile observer's objective was to keep the target bird in view at all times by following the bird as movements occurred. Every effort was made to minimize the impact

of observers on eagle behavior, namely by restricting movements when near nest or perch sites and maintaining a minimum 0.5 km following and observation distance. Observers communicated by hand-held radios to improve their ability to maintain visual contact when birds changed locations.

Locations of eagles and the types and duration of activities were recorded continuously throughout each observation period. I categorized activities as flying (flapping, soaring, or gliding), foraging (active attempts to acquire a food item), sitting/brooding, nest maintenance, feeding (adult feeding nestling), eating (adult eating), drinking/washing, preening, perching, and aggressive interactions, but present here only data for aggressive interactions. I quantified activities in "eagle minutes" such that the activities of each bird in the pair were quantified separately and combined for a total number of minutes per pair.

Because Bald Eagles are sexually dimorphic, I could assign gender to individuals, based on size, only when a pair was seen perching within 1 m of each other (Buehler 2000). Consequently, many observations were of eagles of unknown gender, and in those cases, I report activities based on combined observations of both genders and interaction data were based on combined observations of both genders.

I classified aggressive behaviors into four basic categories: vocalization, stoop, chase, and kleptoparasitism. Territorial Bald Eagles commonly vocalize during encounters with intruders (Verner and Lehman 1982, Eakle et al. 1989). Stooping is defined as an attack from above either through powered flight or with wings tucked. A chase is defined as a powered flight by the aggressor behind and in the same direction as

the recipient. Kleptoparasitism is the attempted confiscation of a food item (either successful or unsuccessful) that has been procured by another individual (Brockman and Barnard 1979). I classified focal eagles and other birds involved in interactions as aggressors or victims and recorded the species (and, in the case of Bald Eagles, the age class) of non-focal birds.

Nestling Measurements

I banded, weighed, and measured nestling eagles at 6-8 weeks of age. To establish the timing of banding, nestling ages were estimated from the ground following descriptions by Bortolotti (1984b). I placed a red anodized aluminum leg band with a unique alpha-numeric label on the left leg of each nestling and a standard USGS aluminum band on the right leg. I also measured bill depth using dial calipers and foot-pad and eighth primary length using a thin metal ruler as described by Bortolotti (1984a). Finally, I weighed each nestling using a spring scale but did not estimate crop content. I calculated a more precise nestling age based on structural measurements of nestlings following the protocol described by Bortolotti (1984a; Appendix B).

Data Analysis

I summed all aggressive interactions within territory and season and categorized interactions into two groups: interactions in which the focal eagle was the aggressor and interactions in which the focal eagle was the recipient. Within the two groups, I divided the number of interactions within each territory by the number of observation periods at the territory. Because observation periods were of relatively uniform length across nest

sites, this standardization removed any bias associated with different levels of observation effort at the territories as the seasons progressed.

Because reproductive success ultimately involves not only the number of offspring produced, but also their quality, I included the size of nestlings in the analysis of the relationship between aggression and reproductive success. I considered nestling size to be an indication of nestling quality, because larger birds are more likely to survive once fledged and be more successful at acquiring food (Knight and Skagen 1988). This assumption is supported by the fact that, in general, larger nestling birds are more likely to be recruited into the population as adults (Magrath 1991, Lindén et al. 1992, Verboven and Visser 1998, Both et al. 1999, Overskaug et al. 1999). I averaged body mass of all nestlings from the same nest. I was unable to band and weigh all nestlings at exactly the same age, so I included average nestling age as a covariate in analyses of nestling mass. Bald Eagles are sexually dimorphic, and after 40 days of age, there is virtually no overlap in body mass between males and females (Bortolotti 1984b). The female to male body mass ratio remains essentially unchanged during this period. Because nests often contained both male and female nestlings and to make direct comparisons among nests, I standardized nestling body mass by multiplying each female's body mass by 0.786 (based on male to female body mass ratios of nestlings of known sex; Bortolotti 1984a) before averaging nestling mass for each nest.

