AN ABSTRACT OF THE THESIS OF

Robert J. Steidl for the degree of Doctor of Philosophy in Wildlife Science presented on September 1, 1994. Title: Human Impacts on the Ecology of Bald Eagles in Interior Alaska.

Abstract approved: Signature redacted for privacy.

Robert G. Anthony

To assess the consequences of increased recreational activity on bald eagles (*Haliaeetus leucocephalus*), we studied factors that influenced their behavior and reproductive success in the Gulkana River basin, Alaska, from 1989 to 1993. Both extrinsic and intrinsic factors were associated with reproductive success. Productivity averaged 0.86 young fledged per occupied territory (SE = 0.05) with 59% nest success ($n = 274$), but productivity varied among years and subdrainages ($P < 0.02$). Further, productivity and nest success, but not density, of pairs along the river corridor were negatively associated with levels of human activity ($P = 0.037$). Pairs that were successful one year were more likely to occupy the same territories, less likely to change nest locations within a territory, more likely to be successful, and fledged more offspring the following year compared to pairs that were previously unsuccessful. Most nesting failure (92%) occurred during incubation. Annual and regional variability in reproductive success of northern bald eagle populations may result from susceptibility to severe spring weather conditions during incubation.

Behavior of breeding eagles changed when humans camped near ($\approx$100 m) versus far ($\approx$500 m) from nests ($P = 0.0036$). Adults decreased the time they fed nestlings and themselves (-30%), preened (-53%), slept (-56%) and maintained nests (-50%), but increased the time they brooded nestlings (14%). Further, adults decreased the frequency with which they performed most nesting behaviors, including the amount of prey they consumed at nests (-26%) and fed to nestlings (-29%). Our results show that human activity near nests altered breeding behavior, and suggest that if disturbances in nesting territories were sustained, eagle populations could be affected adversely.

The context in which human-eagle encounters occurred affected eagle responses to boating activity. The distance a disturbance was first visible to eagles, the distance they perched from the river, perch height, eagle age, julian date, and ambient temperature were among those factors that influenced both flush response and flush distance of nonbreeding eagles. Breeding adults were less likely to flush and flushed at shorter distances (87.5 ± 10.2 m) than nonbreeding adults (113.0 ± 4.5 m) to approaching boats ($P < 0.024$). Based on our studies, we recommend a series of strategies to minimize the adverse effects of human activity on breeding and nonbreeding eagles.

Human Impacts on the Ecology of Bald Eagles in Interior Alaska

by

Robert J. Steidl

A DISSERTATION

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Completed September 1, 1994
Commencement June 1995

Doctor of Philosophy thesis of Robert J. Steidl presented on September 1, 1994

APPROVED:

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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Robert J. Steidl, Author

ACKNOWLEDGEMENTS

Anyone taking the time to read this section surely realizes that this thesis resulted from the collaborative effort of many people. Foremost among these is my major professor, Bob Anthony, who supervised and supported my education while at Oregon State and provided superb logistical support during my field research in Alaska. Bob offered the independence I hoped for and it is for that I am most grateful. Dan Edge, Bill McComb, Cliff Pereira, and Bo Shelby, my graduate committee, all provided guidance and support from different perspectives that added breadth to my research and education. This project was funded by the Bureau of Land Management, Alaska, and performed under the auspices of the Oregon Cooperative Wildlife Research Unit. I offer my sincere thanks to the personnel of both agencies for this unique opportunity. Students and advisors of Oregon State University's Statistical Consulting Center, led by Cliff Pereira, provided suggestions and guidance for many analyses.

I had solid help and encouragement while in Alaska. Most gratitude goes to those who worked with me in the field, for tolerating gracefully the rain, legendary mosquitoes, and ridiculous study design that required us to observe eagles for 24 hours a day: Gregg Steidl, Richard Frenzel, Steve Desimone, Brian Bogaczyk, Jamie Hawk, and Tressa Wang. In addition to their field efforts, I am especially thankful to Gregg Steidl, my brother, for working with and enduring me for two field seasons, and to Richard Frenzel for offering sound advice during the initial phases of this research. I hope fishing on the Gulkana made up somewhat for the "overtime". I am indebted to the personnel of the Glennallen Resource District, Bureau of Land Management, for their ceaseless logistical support and hospitality. I am particularly grateful to Frank Bird, Janelle Ecklund, Gene Keith, and Kurt Sorenson. For guidance when this project was initiated I thank Craig Altop from the B.L.M. Alaska regional office and Skip Ambrose from the U.S. Fish and Wildlife Service. Pilots Jerry Lee and his dad Al had such a complete knowledge of the region's terrain and expert skills that I often wondered if I was really a necessary part of our surveys efforts. Jennifer Fox, Trish Cutler, and Jenna App painstakingly keypunched our data.

This thesis has benefitted from the critical reviews and ideas generated from those around O.S.U.'s Department of Fisheries and Wildlife. These people are also my dearest friends. Foremost among these are Steve DeStefano, Dan Edge, Sally Olson-Edge, Kim Nelson and my fellow graduate students. I owe these folks a humble and sincere thank you. Karin Kozie always reminded me by example that the animals we work with are always our foremost concern. I thank Karin for the opportunity to repeat this research on golden eagles, which broadened my perspective and appreciation for differences among eagles; however, I am most grateful to Karin for introducing me to my future wife. Jenna App, whose support and timing have been near-perfect, has made me a true believer. Last, and certainly not least, I thank my family for always trusting, supporting, and believing in me.

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Human Impacts on the Ecology of Bald Eagles in Interior Alaska

1: GENERAL INTRODUCTION

Bald eagles (*Haliaeetus leucocephalus*) reach both their highest breeding densities and the northern limit of their geographic distribution in Alaska, yet little is known about their breeding biology throughout most of the state. Throughout Alaska's vast interior, there has never been an intensive study of bald eagle breeding behavior and ecology. With its abundant populations of breeding eagles and expansive wilderness areas, Alaska offers an opportunity to study eagles in areas only marginally influenced by humans.

There have been several investigations into how human activity might affect productivity and foraging patterns of breeding bald eagles, and behavior and habitat use of wintering eagles. However, there have been no direct, manipulative attempts to determine the effects of human activity on nesting behavior, a period when bald eagles may be most vulnerable to human impacts. During 1989-1993, we studied the influence of recreational activities on bald eagles nesting along the Gulkana National Wild River in interior Alaska. Our principal objective was to determine the behavioral and reproductive consequences that increasing recreational use might have on breeding and nonbreeding eagles in the Gulkana Basin. Our secondary objective was to describe the ecology of bald eagles in interior Alaska during the summer. A central tenant throughout this thesis is that human activities do not necessarily have to physically alter habitat to affect habitat quality.

Thesis Organization

We investigated how human activity affected the ecology of this bald eagle population using several approaches, each of which constitute a section of this Thesis. In ***Section 2*** we describe factors affecting reproductive success of eagles in the Gulkana Basin between 1989 and 1993. In ***Section 3*** we describe the behavior of breeding eagles in and near nests. In ***Section 4*** we describe the results of an experiment performed to discern how the presence of low-impact, continuous human activity (i.e., camping) affected breeding behavior. In ***Section 5*** we describe how breeding and nonbreeding eagles responded to recreational boating activity, the most prevalent type of human disturbance to which this population was subjected. In ***Section 6*** we describe numbers and characteristics of recreationists in the Gulkana Basin and assess how different levels of human activity were associated with reproductive success of pairs nesting along the river. Lastly, in ***Section 7*** we restate and expand our management recommendations from each of the previous sections and provide suggestions for future research.

2: REPRODUCTIVE SUCCESS OF BALD EAGLES IN INTERIOR ALASKA

INTRODUCTION

Comparing reproductive parameters of a species under varying levels of abiotic factors such as human disturbance or weather, or biotic factors such as resource competition or habitat quality, can provide insights into how reproduction is regulated by these extrinsic factors. Variation in reproductive rates under different levels of these pressures also can provide direction to biologists concerned with the recovery or management of sensitive or endangered species. When resources for protection of threatened or endangered species are limited, one approach is to concentrate conservation measures in areas where fitness, and therefore the likelihood of population persistence, is highest.

Bald eagles breed in a diversity of wetland habitats including estuaries, lakes, rivers, and coastlines throughout much of North America (Stalmaster 1987:119). However, their reproductive success varies temporally and spatially throughout their range (e.g., Sprunt et al. 1973, Grubb et al. 1983, Gerrard et al. 1992). Differences in reproductive success of bald eagles may reflect differences in habitat quality or other factors influencing these populations.

Because bald eagles are so abundant along Alaska's coast, it is considered a stronghold for the species and may represent ideal habitat. There are, however, several smaller nesting populations in Alaska's interior near the northern limits of the species' distribution. Understanding processes that affect a species' reproductive rates on the periphery of its range can reveal aspects of the species' biology where selective pressures are most intense. From 1989 to 1993, we determined the reproductive success of a population of bald eagles located along the Gulkana National Wild River in interior Alaska. We evaluated how different factors were associated with reproductive success of an eagle population near its biogeographical limit.

STUDY AREA

The Gulkana National Wild River is a free-flowing wilderness river in southcentral Alaska that originates north of Summit Lake and south of the Alaska Range (63°07'N, 150°30'W) and flows south into the Copper River. The Main Stem of the Gulkana River is characterized by clear waters with a combination of whitewater rapids, riffles, and meandering reaches. The Gulkana's two major tributaries, the Middle and West Forks, are similar in character to the Main Stem, but meander considerably more. Hundreds of lakes dot these subdrainages and are especially numerous in the area drained by the West Fork. The Gulkana and its tributaries support anadromous runs of chinook (*Oncorhynchus tshawytscha*) and sockeye salmon (*O. nerka*), as well as resident populations of arctic grayling (*Thymallus arcticus*) and rainbow trout (*O. mykiss*).

Higher elevation areas of the basin (>1,000 m) are treeless and vegetated with a moist tundra community. Lower elevation areas are dominated by boreal forest, composed of black (*Picea mariana*) and white spruce (*P. glauca*), with much lower proportions of balsam poplar (*Populus balsamea*), quaking aspen (*P. tremuloides*), and paper birch (*Betula paperifera*). Eagles nest atop all these species except black spruce, which do not grow large enough to support nests. Nests are built at elevations between 400 and 960 m and are usually located near water, the only area where trees grow large enough to support nests.

The weather in this portion of Alaska is changeable, but during the breeding season, rainfall is moderate compared to coastal Alaska. One of the area's most striking environmental characteristics, resulting from its high latitude, is the extended daylight period from May through August, which approaches 24 hours.

The river supports one of the northernmost nesting populations of bald eagles. The nesting season is short compared to lower latitudes, thus these eagles face considerable time constraints. Eagles arrive in mid-April, begin nesting in early May before winter breakup, young begin to fledge by mid-August, and both adults and young begin to leave their nesting territories in early September.

METHODS

Aerial Surveys

We flew 2-3 aerial surveys each year from 1989 to 1993; our initial 1989 surveys were based on a sample of previously known territories ($n = 30$). We flew our earliest surveys between 7 and 14 May to determine territory occupancy, which we defined as a territory with either an incubating adult, an attending pair of adults, or a clutch of eggs. We flew our latest surveys between 26 July and 12

August to determine which occupied territories were successful (those that fledged ≥1 young) and to count the number of young about to fledge (brood size). During 1989 and 1990 we surveyed a sample of nests ($n = 59$ for both years combined) just after peak hatching in early June to estimate the proportion of failures that occurred during incubation. Surveys were flown with a Piper Super Cub aircraft with a pilot and observer. We examined the accuracy of our aerial brood counts with ground checks at 86 nesting attempts (31% of our entire sample); counts agreed 100%.

Statistical Analyses

Territories with an attending adult pair—whether or not they laid eggs—were considered occupied and used to calculate reproductive parameters (Postupalsky 1974). During our 5 years of surveys, we found a total of 15 nests containing young during the latest survey that had not been found earlier during the territory occupancy survey. We included these nests only for calculations based on successful nests but excluded them from calculations based on occupied nests.

We examined variation in reproductive success by considering productivity (young fledged/occupied territory), brood size (young fledged/successful territory), and nest success (percentage of pairs fledging ≥1 young) each year territories were occupied, and also by examining rates of territory occupancy. We wanted initially to examine the associations among nesting habitat, elevation, relative level of human activity, and subdrainage with reproductive rates; however, these factors were confounded because they were more similar within than among subdrainages (Table 2.1). Consequently, we considered only subdrainage for analyses because we believed it best represented this suite of factors.

Because reproductive parameters were collected from the same nesting territories each year, data from the same territory may not be independent among years. Therefore, to appropriately evaluate the relationships that subdrainage and year had on productivity and brood size we used a split-plot analysis of variance (ANOVA) with subdrainage as the whole-plot and year as the subplot. Using a repeated measures ANOVA was impossible because not all territories were occupied each year, resulting in an unbalanced design. However, a split-plot ANOVA is identical to a repeated measures ANOVA if repeated measures on subjects (territories) are equally correlated (Kuehl 1994:504). To compare these approaches, we performed a repeated-measures ANOVA on the balanced subset of our data—territories that were occupied all 5 years ($n = 19$); results were identical to those from the split-plot ANOVA. To evaluate the relationships that subdrainage and year had with nest success we used logistic regression. To calculate rates of territory occupancy (occupied/surveyed), we considered territories the year they were initially occupied and thereafter. To compare rates of territory occupancy among subdrainages, we used a 1-way ANOVA after arcsin square-root transforming these percentages. We used contingency tables to compare factors that influenced nest success and nesting activity within territories between consecutive years.

Table 2.1. Similarity of habitat characteristics within subdrainages of the Gulkana River, Alaska, characterized by percentage of bald eagle nesting attempts (n = 274), 1989-1993.

	Subdrainage		
Habitat characteristic	Main Stem	Middle Fork	West Fork
Habitat (lake, river)	74% river	69% river	70% lake
Elevation[a]	60% low	100% high	54% mid
Human activity (none, some)	93% some	73% none	77% none

[a] low: <634 m, mid: 634-723 m, high: >723 m

RESULTS

From 1989 to 1993, we located a total of 83 bald eagle nesting territories within the entire Gulkana River basin that were occupied for ≥ 1 year. We surveyed 49 (59%) of these territories for all 5 years, 20 (24%) for 4 years, 9 (11%) for 3 years, and 5 (6%) for 2 years. During our 5-year study, each territory that was occupied at least once was surveyed an average of 4.4 ± 0.10 years ($\bar{x}$ ± SE), occupied an average of 3.3 ± 0.15 years, and successful an average of 1.9 ± 0.16 years. We observed 274 nesting attempts, of which 83% were atop white spruce, 10% atop balsam poplar, 5% atop aspen, and 1% atop birch. Nearly all territories surveyed (97%) were classified as active (i.e., adults laid eggs or were observed in an incubating posture). For all years combined, productivity of bald eagles averaged 0.86 ± 0.05 young fledged per occupied territory and 1.48 ± 0.04 young fledged per successful territory (brood size) with 59% nesting success. Modal brood size of successful nests was 1 (54%) but varied by year (Fig. 2.1).

During 1989 and 1991 we surveyed a sample of occupied territories (n = 59) soon after hatching. We found that of nests that ultimately failed, 92% (n = 23 of 25) failed during incubation and only 8% (n = 2) failed after hatching (we excluded 1 pair that occupied a territory but apparently did not lay eggs).

Reproductive Success

Productivity.—Year and subdrainage had significant effects ($P < 0.02$) on productivity (Tables 2.2-2.4). Productivity was higher in the Middle Fork

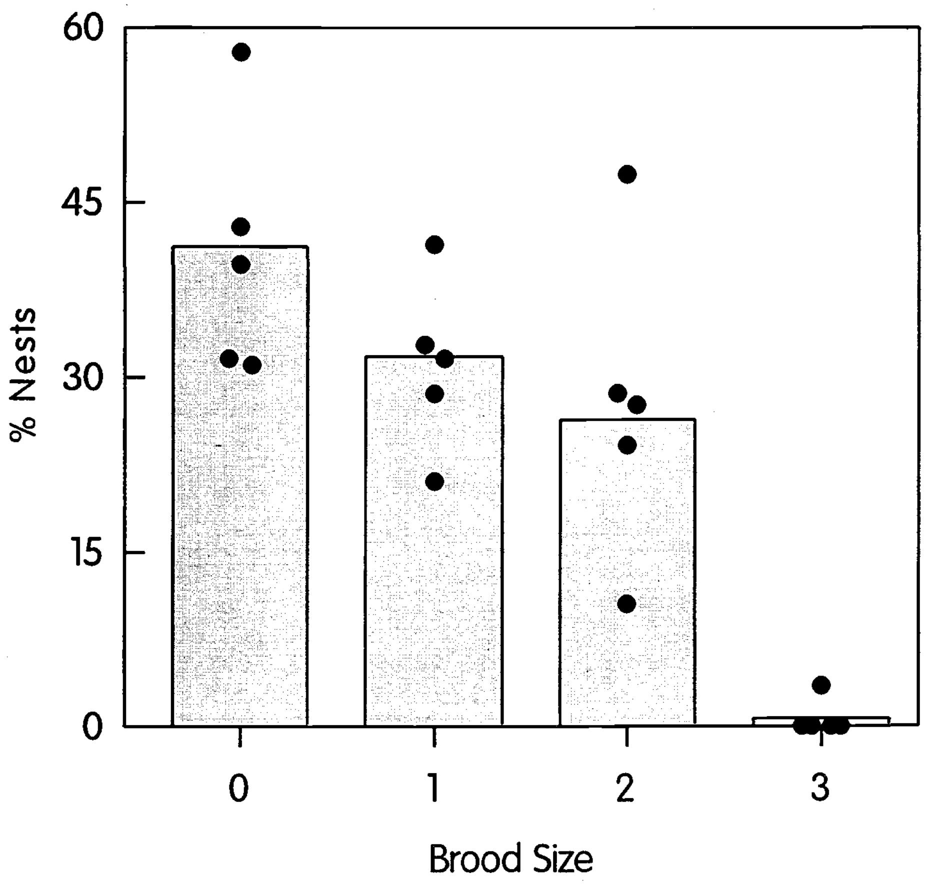

Figure 2.1. Distribution of brood sizes (n = 274) of bald eagles from the Gulkana River, Alaska. Points represent individual data from 1989 to 1993 and bars represent all years combined.

Table 2.2. Split-plot ANOVA model describing the number of young fledged per occupied nest for bald eagles in the Gulkana River basin, Alaska, 1989-1993.

Effect	df	Sums of squares	*F*	*P*
Subdrainage	2	4.0	4.4	0.017
Error (A)	80	53.3		
Year	4	7.5	3.3	0.016
Subdrainage x Year	8	4.7	1.1	0.40
Error (B)	179	105.6		

Table 2.3. Productivity and nest success of bald eagles within the 3 subdrainages of the Gulkana River, Alaska, 1989-1993.

	Occupied territories	Young fledged/ occupied territory		Young fledged/ successful territory		Nest success
Subdrainage	(*n*)	$\bar{x}$	SE	$\bar{x}$	SE	(%)
Main Stem	101	0.96 B[a]	0.09	1.53	0.07	62
Middle Fork	26	1.27 A	0.15	1.50	0.13	85
West Fork	147	0.73 B	0.07	1.44	0.05	52

[a] Means followed by different letters are significantly different ($P < 0.05$, Least Significant Difference test).

Table 2.4. Annual productivity and nest success of bald eagles within the Gulkana River basin, Alaska, 1989-1993.

Year	Occupied territories (*n*)	Young fledged/ occupied territory $\bar{x}$	SE	Young fledged/ successful territory $\bar{x}$	SE	Nest success (%)
1989	38	1.16 A[a]	0.14	1.65	0.09	68
1990	57	0.53 B	0.09	1.29	0.09	42
1991	58	0.91 A	0.12	1.54	0.10	60
1992	57	0.97 A	0.10	1.40	0.08	69
1993	63	0.86 A	0.11	1.50	0.08	57

[a] Means followed by different letters are significantly different ($P < 0.05$, Least Significant Difference test).

subdrainage than either the Main Stem or West Fork subdrainages (Table 2.3). Productivity was generally similar among years except for 1990, when it was significantly lower than all other years ($P < 0.05$) primarily because of low nesting success (Table 2.4). An analysis of brood size revealed similar trends to productivity, however, neither subdrainage or year affected brood size ($F < 1.2$, $P > 0.19$). The lack of substantial annual and regional variability in brood size suggests that nest success was more important than brood size in determining the population's productivity.

Nest Success.—Both subdrainage (drop-in-deviance test: $\chi^2 = 10.0$, $P = 0.0064$) and year ($\chi^2 = 11.1$, $P = 0.025$) influenced nest success (overall model: $\chi^2 = 21.7$, $P = 0.0014$). Like productivity, nest success was highest in the Middle Fork subdrainage, lowest in the West Fork subdrainage (Table 2.3), and noticeably lower in 1990 compared to other years (Table 2.4).

Intraterritory variation.—The overall rate of territory occupancy was 76% (276 of 362) and varied somewhat by subdrainage ($F = 2.8$, $P = 0.066$). Territory occupancy ($\bar{x}$ ± SE) was highest along the Main Stem (85 ± 4%), lowest along the West Fork (70 ± 4%), and intermediate along the Middle Fork (74 ± 12%). Whether or not a pair was successful in a given year was strongly associated with both nest success and nesting activity the following year. Pairs that were successful one year were more likely to be successful the following year (69%, $n = 116$) compared to those that were unsuccessful the previous year (51%, $n = 63$; $\chi^2 = 5.8$, $P = 0.016$). Further, pairs that were successful one year had somewhat higher productivity ($\bar{x}$ ± SE young/occupied territory) the following year (0.99 ± 0.07, $n = 116$) compared to those that were unsuccessful the previous year (0.78 ± 0.11, $n = 63$), although the difference was not significant ($t = 1.6$, $P = 0.11$). Brood size, however, was not correlated between consecutive years within territories ($r = 0.06$, $P = 0.4$, $n = 179$), even for pairs that were successful in both years ($r = -0.02$, $P = 0.8$, $n = 80$). This result was likely a consequence of the annual differences in productivity (Table 2.4).

Whether a pair changed the location of their nest within a territory (assuming pairs were site faithful; Gerrard et al. 1992, Jerkins 1992) was associated with whether they were successful the previous year ($\chi^2 = 19.2$, $P < 0.0001$). More successful pairs reoccupied the same nest the following year (86%, $n = 180$) compared to those that were unsuccessful the previous year (57%). Also, more successful territories were reoccupied the following year (82%, $n = 229$) compared to those that were unsuccessful the previous year (73%), although the difference was not significant ($\chi^2 = 2.3$, $P = 0.13$).

Comparing Reproductive Success Among Populations

Productivity (young fledged/occupied territory), brood size (young fledged/occupied territory), and nest success (% of nests fledging ≥1 young) are the parameters typically examined to assess the reproductive condition of bald eagle populations. Sprunt et al. (1973) suggested that populations that meet or exceed some value for *both* productivity and nest success are stable. However, these 2 parameters are highly correlated ($r = 0.77$, $P = 0.0001$, $n = 17$) (Table 2.5) and therefore provide similar information. The lack of a perfect correlation

Table 2.5. Reproductive parameters of bald eagle populations not influenced by environmental contaminants.

Geographic region	Occupied territories (n)	Young fledged/ occupied territory	Young fledged/ successful territory[a]	Nest success (%)	Study period	Source
Inland Wisconsin	1,469	1.30	1.69	77	1983-88	Kozie and Anderson (1991)
Colorado and Wyoming	85	1.21	1.92	63	1981-89	Kralovec et al. (1992)
Saskatchewan, Canada	264[b]	1.17	1.60	73	1973-81	Gerrard et al. (1983)
Saskatchewan, Canada	48	1.06	1.82	58	1984-87	Dzus and Gerrard (1993)
Yukon Territory, Canada	39	1.05	1.46	72	1980-82	Blood and Anweiler (1990)
Kodiak Island, Alaska	312	1.00	1.59	63	1963-70	Sprunt et al. (1973)
Oregon	606	0.92	1.37	67	1978-82	Isaacs et al. (1983)
Wisconsin	492	1.00	1.52	66	1962-70	Sprunt et al. (1973)
Yellowstone Ecosystem	232	0.98	1.63	60	1976-82	Swenson et al. (1986)
Washington	866	0.87	1.32	66	1981-85	McAllister et al. (1986)
Gulkana River, Alaska	274	0.86	1.48	59	1989-93	This study
Amchitka, Alaska	68	0.86	1.43	60	1969-84	Sherrod et al. (1976)
San Juan Islands, Wash.	275	0.84	1.35	62	1975-80	Grubb et al. (1983)
California	140	0.81	1.45	56	1970-91	Jerkins (1992)
Arizona	45	0.80	1.63	49	1975-80	Grubb et al. (1983)
New Brunswick, Canada	55	0.73	1.33	55	1974-80	Stocek and Pearce (1981)
Coastal Florida	592	0.73	1.46	50	1961-70	Sprunt et al. (1973)

[a] Young fledged/successful territory calculated as young fledged/occupied territory ÷ nest success.