I performed all statistical analyses using the JMP® 8.0 statistical package (SAS Institute Inc., Cary, NC, USA). For all statistical analyses I defined productivity as the number of nestlings that reached at least 80% of fledging age (i.e., approximately 60 days

of age; Steenhof 1987). I performed Student's *t*-tests to test for between-year differences in aggressive interactions and productivity. I used simple linear regressions to describe relationships between aggression and productivity and between aggression and nestling mass. Linear regressions inherently imply a causative relationship between variables, but I do not make that assumption in the interpretation of the results. Data from nests that were used in consecutive years are likely to be ecologically dependent, so for each of these nests I randomly selected data from one season to use in all regression analyses. I used a Bonferroni-corrected α-level of 0.0125 for between year differences in aggressive interactions and used an α-level of 0.05 to establish significance in all other tests.

Results

I conducted more than 556 hr of observations at nine occupied breeding territories at Lake Cascade in 2000 for an average of 61.8 hr per occupied territory. In 2001, I monitored eight territories that had been used in 2000 and one new territory, for 358 hr (39.8 hr per occupied territory). Observation effort for both years exceeded 914 hr and averaged 50.8 hr per occupied territory (Table 2).

Aggressive Interactions

I recorded 119 aggressive interactions involving Bald Eagles with conspecifics and other bird species. The total number of interactions did not differ between years (t_{16} = -0.702, P = 0.493; Table 2). Nesting Bald Eagles instigated 53 interactions, whereas 66 were directed at nesting eagles. None of the interactions was between two adult eagles. Ospreys were attacked by eagles on 12 (22.6%) occasions and acted aggressively toward

adult nesting eagles on 34 (51.5%) occasions. The next most common aggressors toward

adult nesting Bald Eagles were Red-tailed Hawks (17 occasions or 4.6%), though a hawk

was attacked by an adult eagle on only one occasion. Immature Bald Eagles never

instigated interactions with territorial eagles but were attacked by adult Bald Eagles 22

(41.5%) times. Other notable encounters involving eagles included nine interactions with

Common Ravens, six interactions with American Crows, and four interactions with

Canada Geese (*Branta canadensis*). On one occasion I observed a Long-billed Curlew

(*Numenius americanus*) chase a territorial eagle.

Stoops and chases were the most common forms of aggressive interaction at Lake

Cascade (53 (44.5%) and 49 (41.2%) incidents, respectively). Nesting Bald Eagles were

most likely to be stooped at by individuals of other species (49 times, or 74.2%) but were

most likely to instigate chases (32 times, 60.4%). Although kleptoparasitism was not a

common type of interaction (10 occasions, 18.9%), all acts of kleptoparasitism were

instigated by nesting eagles, and 70% were directed against Ospreys. All attempts at

kleptoparasitism occurred over water, which may have contributed to the low success rate

(50%) due to fish being dropped in the water where they could not be recovered.

Vocalizations were of minor importance as a means of aggressive interaction by Bald

Eagles (seven occurrences, 13.2%) and was never seen directed at eagles.

Territorial Bald Eagles instigated a mean of 0.68 aggressive interactions per

observation period in 2000 and only 0.28 aggressive interactions per observation period

in 2001; however, the difference was not significant ($t_{16} = $ -1.522, $P = 0.148$; Table 2).

Territorial Bald Eagles were the recipients of aggression 0.63 times per observation

period during 2000 and 0.45 times per observation period during 2001. Again, the difference was not significant (t_{16}= -0.057, P = 0.956; Table 2).

Productivity

I found no difference in eagle productivity between the two years of the study (t_9 = 0.31, P = 0.76; Table 2). In 2000, seven pairs produced 13 fledglings for an average of 1.9 young per successful pair. In 2001, four pairs produced only eight fledglings for an average of 2.0 young per successful pair.

I detected no significant relationships between productivity and the number of total aggressive interactions ($F_{1,8}$ = 2.869, P = 0.129, r^2 = 0.264; Fig. 4), those instigated by territorial Bald Eagles ($F_{1,8}$ = 0.957, P = 0.357, r^2 = 0.107; Fig. 4), or those in which territorial eagles were the recipients ($F_{1,8}$ = 1.964, P = 0.199, r^2 = 0.197; Fig. 4). Nevertheless, pairs with higher productivity tended to be involved in more aggressive interactions (Fig.2).