[b] Using midpoint of estimates.

between these 2 parameters results from differences in brood size, which is not correlated with nest success ($r = 0.08$, $P > 0.7$). Because the product of brood size and nest success equals productivity, we suggest that productivity be used when a single measure is needed to compare reproductive output among populations. Hence, when considered as a group, bald eagles nesting within the Gulkana Basin (productivity = 0.86) were reproducing at levels comparable to other populations ($\bar{x} = 0.95$) (Table 2.5).

DISCUSSION

Several factors, both within and across nesting territories, were associated with reproductive success of this northern bald eagle population. A successful nesting attempt in one year was associated with the choice of nesting location, territorial occupancy, and reproductive success in that territory the following year. These within-territory effects on reproduction suggest that either the resident pair or some features of the territory (or both) might also be influencing reproductive output of eagle populations. Further, there was significant annual and regional (subdrainage) variation in reproduction (Tables 2.2-2.4), as has been reported elsewhere in the bald eagles' range (e.g., Grubb et al. 1983, Isaac et al. 1983, McAllister et al. 1986, Swenson et al. 1986) (Table 2.5). Reproductive variability, therefore, seems a fundamental characteristic of bald eagle reproductive ecology. The variability we observed was largely a result of differences in the proportion of nesting attempts that were successful (nest success) rather than the number of young fledged per successful pair (brood size). Regional variability in reproductive success of bald eagles among subdrainages of the Gulkana River and elsewhere (Sprunt et al. 1973, Grubb et al. 1983) is likely a result of regional differences in factors such as weather, length of available breeding season, nesting density, human impacts such as disturbance or environmental contaminants, and prey abundance. Annual variability, however, seemed attributable simply to an occasional "poor" year such as 1990 (Table 2.4); similar observations have been reported from other northern eagle populations (Gerrard et al. 1992).

Variability in reproductive success and nesting activity within and among bald eagle populations has been examined with respect to differences in nesting habitat, levels of human disturbance, weather, and some indicator of prey abundance (e.g., McEwan and Hirth 1979, Swenson et al. 1986, Hansen 1987). Although habitat structure explained some aspects of nest-site selection (Grubb 1980, Anthony and Isaacs 1989), the most critical component for site-selection may simply be the presence of a suitable nest tree (McEwan and Hirth 1979, Swenson et al. 1986); hence, differences in habitat structure probably have only minor impacts on reproductive success (e.g., Hansen 1987).

We suggest that prey availability and spring weather conditions may explain most of the variation in reproductive success and nesting activity among bald eagle populations. Years of poor productivity have been associated with inclement spring conditions (Swenson et al. 1986, Gerrard et al. 1992). On the Gulkana River, spring conditions were most severe during 1991, a year of "normal" reproductive success, and were mild during 1990, a year of poor productivity.

Hence, severity of spring weather may not be responsible for low productivity but may act to suppress prey levels that regulate reproduction, at least in northern populations. Several examples provide evidence that prey levels can control bald eagle reproductive rates. Nesting activity, nestling survival, and therefore productivity, increased when prey was placed within nesting territories of bald eagles in southeastern Alaska (Hansen 1987). A difference in densities of bald eagles breeding along two northern lakes was associated with differences in prey characteristics (Dzus and Gerrard 1993). Lastly, high variability in breeding rates of eagles in southeastern Alaska (14-84% of adults breed/year) was attributed to variability in prey abundance (Hansen and Hodges 1985). It seems possible, therefore, that the annual differences in nesting success observed in the Gulkana Basin and elsewhere may have been a function of prey availability. Further, because most nesting failure occurred before hatching (which corresponds roughly to when lakes and rivers become free of ice) on the Gulkana and elsewhere (Fraser 1981), prey levels during incubation seem most critical.

This hypothesis of reproduction success based on prey availability during incubation is further supported by our observation of only minor annual variability in brood sizes of successful nests (Table 2.4). If annual variability in prey levels during the nestling period was significant, brood size also would vary annually because brood reduction occurs in populations of eagles (Bortolotti 1986) and other raptors (Steidl and Griffin 1991) where prey is limited. Lastly, annual variability in reproductive success affected all 3 Gulkana River subdrainages similarly because we found no interaction between year and subdrainage. Thus, we believe that prey availability during incubation, regulated by spring severity or perhaps other factors, may be responsible for the observed annual variation in reproductive success on the Gulkana and elsewhere.

RESEARCH AND MANAGEMENT IMPLICATIONS

Most bald eagles within the Gulkana Basin inhabit areas that represent nearly pristine habitat. Their reproductive performance in most areas of the basin, therefore, is likely representative of northern regions that have not been substantially impacted by humans. Annual variability in reproductive success observed in this and other northern populations may result because eagles are nesting near the limits of their geographical range and therefore are susceptible to fluctuations in spring weather conditions that may affect prey availability. To better understand how weather and prey levels influence bald eagle reproduction, populations with varying levels of prey abundance and weather severity, but with similar levels of other potentially influential factors such as human disturbance, could be compared to assess the importance of these factors.

Measures of reproductive success are typically used to gauge human impacts on breeding bald eagle populations (e.g., Mathisen 1968, Grier 1969, Fraser et al. 1985). However, we suggest other long-term population parameters such as nesting density and within-territory rates of nest changes and occupancy be investigated. Using reproductive success as the only response variable when assessing impacts to bald eagle populations could be seriously deficient and even misleading because more subtle effects are easily overlooked. Instead, we suggest that disturbances that do not destroy habitat be assessed with measures that are more sensitive and less consequential than reproductive success. Two examples of this type of measure are changes in foraging patterns and nesting behaviors. We feel that these and similar measures are more appropriate for evaluating short-term impacts on breeding populations of bald eagles.

3: BREEDING BEHAVIOR OF BALD EAGLES IN INTERIOR ALASKA

INTRODUCTION

Organisms inhabiting arctic and subarctic regions are exposed to wide fluctuations in temperature and weather throughout the year. However, a myriad of birds migrate to and breed in these regions, thereby avoiding the severe winter environment and exploiting the abundant resources during the summer. Because the summer season is far shorter than in temperate regions, larger birds may face a significant time constraint within which to complete nesting. One factor that could functionally ameliorate the brevity of this season is the long daylight that these areas receive during the summer. Perhaps with this extended daylight regime, birds can adjust their activity budgets to effectively "compress" a breeding season into a shorter period.

Bald eagles (*Haliaeetus leucocephalus*) reach the limits of their geographic distribution near the arctic circle. Because of their relatively long breeding-season requirements (approximately 136 days from egg laying to fledging), eagles provide an example of a large, migratory species that exploits the seasonally abundant resources of this region. However, compared to their counterparts nesting in the temperate zone, eagles in the subarctic may need to adjust their breeding behaviors to accommodate the short breeding season.

We studied the behavior of nesting bald eagles from hatching to fledging along the Gulkana River in interior Alaska during 1989-1992. Our objectives were to quantify and describe the time and activity budgets of bald eagles breeding in interior Alaska, an area where the breeding season is brief.

FIELD METHODS

From 1990 to 1992, a group of 2-3 observers used inflatable rafts to access and observe eagles at nests located along the Main Stem and West Fork of the Gulkana River (see ***Section 4*** for a detailed description of the study area). For inclusion in the study, we chose randomly from those nests whose nest platforms and surrounding areas were observable.

We quantified behavioral patterns of nesting bald eagles during 50 continuous 24-hour observation bouts at 20 nests. Each nest was observed 1-3 times ($\bar{x} = 2.5$, mode = 3) with at least 3 weeks separating repeated observations at the same nest. Each observation bout consisted of a 24-hour period camped approximately 500 m from the nest, a distance we believed would have no effects on the nesting behaviors of adults (Fraser et al. 1985). Because of the extended daylight period in this region, we were able to record behaviors for an average of 22.2 hours per day, for a total of 1,108 hours.

We recorded continuously the behaviors, sex, and number of adult eagles on or near nests. The amount of time adults performed the following suite of behaviors was recorded while at their nests: brooding, shading, feeding, nest maintenance, preening, perching, dozing, empty (no adults on nest). We also recorded continuously the number of times adults vocalized and the amount of prey they consumed and fed to nestlings on nests. Eagles conspicuously tear off and consume discrete portions of prey ("bites") when feeding themselves or their nestlings. Therefore, we quantified the amount of prey consumed at nests by counting the number of bites consumed by adults and nestlings. Lastly, we recorded the number of adults and the amount of time they perched within 200 m of the nest (= nest area). Behaviors were recorded to the nearest minute but occasionally to the nearest second.

STATISTICAL ANALYSES

Each nesting behavior was usually performed independently, however, brooding was sometimes performed simultaneously with nest maintenance, preening, sleeping, or dozing behaviors. In these few instances, we counted both behaviors individually for analyses. As a result, activity budgets sometimes summed to >100% ($\bar{x}$ = 107%, SE = 1.1, n = 100).

We calculated activity budgets as the percentage of time adults performed each nesting behavior based on the total number of hours the nest was observed during a visit. We assessed the relationships that the number and age of nestlings (estimated soon after hatching to the nearest 1/2 week), ambient temperature, rain (raining or not), wind speed (windy or calm), time-of-day (grouped into 6 4-hr blocks), and sex of the attending adult had on both the duration and frequency of nesting behaviors.

Most of our analyses considered behavior on a daily basis. However, we also examined brooding and feeding behaviors individually so we could more precisely examine the effects of the above factors on these important behaviors. For these behaviors, we developed multiple regression models to describe the relationships between these factors and the duration of brooding and feeding bouts as well as the amount of prey consumed per feeding bout. For all regression analyses, we fit full models that included all parameters, then sequentially eliminated parameters if they did not provide a significant contribution to the model ($P > 0.10$) (Myers 1990:95).

We developed logistic regression models to assess whether the initiation of a particular nesting behavior was associated with changes in temperature, rain, wind, and time-of-day. We fit a main effects model for each behavior using variance estimates scaled by model deviance (Collett 1991). The interactive effects among environmental factors were then examined using only those subsets of our data where factorial treatment combinations were complete (those combinations where factor levels had ≥ 5 observations). This was necessary because certain environmental conditions never occurred or occurred rarely (e.g., high temperatures late at night), thereby precluding simultaneously examination of interactions for all factors.

We transformed data when necessary to meet assumptions of statistical tests, often using natural log transformations for duration of behaviors and square-root transformations for counts. Although some statistical analyses were performed with transformed data, we report arithmetic means ± 1 standard error throughout the paper unless otherwise noted.

RESULTS

Nesting Activity Budgets

Nesting behaviors of adult bald eagles were strongly associated with the age of their nestlings; all components of adult activity budgets changed significantly as nestlings matured (Table 3.1, Figs. 3.1*a* and 3.1*b*). Overall, the amount of time adults attended nestlings declined as nestlings matured and they became more aggressive to their parents. The amount of time adults brooded or shaded nestlings and time the nest was left empty were the behaviors that changed most dramatically as nestlings aged (Fig. 3.1*a*).

Females performed most of the nest-related duties during brood rearing. For those behaviors most consequential for successful reproduction, females performed 93 ± 2% ($\bar{x} \pm$ SE) of the total time spent brooding or shading nestlings, 69 ± 5% of the time spend feeding, 76 ± 5% of the time maintaining the nest, and 76 ± 4% of the time attending the nest (Fig. 3.2). Males performed most of the remainder of these duties with few (0-4%) performed by both adults together (Fig. 3.2).

Nest and Nest-Area Attendance.—The percent time that 1 adult attended the nest was essentially the converse of the time the nest was empty (Fig. 3.1*a*, Table 3.1) and followed a sigmoid curve that declined as nestlings aged (Fig. 3.3)

Table 3.1. Relationships between nesting behaviors (Y = % day) of adult bald eagles and nestling age (n = 50), Gulkana River, Alaska, 1990-1992.

Nesting behavior	Regression equation	r^2	F	P
Feed[a]	$Y = 6.4 - 0.52\ (\text{age})$	0.42	34.2	0.0001
Brood/Shade[b]	$Y = 100.7 - 21.34\ (\text{age}) + 1.11\ (\text{age}^2)$	0.82	98.6	0.0001
Perch	$Y = 17.3 - 1.33\ (\text{age})$	0.21	12.9	0.0008
Preen	$Y = 7.5 - 0.75\ (\text{age})$	0.27	18.2	0.0001
Sleep	$Y = 9.3 - 0.95\ (\text{age})$	0.30	20.7	0.0001
Nest Maintenance[b]	$Y = 4.9 - 0.57\ (\text{age})$	0.53	48.2	0.0001
Doze[b]	$Y = 12.7 - 1.47\ (\text{age})$	0.38	26.5	0.0001
Nest Empty	$Y = -11.6 + 86.3/(1 + 10^{1.25-0.29[\text{age}]})$	0.83	219.4	0.0001

[a] n = 49; excludes 1 observation while adults still incubating.

[b] n = 45; excludes observations when nestings were > 10 weeks old (all values = 0).