Nestling Body Mass

I banded 21 nestling Bald Eagles during the two breeding seasons (13 in 2000 and 8 in 2001). None of the eaglets had an enlarged crop when weighed, so I assumed that the effect of crop content mass was negligible. After adjusting nestling body mass for sex, mean ($\pm$ SE) nestling body mass was 4.03 $\pm$ 0.08 kg in 2000 (range 3.46 - 4.48 kg; Table 1) and 4.15 $\pm$ 0.15 kg in 2001 (range 3.77 - 4.50 kg), with no difference between years (t_9 = 1.03, P = 0.32). I also averaged adjusted nestling body mass within nest (Table 2). Mean ($\pm$ SE) adjusted body mass was 4.01 $\pm$ 0.10 kg per nest in 2000 (range

3.46 - 4.40 kg) and 4.15 ± 0.13 kg per nest in 2001 (range 4.02 - 4.37 kg), with no

difference between years ($t_9 = 0.95$, $P = 0.38$).

Nestling age at the time of weighing ranged from 41 to 61 days. Nestlings

averaged 53.0 days per nest in 2000 (range 45.3 - 59.0 days) and 52.0 days in 2001

(range 49.0 - 54.5 days). Linear regression models using average nestling age as a

covariate indicated that the number of total aggressive interactions involving territorial

bald eagles per observation period and nestling body mass were unrelated ($F_{2,3} = 1.758$, P

$= 0.312$, $r^2 = 0.539$; Fig. 5). I also found no relationship between nestling body mass and

either the number of aggressive interactions per observation period instigated by

territorial bald eagles ($F_{2,3} = 1.793$, $P = 0.307$, $r^2 = 0.545$; Fig. 5) or interactions per

observation period directed at eagles ($F_{2,3} = 2.813$, $P = 0.205$, $r^2 = 0.652$; Fig. 5).

Discussion

Bald Eagles at Lake Cascade were involved in aggressive interactions, on

average, once per observation period during 2000 and 2001. Interactions at Lake

Cascade usually involved Ospreys, Red-tailed Hawks, and non-breeding Bald Eagles.

Ospreys generally are considered to be the Bald Eagle's most common competitor

(Stalmaster 1987, Buehler 2000), and this proved to be the case at Lake Cascade.

Nevertheless, these interactions appeared to have little effect on eagle nesting success.

The results of this study do not show a significant relationship between aggression

and nest success in Bald Eagles. Several factors may explain why aggression was not

related to the reproductive success at Lake Cascade. Nesting densities of Bald Eagles

and their competitors at Lake Cascade may not have been high enough to cause the levels of competition for prey and aggression that can affect reproduction. Lake Cascade provides a large and diverse prey base for eagles and their competitors (US Bureau of Reclamation 2002). No Bald Eagle nests failed at Lake Cascade during this study once eaglets hatched (though two nesting attempts by eagles failed to produce clutches in 2001), nor did I observe any evidence of brood reduction. In short, prey may not be a limiting factor at Lake Cascade.

If a relationship exists between aggression and reproductive success, it may be obscured for several reasons. The sample size used in this study is too low to detect any but a strong relationship between aggression and nest success. These small sample sizes are an inherent consequence of working with the Bald Eagle population at Lake Cascade, and raptors, in general. Nevertheless, a larger study using more pairs of eagles would likely be necessary to detect a relationship if one exists (or if the relationship is weak). In addition to the small sample size used in this study, Bald Eagle productivity at Lake Cascade was relatively low in 2001. In 2001, early spring storms and late spring periods of freezing weather may have contributed to the decrease in productivity.

The frequency of kleptoparasitism also may be related to prey availability. If foraging conditions are poor, kleptoparasitism may increase. During the two breeding seasons, I witnessed nine acts of kleptoparasitism (both successful and unsuccessful attempts) by nesting eagles, most directed at Ospreys. These nine incidents of kleptoparasitism accounted for nearly 19% of all aggressive interactions instigated by eagles, and 20% of all documented attempts to capture prey. Rates of kleptoparasitism

were low when compared to potential rates (as high as 54%) of kleptoparasitism in poor

foraging conditions in winter (Fischer 1985, Knight and Skagen 1988). In winter,

kleptoparasitism rates were lowest during periods of high prey abundance (Knight and

Skagen 1988). Consequently, I believe that prey availability at Lake Cascade was

relatively high because incidences of kleptoparasitism were relatively infrequent.