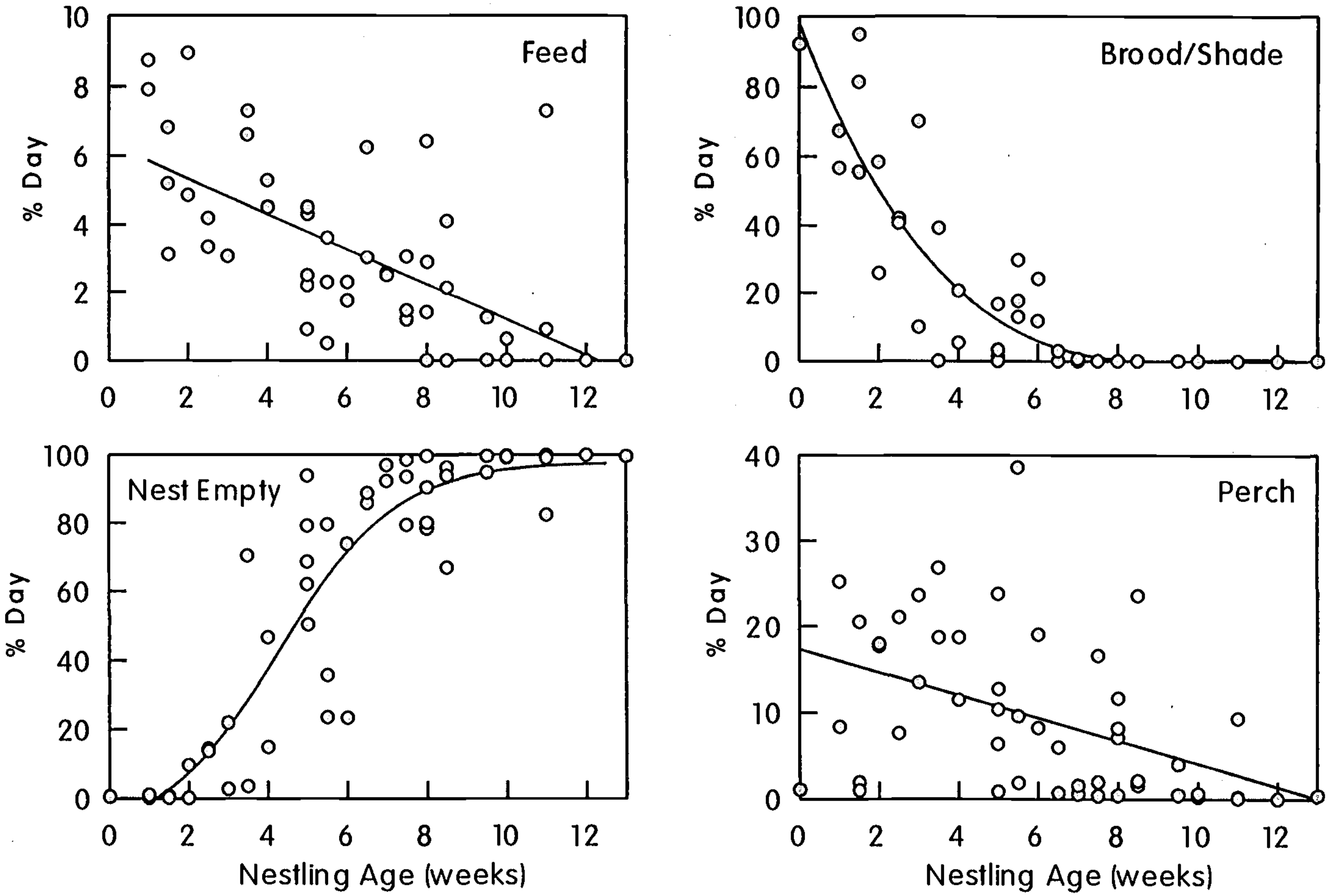

Figure 3.1*a*. Percent day that adult bald eagles performed nesting behaviors changed dramatically as nestling aged.

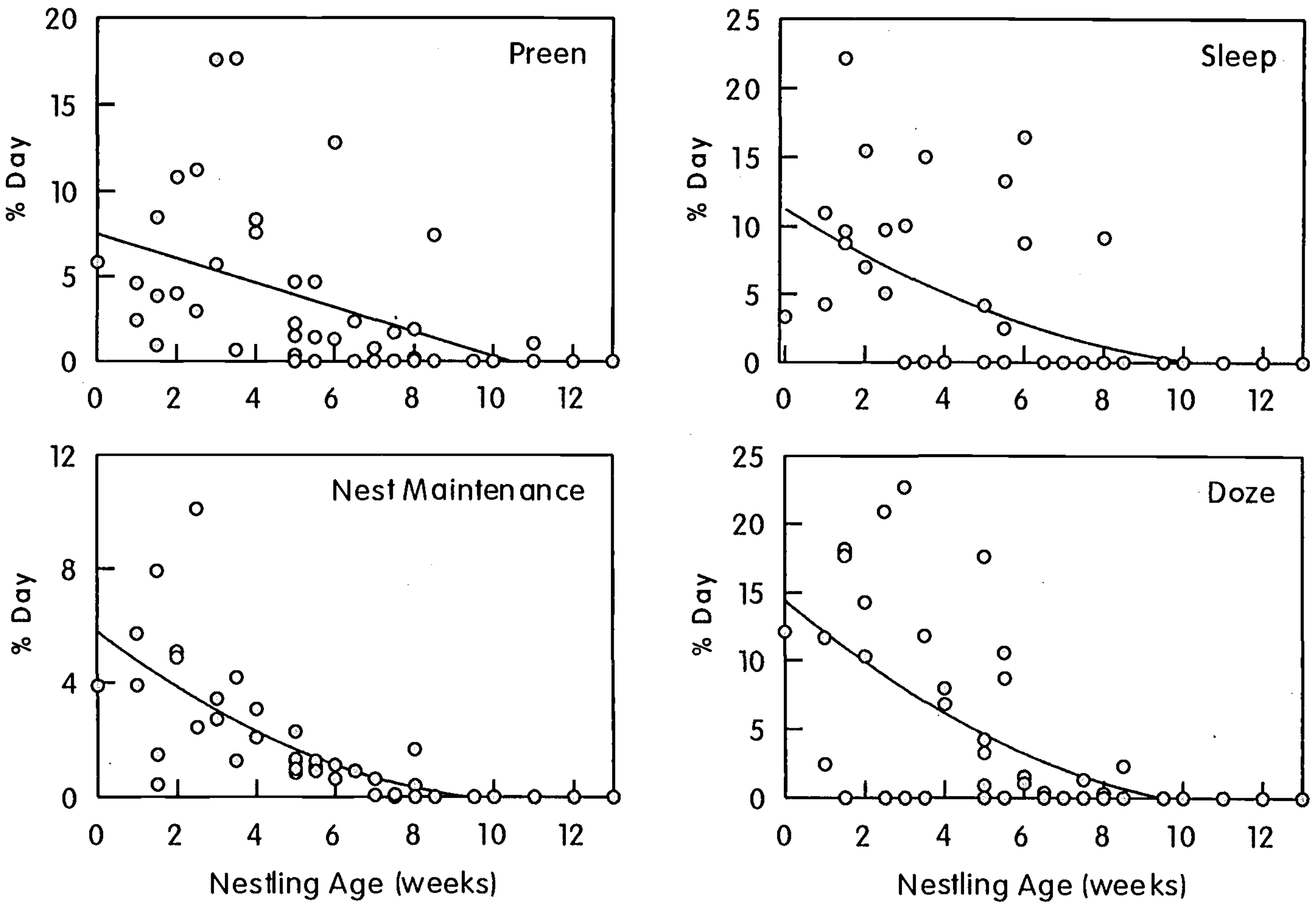

Figure 3.1*b*. Percent day that adult bald eagles performed nesting behaviors changed dramatically as nestling aged.

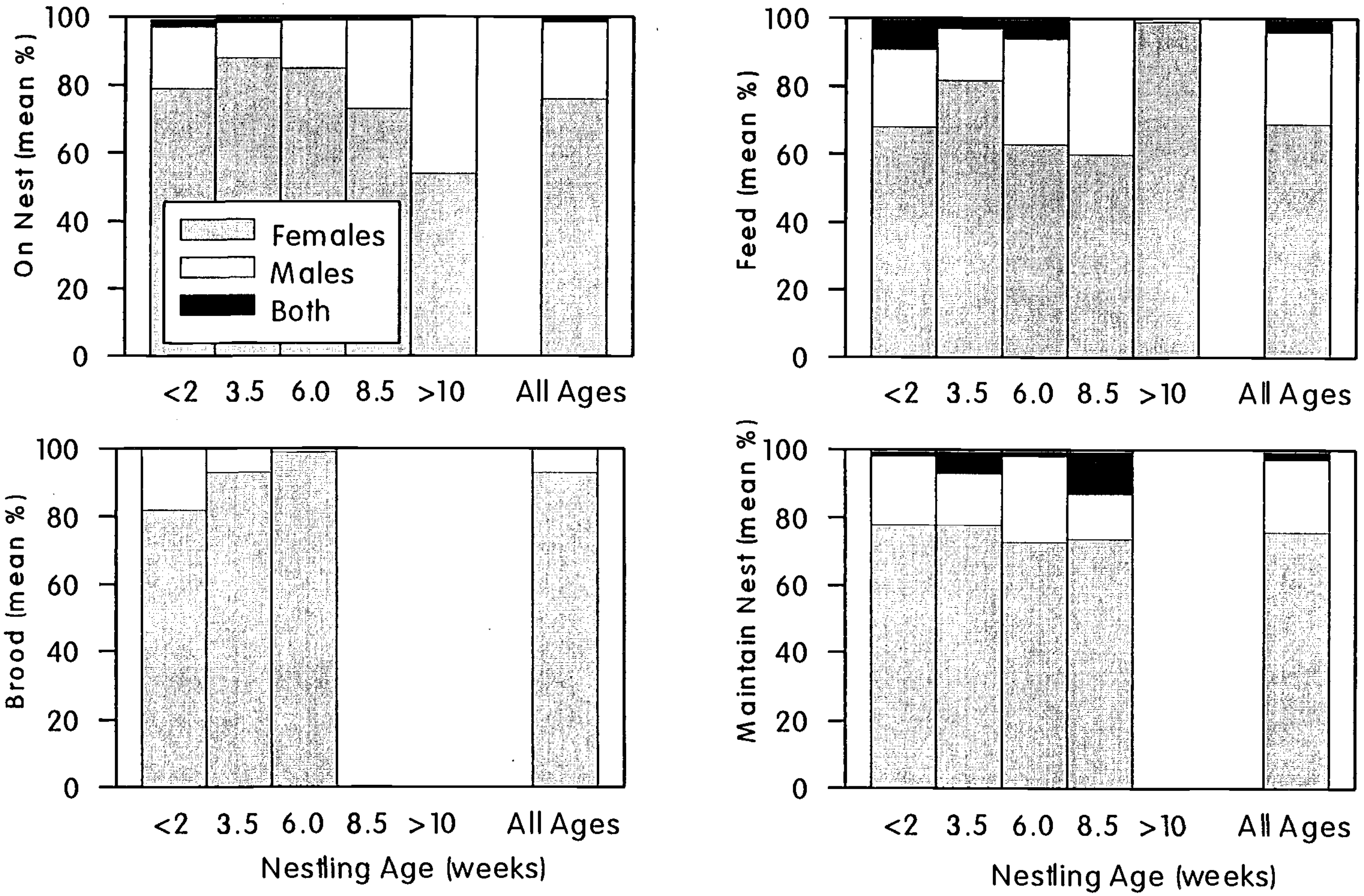

Figure 3.2. The majority of nesting behaviors were performed by female bald eagles.

(% time 1 adult at nest = $110.2 - 108.5/[1 + 10^{1.25-0.29\{age\}}]$, $F = 125.1$, $P < 0.0001$). Rarely did both adults attend the nest together ($\bar{x} = 0.5\%$ day ± 0.1), however, the percentage of time they did also declined as nestlings matured (Fig. 3.3) (slope = -0.14 ± 0.03, $t = 4.7$, $P < 0.0001$, $n = 50$).

The percent time that 1 (slope = -6.1 ± 0.73, $t = 8.4$, $P < 0.0001$) or both (slope = -1.6 ± 0.58, $t = 2.7$, $P = 0.009$) adults attended the nest area (within 200 m of the nest) decreased linearly as nestlings aged (Fig. 3.4) but much less dramatically than percent time adults attended the nest (Fig. 3.1*a*). Although adults spent increasingly more time off the nest as nestlings matured, much of that time was spent in the vicinity of the nest.

Brooding Behavior

For several weeks after hatching, nestlings relied on their parents for protection from temperature and weather extremes. Accordingly, adults brooded more than 50% of each day until nestlings were 3 weeks old and did not completely cease brooding until nestlings were >7 weeks old (Fig. 3.1*a*). The number of brooding bouts per day decreased with nestling age (Fig. 3.5) (slope = -0.62 ± 0.10; $t = 6.1$, $P < 0.0001$, based on square-root transformed data). Also, females performed more brooding bouts per day than males ($\bar{x} = 7.0 \pm 1.3$ versus 1.4 ± 0.5, respectively) ($t = 7.1$, $P < 0.0001$, $n = 28$ days).

We investigated whether the duration (min) of each brooding bout was related to nestling age, ambient temperature, sex of the brooding adult, rain, wind, and time-of-day. Duration of brooding bouts decreased as ambient temperature

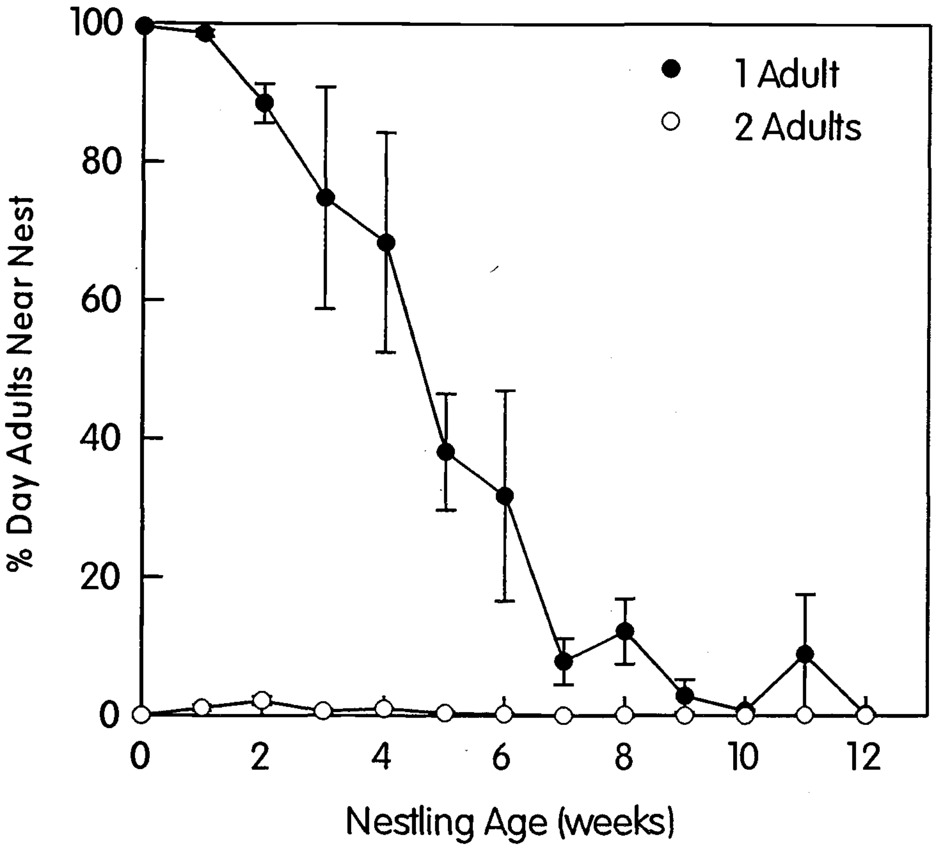

Figure 3.3. Percent day that adult bald eagles attended nests declined as nestlings aged.

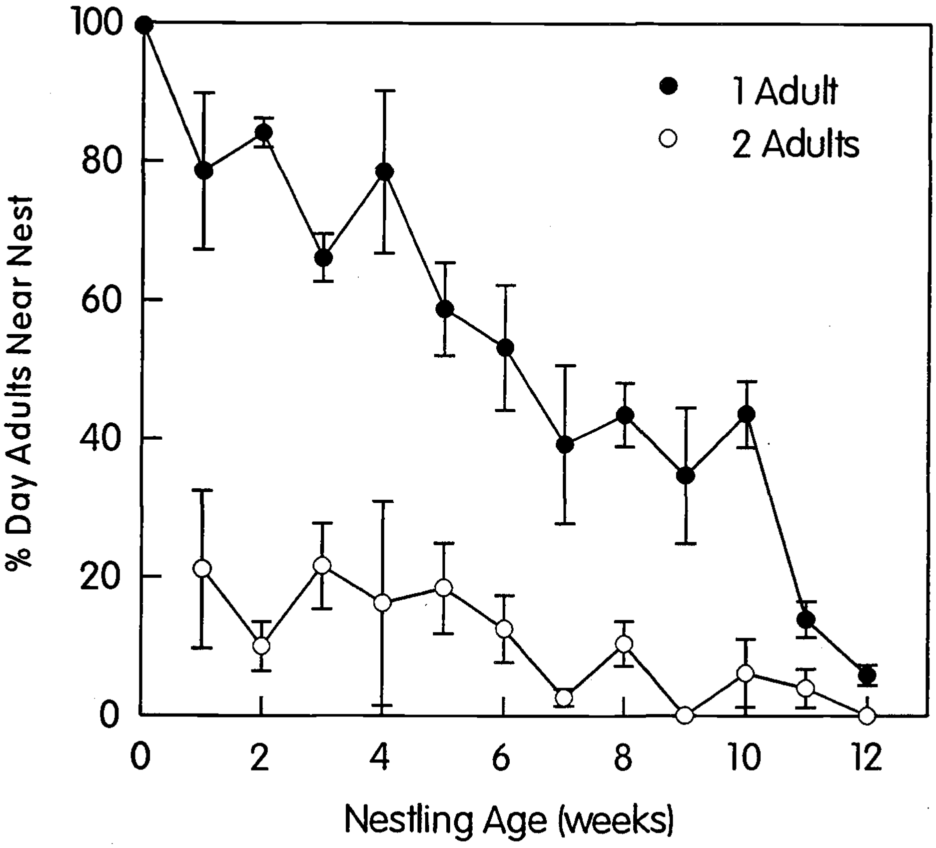

Figure 3.4. Percent day that adult bald eagles attended the nest area (within 200 m from nests) declined as nestlings aged.

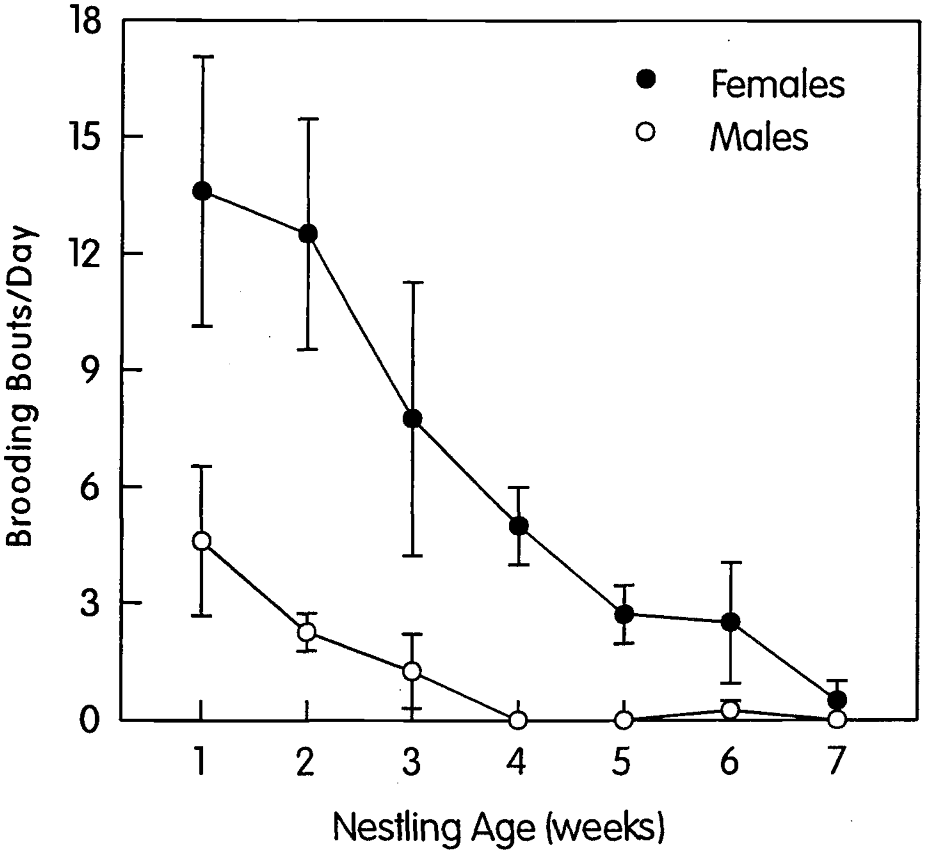

Figure 3.5. Number of brooding bouts ($\bar{x}$ ± SE) by adult bald eagles declined as nestlings aged. Data are grouped by week.

increased (Fig. 3.6) ($F = 15.1$, $P < 0.0001$), were longer when it was raining than not ($P = 0.0003$), were longer for females than males ($P = 0.053$), and were also somewhat longer when it was windy than not ($P = 0.074$) (Table 3.2). We found no influence of nestling age and time-of-day on duration of brooding bouts ($P > 0.3$).

Feeding Behavior

Nestlings began to handle prey when they reached 3 weeks old, but did not become capable of tearing prey and feeding themselves until about 5 weeks. Therefore, nestlings were fed completely by adults until they reached about 5 weeks. Once nestlings began to feed themselves, however, the percentage of prey they consumed independently increased steadily as they matured (Fig. 3.7). Compared to adults, nestlings were far less efficient at tearing and consuming prey. Adults fed nestlings 4.7 ± 0.2 ($\bar{x} \pm$ SE) bites per minute whereas nestlings fed themselves only 2.2 ± 0.1 bites per minute ($t = 8.5$, $P < 0.0001$). As nestlings matured, however, the rate at which they fed themselves increased significantly (slope = 0.32 ± 0.09; $t = 3.6$, $P = 0.0005$, $n = 86$, based on square-root transformed data).

Number of feeding bouts per day.—The number of feeding bouts per day by adults declined as nestlings aged (slope = -0.25 ± 0.03; $t = 10.0$, $P < 0.0001$, based on square-root transformed data) (Fig. 3.8). Over the entire nestling period ($n = 49$), females fed nestlings an average of 1.5 times more per day than males ($t = 4.6$, $P < 0.0001$). When considering only those days during which adults fed

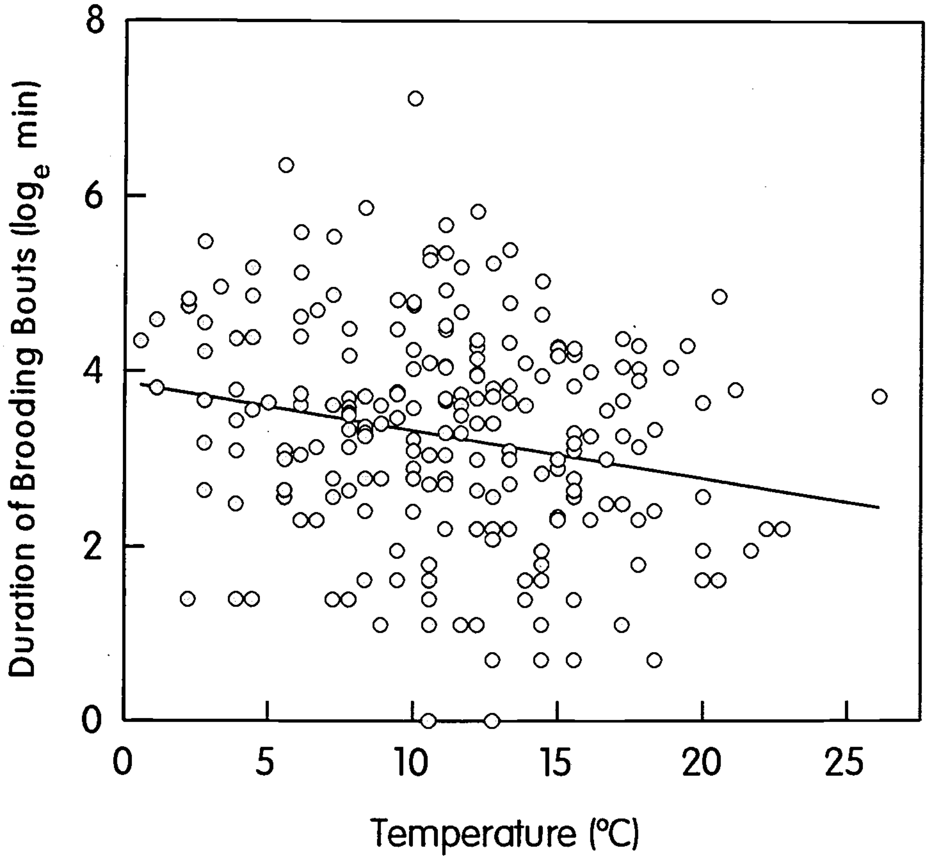

Figure 3.6. Duration of brooding bouts by bald eagles decreased as temperature increased.