Although I detected no significant relationship between nestling mass and

aggression, I did detect a non-significant positive trend in the relationship between

productivity and the number of cases in which eagles were involved in aggressive

interactions. This trend occurred regardless of whether eagles initiated the aggression or

were the recipients. More aggressive interactions by eagles would be expected if nests

were located in areas of highest prey availability, because high prey availability should

lead to increased competitor density and, hence, increased encounter rates with potential

competitors. High competitor density could lead to more interactions with nesting eagles,

because eagles are not only potential competitors for resources, but are potential

predators of other raptors' nestlings (Flemming and Bancroft 1990 and Liston 1996).

The reverse is also true in California, where Red-tailed Hawks are known predators of

Bald Eagle nestlings (Perkins et al. 1996). Therefore, when prey availability is high,

Bald Eagle nesting success is probably influenced more by availability and diversity of

prey and less by aggression levels, *per se*.

Because I did not measure prey availability in this study, I cannot draw any

conclusions about the relationship of aggression levels to reproductive success and the

relative role of food supply. This is due in part to the observational and descriptive

nature of the study. A manipulative or experimental approach might address these questions more effectively; unfortunately, sample sizes for such an experiment at Lake Cascade would likely be small, even if logistical constraints to manipulations were alleviated. Nevertheless, a better understanding of the relationship between aggression and reproductive success might be obtained by manipulating aggression levels of nesting Bald Eagles. Large-scale field experiments manipulating hormone levels and food availability (via supplementation) in breeding Bald Eagles might also clarify the relative contributions of aggression and prey availability to the reproductive success of the species.

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Table 2. Summary of variables associated with aggression and productivity of Bald Eagles breeding at Lake Cascade, Idaho, during 2000 and 2001 (all measures, except breeding pairs, presented as $\overline{X} \pm S_{\overline{X}}$; AI/OP = aggressive interactions per observation period).

Variable	2000	2001	t	p
breeding pairs	9	9		
observation effort (hr)	61.8 ± 9.5	39.8 ± 6.4		
Aggressive Interactions				
total	7.9 ± 2.0	5.9 ± 2.0	-0.702	0.493
eagles as aggressors	3.9 ± 0.9	2.0 ± 0.9	-1.522	0.148
eagles as receivers	4.0 ± 1.4	3.9 ± 1.4	-0.057	0.956
AI/obs. period				
total	0.63 ± 0.19	0.44 ± 0.19	-1.615	0.126
eagles as aggressors	0.68 ± 0.13	0.28 ± 0.13	-2.184	0.044
eagles as receivers	0.63 ± 0.18	0.45 ± 0.18	-0.750	0.464
Young/occupied pair	1.4 ± 0.36	0.9 ± 0.36	-1.078	0.297
Avg. nestling weight (kg)	4.01 ± 0.10	4.15 ± 0.13	0.886	0.387
nestling mean age (d)	53.0 ± 2.0	52.0 ± 1.3		

Figure 3. Lake Cascade study area with locations of occupied Bald Eagle and Osprey

nests during 2000 and 2001.