Table 3.2. Parameters that influenced duration (min) of brooding bouts by bald eagles (n = 227). Geometric means are back-transformed from $\log_e$ transformations used for analysis. F-statistics and P-values from ANCOVA models.

Parameter	Category	n	Geometric $\bar{x}$	F	P
Sex	Female	189	27.7	3.8	0.053
	Male	38	18.7		
Raining	No	198	23.3	13.4	0.0003
	Yes	29	54.1		
Wind >5 kph	No	120	23.8	3.2	0.074
	Yes	107	28.5		

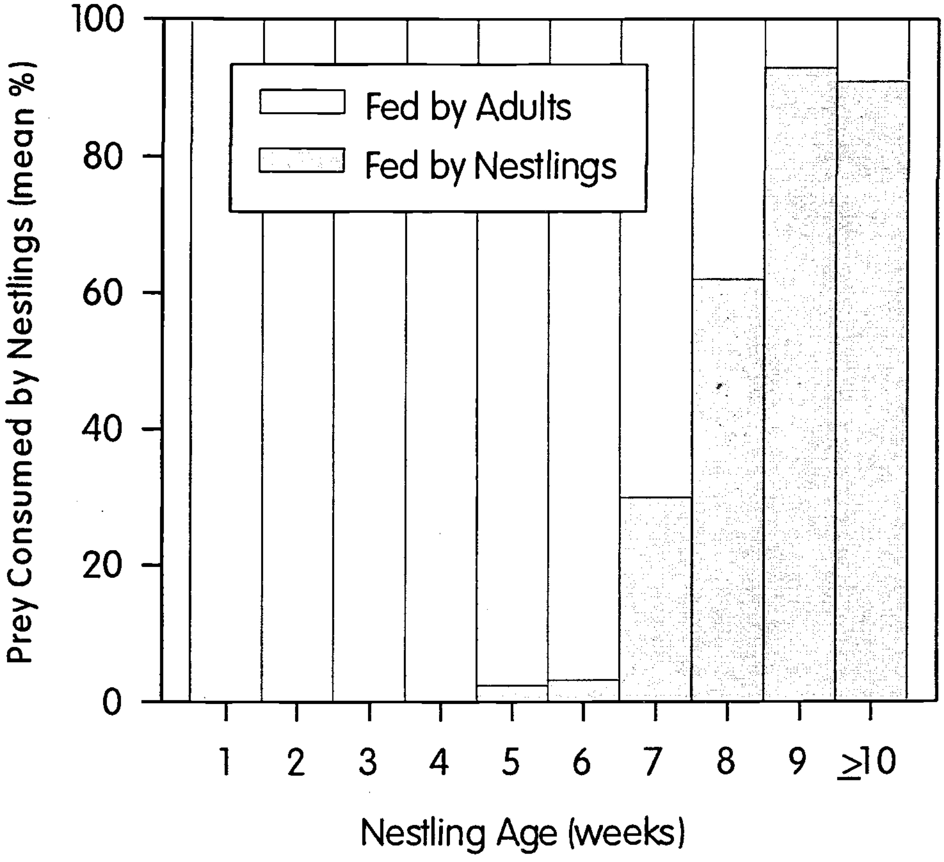

Figure 3.7. The percent of prey that nestling bald eagles consumed independently increased as they aged.

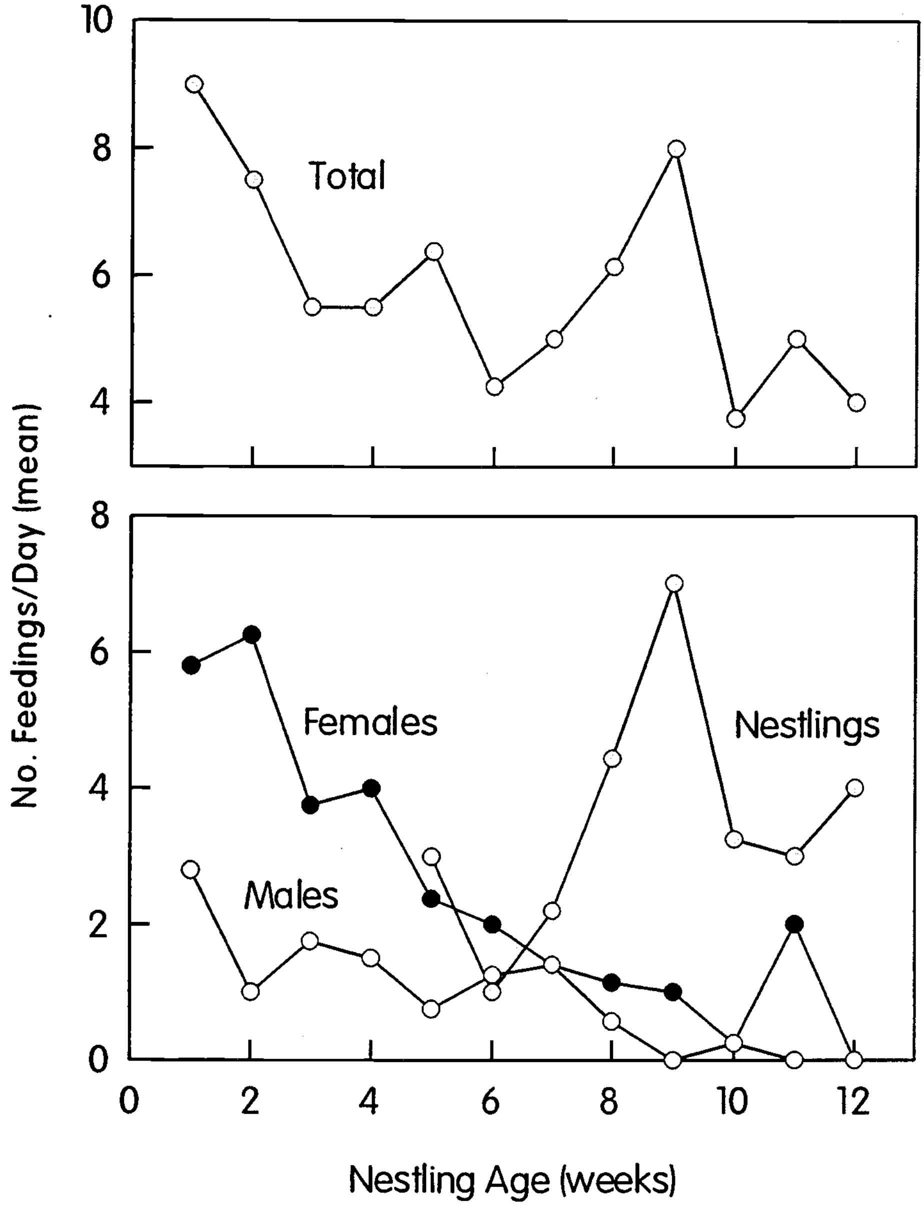

Figure 3.8. The number of feeding bouts per day by adult bald eagles declined as nestlings aged, while the number performed by nestlings increased. Data are grouped by week.

nestlings ($n = 41$), females averaged 1.8 more feedings per day than males ($t = 4.7$, $P < 0.0001$) (Table 3.3). Females performed 69% of all adult feeding bouts ($n = 183$), males 28%, and both adults 3%. As nestlings matured and became better able to feed themselves, the number of feeding bouts performed by adults decreased and the number performed by the nestlings themselves increased accordingly (Fig. 3.8). In later stages of the nestling period, adults usually visited the nest solely to deliver prey.

Prey consumed per feeding bout.—We investigated whether the amount of prey consumed (number of bites) per feeding bout by adults ($n = 178$) was related to the number of nestlings, nestling age, sex of the feeding adult, and duration of the feeding bout (min). We modeled how these parameters influenced the number of bites that adults fed to nestlings and consumed themselves (Table 3.4). Both responses were affected by the duration of feeding bouts which was strongly correlated with the total number of bites per feeding bout (Fig. 3.9). This correlation suggests that adult eagles fed at a fairly constant rate (bites/min). Therefore, duration of feeding bouts would be a suitable measure of the amount of prey that adults feed to nestlings and consume themselves when it is impossible to count bites directly (Fig. 3.9).

In addition to the effect that duration had in this model, the number of bites fed to nestlings per bout was significantly higher for nests with 2 nestlings ($\bar{x} = 55.3 \pm 4.5$) than those with 1 (46.3 ± 4.8). The number of bites that adults fed themselves was significantly lower for nests with 2 nestlings (13.4 ± 2.4) than those with 1 (19.2 ± 2.5), decreased with nestling age (slope = -0.09 ± 0.05), and

Table 3.3. Number of feeding bouts per day by adult bald eagles.

		Female		Male		Total	
Observation period	n	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Entire nestling period	49	2.57	0.34	1.04	0.20	3.71	0.45
Days adults fed nestlings	41	3.07	0.35	1.24	0.22	4.44	0.46

Table 3.4. Influence of 5 parameters on the amount of prey consumed (bites) per feeding bout by adult bald eagles. *P*-values from multiple regression models reported only if $P < 0.10$ ($n = 178$).

	No. bites	
Regressor variables	Fed to nestlings	Consumed by adults
No. nestlings	0.011	0.012
Nestling age		0.061
Sex of adult		0.060
Duration of feeding	0.0001	0.0001
Time since last feeding[a]	0.0001	0.0038
Model r^2	0.59	0.38

[a] Excludes first feeding observed per day ($n = 160$).

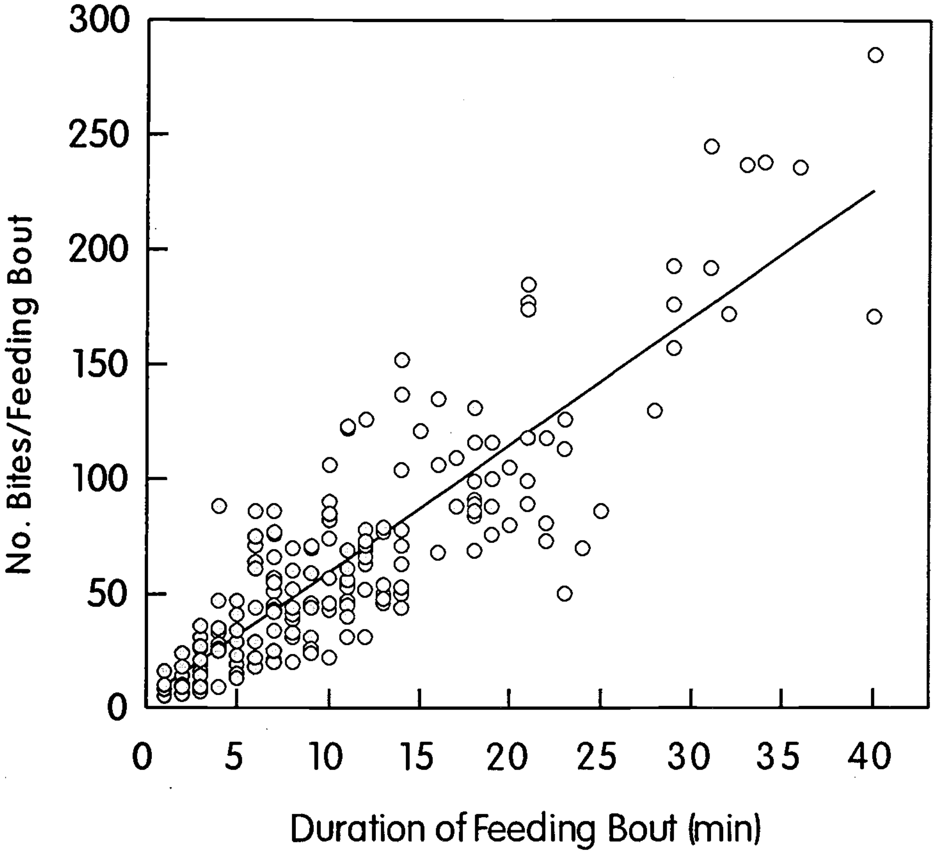

Figure 3.9. The number of bites per feeding bout was highly correlated ($r = 0.86$, $P < 0.0001$) with the duration of the feeding bout for bald eagles.

differed by sex. At nests, females fed themselves somewhat less (15.4 ± 2.1) than males (17.2 ± 3.3), but the number of bites consumed in total (adults+nestlings) was marginally higher for feedings performed by females (67.9 ± 4.9) than males (65.9 ± 6.6).

We investigated how the time elapsed since the previous feeding bout affected the amount of prey consumed per feeding. For this analysis, we examined only those feedings that occurred after the first feeding we observed (n = 160). Time since previous feeding had an additional effect on both measures of feeding. The amount of prey consumed increased as the time elapsed since a previous feeding increased, including the number of bites per bout that adults fed to nestlings (slope = 0.003 ± 0.0006, both models based on square-root transformed data) and that adults consumed themselves (slope = -0.002 ± 0.0006) (Table 3.4).

Prey consumed per day.—The amount of prey consumed per day by adults at nests declined steadily as nestlings matured (Fig. 3.10). The amount of prey consumed by nestlings, however, showed 2 distinct trends with age (Fig. 3.10). Through 5 weeks of age, when nestlings were solely being fed by adults, the amount of prey nestlings consumed increased steadily. When nestlings began to feed themselves at 5 weeks, however, the amount of prey they consumed (that was either fed to them by adults or consumed themselves) dropped abruptly, but then increased gradually as they aged (Fig. 3.10). We observed that bite size seemed to increase somewhat as nestlings aged, which may have changed how bites and prey consumed were related throughout the season; however, we were unable to quantify changes in bite size.

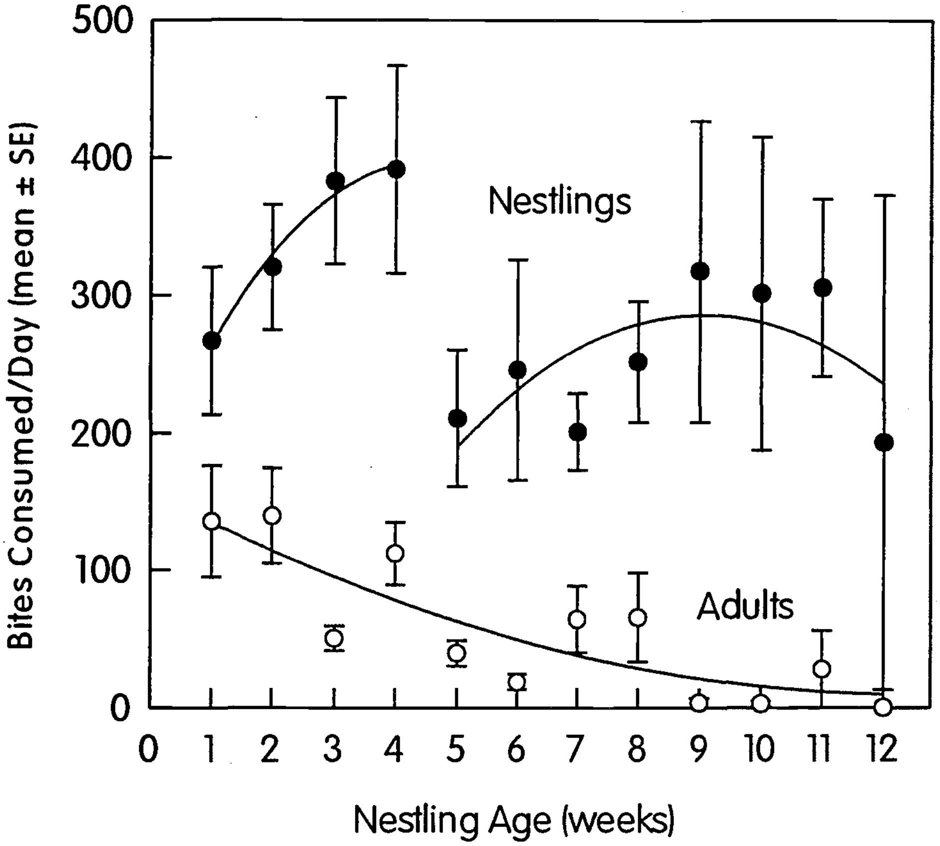

Figure 3.10. The amount of prey ($\bar{x}$ ± SE number of bites) consumed by adult bald eagles at nests declined while the amount consumed by nestlings increased until they were able to feed independently at 5 weeks. Data are grouped by week.

We assessed the relationship that the age and number of nestlings had on the amount of prey consumed per day at nests (n = 41 days with ≥1 feeding bout by adults). As nestlings aged, both the number of bites that adults fed to nestlings (slope = -0.96 ± 0.23; F = 17.5, P = 0.0002) and that adults consumed themselves (slope = -0.65 ± 0.20; F = 10.4, P = 0.003) decreased. However, only the number of bites that adults fed to nestlings (F = 4.9, P = 0.031) was influenced by the number of nestlings in a brood, which was higher for nests with 2 ($\bar{x}$ = 256.7 ± 27.8, n = 23) than 1 nestling (181.0 ± 30.5, n = 18). Because females performed more frequent and longer feedings than males, both the number of bites per day that females fed to nestlings (162.8 ± 20.4) and consumed themselves (47.6 ± 8.1) was greater than males (60.7 ± 11.4, 21.4 ± 5.2, respectively) ($t > 3.4$, $P < 0.009$).

Weather and Time-of-Day

We examined how ambient temperature, wind, rain, and time-of-day related to the likelihood that adults initiated particular nesting behaviors. For these analyses, we combined data from all nests (n = 2,753 behaviors). Ambient temperature varied considerably during the nestling period, and ranged from -3 to 34°C ($\bar{x}$ = 14°C) during observations. Temperature had a marked influence on 4 of 8 behaviors that adult eagles performed while on their nests (Table 3.5). When temperatures were low, adults were much more likely to brood or sleep, which often coincided with late-night and early-morning periods. When temperatures were high, adults were more likely to shade nestlings (Table 3.5).

Table 3.5. Odds ratios for the likelihood that a behavior was performed at a given temperature class relative to the highest temperature class (>20-30°C). Chi-square statistics and *P*-values from logistic regression models represent the overall effect that temperature had on nesting behaviors while also considering the effects of rain, wind, and time-of-day.

	Temperature (°C)					
Behavior	0-10	>10-15	>15-20	>20-30	χ^2	*P*
Brood	19.6[a]	12.5[a]	6.8[a]	1	49.4	<0.0001
Doze	0.6	0.5	0.8	1	3.4	0.33
Feed	1.3	1.1	1.4	1	2.1	0.55
Maintain nest	1.1	1.4	1.4	1	4.6	0.20
Perch	0.7	1.2	1.2	1	8.6	0.035
Preen	1.3	1.4	1.1	1	3.9	0.27
Shade	0.1[a]	0.2[a]	0.2[a]	1	52.0	<0.0001
Sleep	51.4[a]	18.5[b]	5.5	1	26.8	<0.0001

[a] Odds of performing behavior at this temperature differed significantly ($P < 0.05$) from >20-30°C temperature class, assigned arbitrarily using an indicator-variable approach.

[b] $P = 0.055$.

Rain and wind also affected adult behavior. Adults were more likely to maintain nests (odds ratio = 1.6; $\chi^2 = 3.9$, $P = 0.049$) and to doze (1.8; $\chi^2 = 2.9$, $P = 0.088$) when it was raining compared to when it was not (odds ratio = 1). Adults were more likely to just perch atop nests (1.3; $\chi^2 = 4.8$, $P = 0.028$) and somewhat less likely to preen (odds ratio = 0.8; $\chi^2 = 2.9$, $P = 0.087$) when it was windy compared to when it was not (odds ratio = 1).

During much of the nestling period, the amount of available daylight (which we defined as sufficient daylight in which to adequately observe behaviors) in this region extended to a full 24 hours. From 5 June, when we began our nest observations, until 25 July, we had sufficient available daylight to observe nesting activity for 24-continuous hours. The shortest amount of available daylight was 17 hours on our latest observation date, 24 August. Therefore, throughout most of the nestling period, adult eagles could have been active throughout most of the day. Activity patterns of adults at nests, however, were strongly associated with time-of-day, which significantly affected 5 of 8 nesting behaviors (Table 3.6). Adults were more likely to sleep and doze and least likely to feed during the very early part of the day (001-0400), and were more likely to shade nestlings and simply perch atop the nest during daytime hours (0801-2000) (Table 3.6).

These environmental parameters sometimes interacted to affect behavior in complex ways (Table 3.7). For example, the likelihood of feeding was not affected by ambient temperature ($P = 0.55$; Table 3.6) or time-of-day ($P = 0.16$; Table 3.6). However, the likelihood of feeding at certain times of the day differed depending on ambient temperature (interaction: $P = 0.031$; Table 3.7). Within each

Table 3.6. Odds ratios for the likelihood that a behavior was performed at a given time-of-day class relative to the latest time class (2000-2400). Chi-square statistics and P-values from logistic regression models represent the overall effect that time-of-day had on nesting behaviors while also considering the effects of rain, wind, and temperature.

	Time-of-day							
Behavior	0001-4000	0401-8000	0801-1200	1201-1600	1601-2000	2001-2400	χ^2	P
Brood	0.6	0.8	0.9	1.0	1.2	1	3.1	0.68
Doze	1.7	1.2	0.7	0.6	0.7	1	7.5	0.19
Feed	0.4	0.8	1.0	0.8	1.1	1	7.9	0.16
Maintain nest	0.8	0.8	0.8	0.6[a]	0.5[a]	1	12.6	0.027
Perch	0.5[a]	1.7[a]	1.3[a]	1.2	1.3[a]	1	29.0	<0.0001
Preen	1.4	0.7	0.9	1.1	1.4	1	12.5	0.029
Shade	0.5	0.8	2.2[a]	2.6[a]	1.7	1	13.6	0.018
Sleep	2.0[a]	0.8	0.3[a]	0.5	0.4	1	21.6	0.0006

[a] Odds of performing behavior at this temperature differed significantly ($P < 0.05$) from 2001-2400 time class, assigned arbitrarily using an indicator-variable approach.

Table 3.7. Results of tests for calculable interactions between 4 environmental parameters and their effects on initiation of nesting behaviors. P-values from logistic regressions reported only for behaviors with significant interactions ($P < 0.05$). Interactions are interpretable only within the range of environmental conditions examined[a,b].

Behavior	time-of-day[a] x temperature[b]	time-of-day x wind	time-of-day x rain	temperature x wind	temperature x rain
Brood			0.025 -		
Doze	0.015 +				0.0002 +
Feed	0.031 -				0.007 -
Perch	0.044 -				
Preen				0.011 -	
Shade			0.0007 -		
Sleep	0.029	0.0001 o			0.024 -

[a] Interactions with time-of-day excluded time period 2001-2400.

[b] Interactions with temperature excluded temperature class >20-30°C, and also excluded temperature class >15-20°C in the morning (001-800) and temperature class 0-10°C in the afternoon (1201-2000).

[c] For those significant interaction combination levels, a (+) indicates that the likelihood of performing this behavior always increased as the second variable listed in the interaction increased while the first variable was held constant; a (-) indicates the opposite relationship; a (o) indicates that the effect of the second variable on this behavior was not monotonic; i.e., the effect changed with levels of the first interaction variable (both + and -); no symbol indicates that no individual interaction levels were significant.

particular time class, adults were more likely to feed nestlings when the temperature was low (Fig. 3.11).

Vocalizations

We observed and heard adult eagles vocalizing in 3 different contexts: during the early morning or late evening when the pair concurrently called to each other ("location"), as one pair member approached the nest ("greeting"), and when seemingly disturbed ("alarm"), such as when a human or subadult eagle approached a nest with nestlings. The number of vocalizations per day averaged (geometric $\bar{x}$) 11.9 for all pairs combined but varied considerably among pairs (range = 1-134/day/pair). We were unable to assign gender to 11% (108 of 963) of the vocalizations we heard, which represented an arithmetic mean of 2.2 vocalizations per day. Of the gender-classified vocalizations, females (geometric $\bar{x} = 5.4$) vocalized 3.1 times more per day than males (1.7) ($t = 5.2$, $P < 0.0001$). Adults vocalized less often late at night and most frequently in the early morning hours (Fig. 3.12) ($F = 8.4$, $P < 0.0001$). There was no apparent relationship between nestling age and the number of vocalizations per day by males, females, or both adults combined ($P > 0.35$).