Bald Eagle nest sites
Osprey nest sites
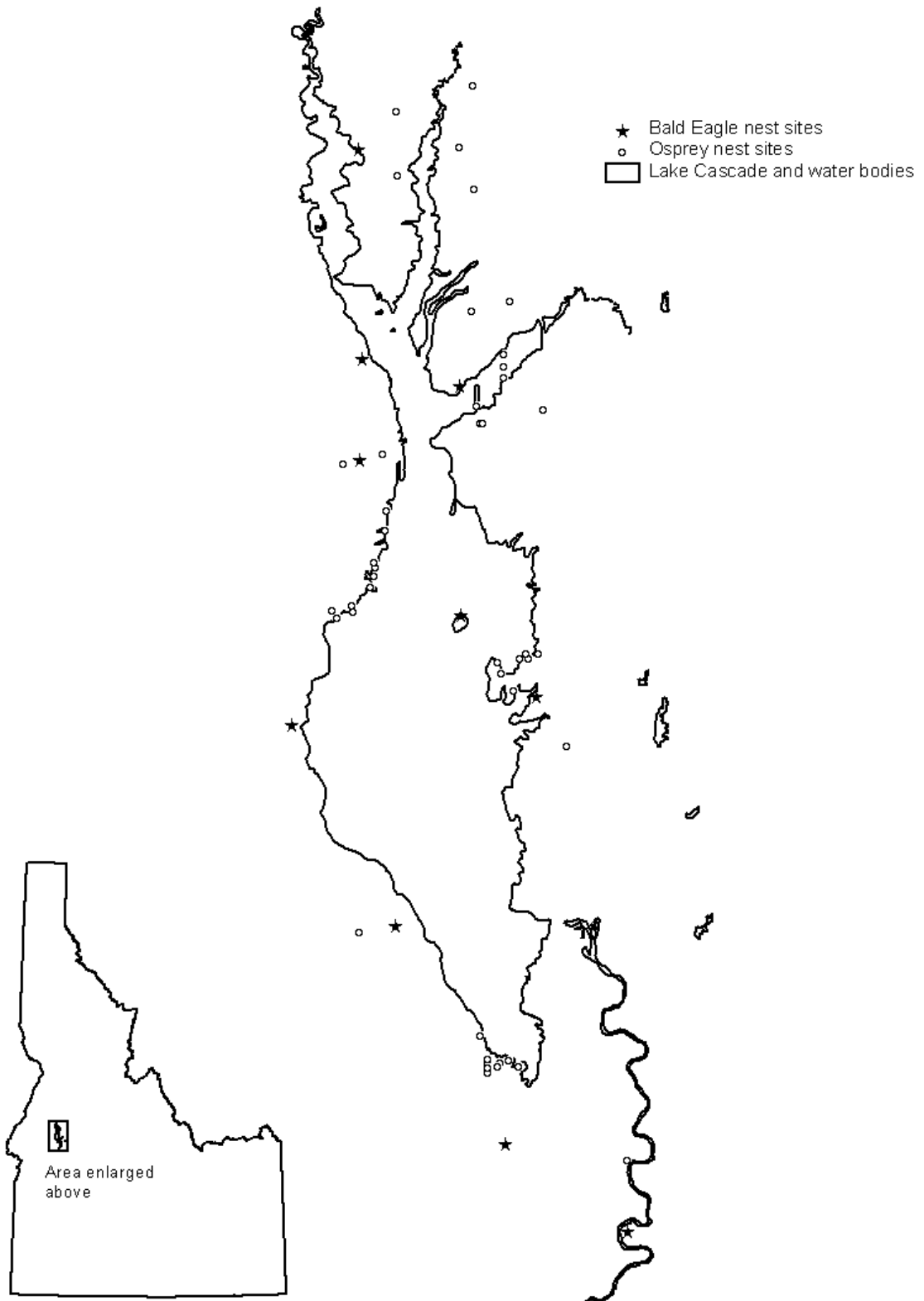Lake Cascade and water bodies

Area enlarged
above

Figure 4. Relationship between Bald Eagle productivity in 2000 and 2001 and A) total number of aggressive interactions per observation period (AI/OP) (Prod = 0.265 + 0.907* Total AI/OP; adj. R^2 = 0.172), B) AI/OP when territorial Bald Eagles were aggressors (Prod = 0.663 + 1.114*Aggressor AI/OP; adj. R^2 = -0.005), and C) AI/OP when territorial Bald Eagles were recipients (Prod = 0.722 + 1.004*Receiver AI/OP; adj. R^2 = 0.097).
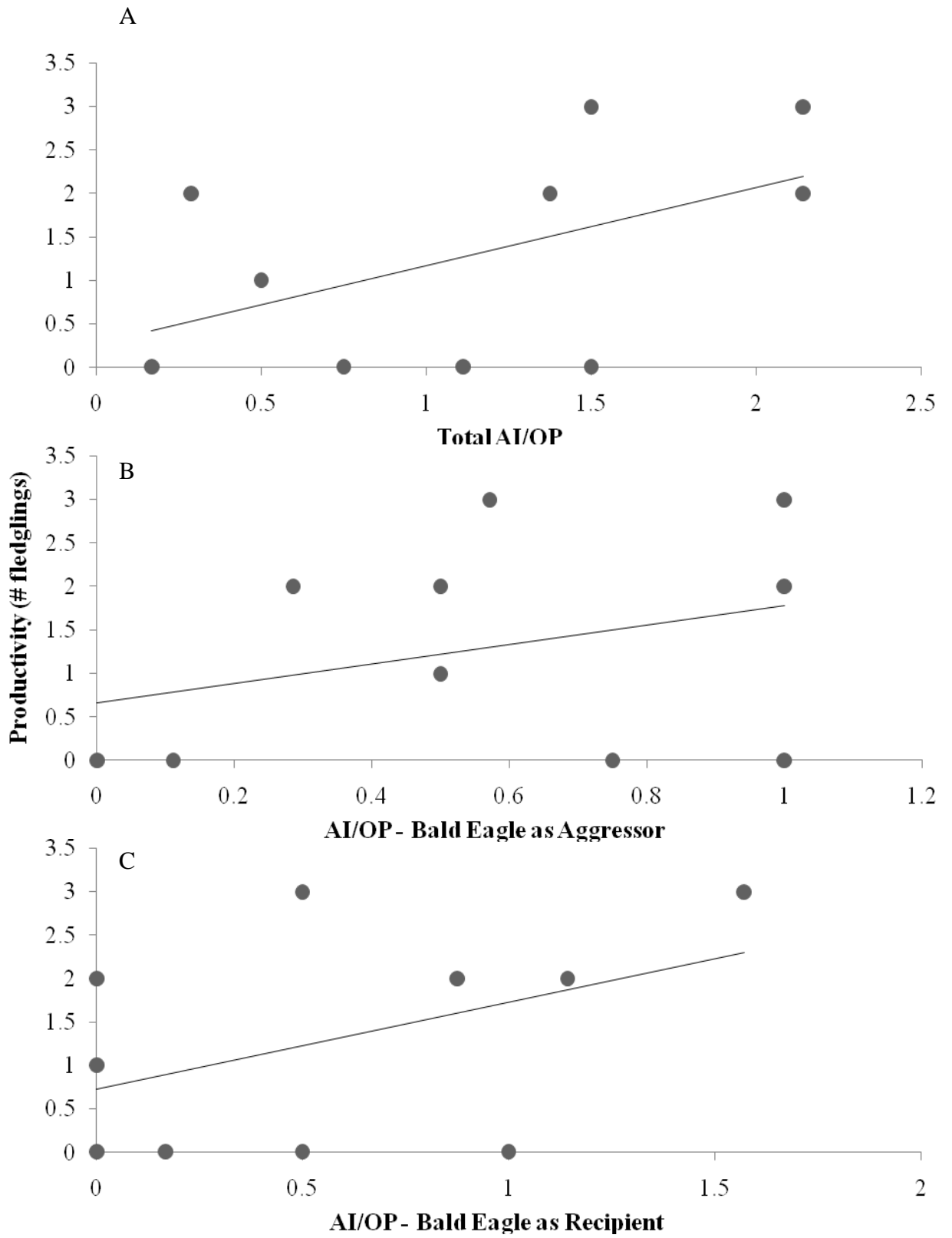
Figure 5. Relationship between Bald Eagle mean nestling mass adjusted for sex in 2000 and 2001 and A) total number of aggressive interactions per observation period (AI/OP) (Mass = 2.501 - 0.051*AI/OP + 0.032*Age; adj. R^2 = 0.233), B) AI/OP when territorial Bald Eagles were aggressors (Mass = 2.601 + 0.128*AI/OP + 0.027*Age; adj. R^2 = 0.241), and C) AI/OP when territorial Bald Eagles were recipients (Mass = 2.203 - 0.130*AI/OP + 0.038*Age; adj. R^2 = 0.420).
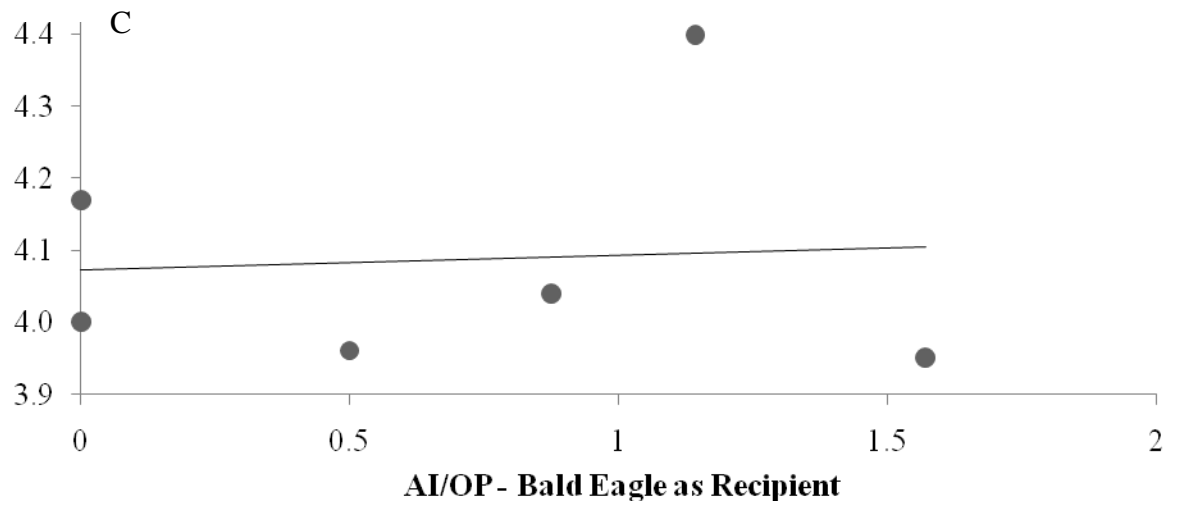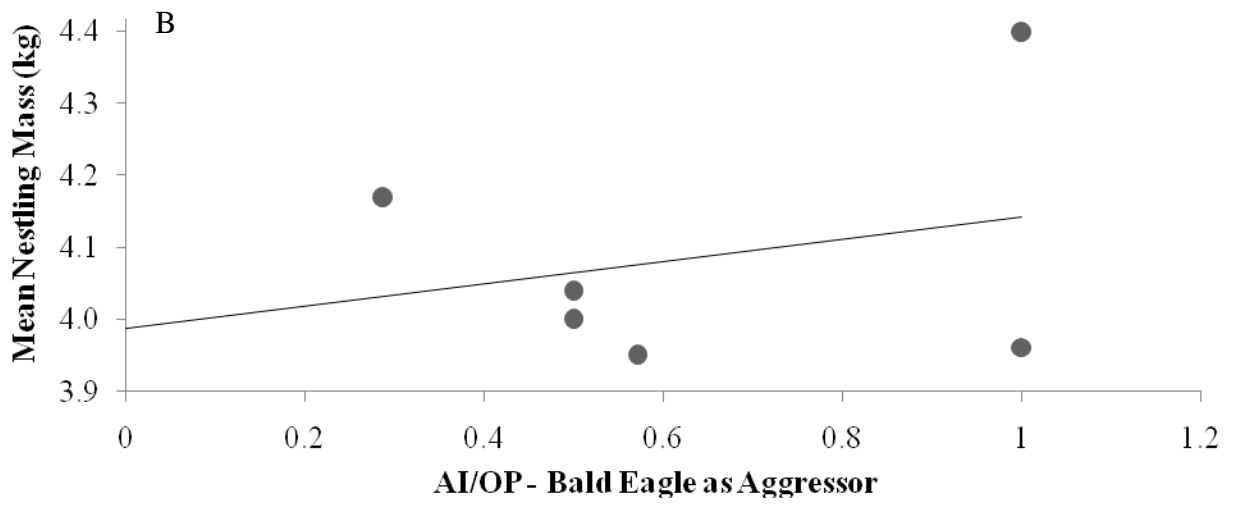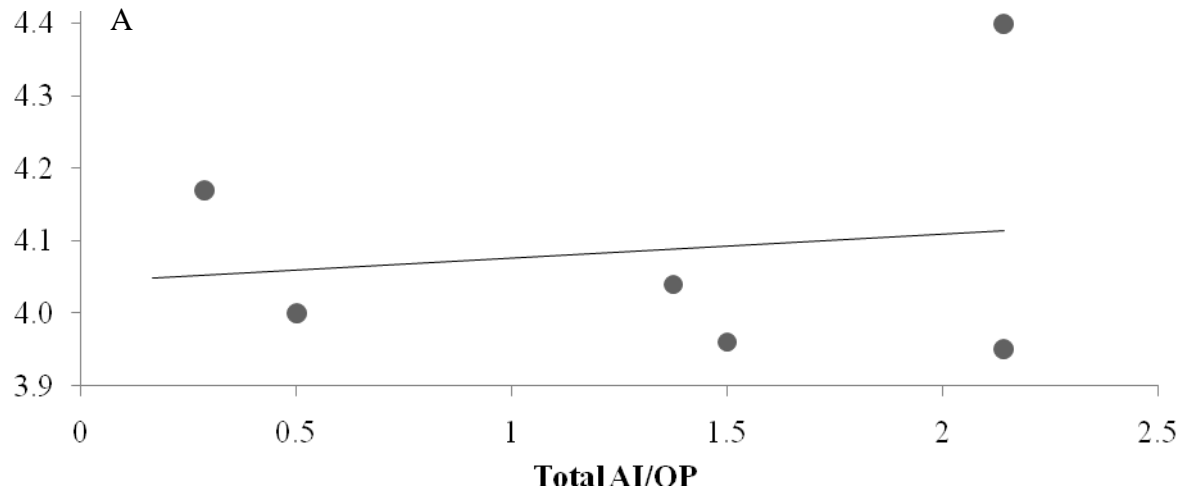
APPENDIX A

Bald Eagle Activities at Lake Cascade, ID, in 2000

Bald Eagle Activities at Lake Cascade, ID, in 2000.

Territory	2000 Activity (hours)											
	Perch	Sit/ Brood	Preen	Fly	Feed	Eat	Aggr. Inter.	Nest Maint.	Forage	Other	Out of View	Total
Buttercup	53.33	22.95	7.1	3.62	1.52	0.67	0.27	0.05	0.15	0.82	80.78	90.47
Donnelly	31.05	20.93	1.23	1.85	1.87	0.08	0.07	0.12	0	1.52	70.8	58.72
French Creek	17.13	12.62	0.83	1.63	1.62	1	0.02	0.1	0.05	0	61.62	35
Gold Fork	64.32	12.8	4.85	2.48	2.1	2.12	0.35	0.5	0.05	0.52	78.8	90.08
Hurd Creek	1.52	12.7	0.35	0.67	0	0	0.03	0.1	0	0	14.83	15.37
Poison Creek	6.82	0	0.13	0.85	0	0.12	0	0	0	0.32	31.97	8.23
Raspberry	33.48	11.82	0.97	1.35	1.32	0.65	0.2	0.07	0.08	0.48	76.1	50.42
Sugarloaf	52.08	20.12	1.82	2.58	1.4	0.38	0.3	0	0.18	0.65	56.57	79.52
												427.8
Mean	32.47	14.24	2.16	1.88	1.23	0.63	0.15	0.12	0.06	0.54	58.93	53.48
Percent	0.61	0.27	0.04	0.04	0.02	0.01	0	0	0	0.01		

APPENDIX B

Bald Eagle Productivity at Lake Cascade, ID, in 2000 and 2001

Bald Eagle Productivity at Lake Cascade, ID, in 2000 and 2001.

Territory	2000				2001			
	Occupied	Eggs	Successful	# Young	Occupied	Eggs	Successful	# Young
Buttercup	Y	Y	Y	2	Y	Y	Y	2
Cabarton	Y	Y	Y	3	Y	Y	N	0
Donnelly	Y	Y	Y	1	Y	Y	Y	2
French Creek	Y	Y	Y	1	Y	Y	Y	2
Gold Fork	Y	Y	Y	1	Y	Y	N	0
Hurd Creek	Y	Y	N	0	Y	Y	N	0
Island	-	-	-	-	Y	N	N	0
Poison Creek	Y	Y	N	0	Y	N	N	0
Raspberry	Y	Y	Y	2	Y	Y	Y	2
Sugarloaf	Y	Y	Y	3	Y	N	N	0
Total	9	9	7	13	10	7	4	8
# Fledged/Occupied				1.4				0.8
# Fledged/Successful				1.9				2.0