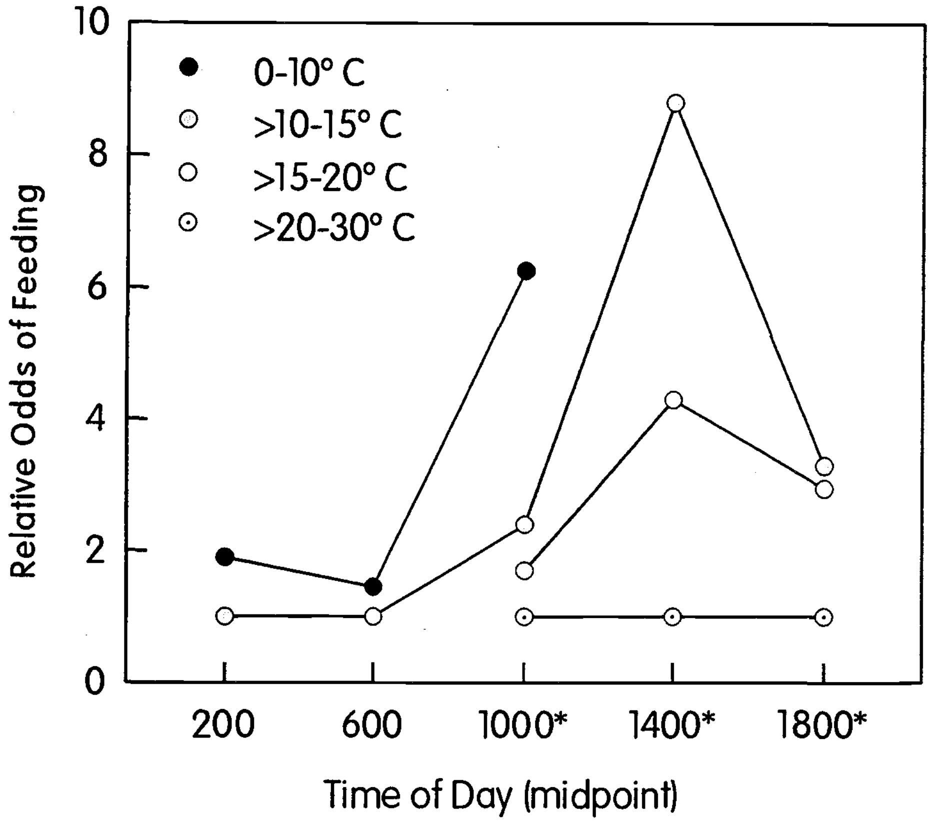

Figure 3.11. At a given time-of-day odds of feeding increased as temperature decreased; i.e., adults were more likely to feed nestlings when the temperature was low. Asterisks along x-axis labels indicate that the odds of feeding differed significantly ($P < 0.05$) among temperature classes at that time-of-day.

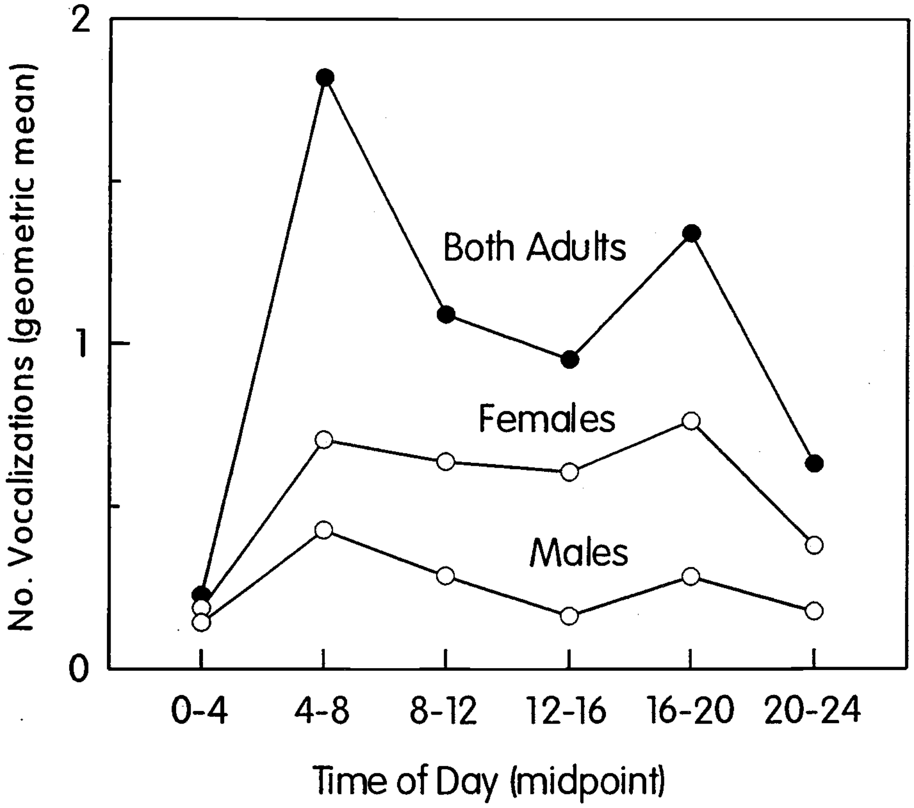

Figure 3.12. The number of vocalizations (geometric $\bar{x}$) by adult bald eagles varied by time-of-day.

DISCUSSION

Nesting Behavior

Three factors had overwhelming effects on patterns of adult bald eagle nesting behaviors in interior Alaska: nestling age, brood size, and environmental conditions.

Nestling Age.—The most important factor governing adult nesting behaviors was the age of their nestlings. As nestlings matured, the amount of time that adult bald eagles performed most behaviors and attended nests declined, as has been observed in other raptors, including golden eagles (*Aquila chrysaetos*) (Ellis 1979, Collopy 1984), ospreys (*Pandion haliaetus*) (Levenson 1979), and prairie falcons (*Falco mexicanus*) (Holthuijzen 1989). Further, the frequency with which many behaviors were performed, such as the number of times and amount of prey adults fed nestlings, also declined as nestlings aged, as similarly observed for golden eagles (Ellis 1979, Collopy 1984) and bald eagles in southeastern Alaska (Cain 1985). These changes in adult behavior with nestling age corresponded to the rapidly increased ability for nestlings to thermoregulate and the increased efficiency with which they were able to feed themselves.

The decreasing sigmoidal trend in nest attendance with nestling age that we observed (Fig. 3.3) has been observed for bald eagles in Canada (Bortolotti et al. 1983) as well as for other raptors (Collopy 1984, Holthuijzen 1989). Similarly, the amount of time that adult bald eagles spent perched off, but in the vicinity of, the nest decreased as nestlings matured (Fig. 3.4), which has been observed for bald eagles in Ohio (Herrick 1924) and ospreys in California (Levenson 1979).

Brood Size.—The number of nestlings in a brood affected adult nesting behaviors, especially how adults provisioned prey. We observed that 2-nestling broods received more prey per feeding bout and more prey per day in total than 1-nestling broods, suggesting that adults with larger broods increased their foraging effort. However, on a *per nestling* basis, nestlings from 1-nestling broods received more prey than those from 2-nestling broods. Similar patterns of increased feeding levels with increased brood size has also been observed in peregrine falcons (Enderson et al. 1972, Steidl 1990) and golden eagles (Collopy 1984).

Environmental Conditions.—Many adult behaviors were initiated in response to particular environmental conditions (Tables 3.5 and 3.6), most of which represented adult responses to reduce energy burdens of their nestlings. For example, the likelihood of adults brooding nestlings and the duration of brooding bouts both increased as ambient temperature decreased; brooding bouts were significantly longer when it was raining or windy than when it was not. Similarly, the amount of time that bald eagles (Cain 1985) and prairie falcons (Holthuijzen 1989) brooded nestlings per day decreased as ambient temperature increased.

Sexual Partitioning of Nesting Duties

Raptors have evolved several strategies for dividing brood-rearing duties, ranging from species where males spend almost no time at the nest but perform nearly all the hunting, to those where both sexes share more equally in brood-rearing duties (Newton 1979:159). In the population of bald eagles we studied, females performed 69 to 93% of the most consequential nesting duties during brood rearing (Fig. 3.2). The high percentage of brooding by female bald eagles (93%) was similar to that observed for other raptors, including golden eagles (≈100%; Ellis 1979, Collopy 1984), ospreys (95-100%; Levenson 1979, Jamieson et al. 1982), peregrine falcons (*Falco peregrinus*) (99%; Enderson et al. 1972), and gyrfalcons (*Falco rusticolus*) (87%; Jenkins 1978). Further, female bald eagles performed longer and more frequent feedings than males throughout the nestling period. Similar to Cain (1985), we observed that females almost invariably brooded nestlings during periods of inclement weather.

Unlike many raptors, such as ospreys (Levenson 1979), golden eagles (Ellis 1979, Collopy 1984), and peregrine falcons (Enderson et al. 1972) where males provide food for but rarely attend offspring, we found that male bald eagles performed up to 29% of brood-rearing duties. Cain (1985) also found that male bald eagles performed a comparatively high percentage of these duties.

CONCLUSIONS

Nesting behaviors of adult eagles and other raptors are governed largely by the age of their nestlings. After nestlings attain a certain size and become able to thermoregulate, adults can spend proportionately less time on and in the immediate vicinity of their nest without apparent consequences to nestlings. Therefore, this decreased need for nestling attendance probably allows adults to reduce their reproductive costs by attending to their own survival needs, perhaps by inhabiting areas of lower risk within their territory than those immediately surrounding nests.

4: HUMAN ACTIVITY AS HABITAT DISTURBANCE: AN EXPERIMENT WITH BREEDING BALD EAGLES

INTRODUCTION

As human activities in wilderness areas increase, the number, type, and intensity of human-caused disturbances to species and habitats in these areas also increase. Disturbances to habitat can be classified as direct and indirect. Direct disturbances include activities such as cutting trees and draining wetlands that physically destroy habitat and reduce a species' likelihood of survival, its chances for successful reproduction, or force it to occupy lower quality habitats. In contrast, indirect disturbances do not make overt physical changes to habitat but reduce habitat quality through more subtle mechanisms. Indirect disturbances result when humans temporarily exclude animals from preferred habitats or alter behavioral patterns necessary for survival and reproduction; these include non-consumptive forms of recreation such as hiking and boating. Compared to direct disturbances, the effects of indirect disturbances are more difficult to recognize. Determining how indirect disturbances affect habitat quality and viability of wildlife populations, and devising strategies to mitigate their effects, has become an increasing challenge for resource managers.

Indirect forms of human disturbance have been shown to have both short- and long-term effects on birds (e.g., Burger 1981, Henson and Grant 1991, Fernandez and Azkona 1993, Holmes et al. 1994). These effects include reduced productivity through nest abandonment and decreased nestling survival (Tremblay and Ellison 1979, White and Thurow 1985), increased energetic stresses (Bélanger and Bédard 1990), and displacement from preferred habitats (McGarigal et al. 1991). Most studies of indirect disturbance on nesting birds have concentrated on the impacts and biases associated with researchers visiting nests or nesting areas (Grier 1969, Bart 1977, Westmoreland and Best 1985). Far less research has focused on the types of disturbances that birds are typically exposed to at nests. Studies of human activity in natural settings will best promote our understanding of how indirect disturbances affect populations and will provide guidance for management and mitigation efforts to ameliorate their effects (Anthony et al. 1994).

Most attempts to discern the impacts of human activity on breeding bald eagles have used measures of reproductive success as the response variable (e.g., Mathisen 1968, Grier 1969, Fraser et al. 1985). These measures can be problematic because they ignore changes in behavior that can have long-term consequences to populations (Holthuijzen 1989, Anthony et al. 1994, *Section 2*). However, impacts of human activity have been assessed on behavior of eagles in winter, a period when food stress can be severe (e.g., Stalmaster and Newman 1978, Knight and Knight 1984). Raptors and other birds are at least as vulnerable to disturbances during the breeding season, when their activities are restricted to nesting territories. Changes in behavioral patterns during breeding may lower rates of offspring survival which would reduce population viability, especially for endangered or threatened species. Species breeding in riparian habitats are particularly vulnerable to these disturbances because both human and wildlife activities tend to be concentrated in these areas, greatly increasing the likelihood of conflict.

We studied the behavior of bald eagles (*Haliaeetus leucocephalus*) nesting along the Gulkana River in interior Alaska during 1989-1992. Our objective was to assess the effects of recreational activity on behavior of breeding adults. We performed an experiment designed to measure differences in nesting behavior when activity was located near ($\approx$100 m) versus far ($\approx$500 m) from nests. This allowed us to mimic and assess the impacts of this increasingly common and representative form of habitat disturbance on a regionally abundant, top trophic-level predator.

STUDY AREA

The Gulkana National Wild River in southcentral Alaska originates at the base of the Alaska Range (63°07'N, 150°30'W) and flows south into the Copper River. The Gulkana is characterized by clear waters with a combination of whitewater rapids, riffles, and meandering reaches. The Gulkana's 2 major tributaries, the Middle and West Forks, are similar in character to the Main Stem, but are considerably more meandering. The Gulkana and its tributaries support anadromous runs of chinook (*Oncorhynchus tshawytscha*) and sockeye (*O. nerka*) salmon, as well as abundant resident fish populations, including arctic grayling (*Thymallus arcticus*) and rainbow trout (*O. mykiss*).

Higher elevation areas of the basin ($>$1000 m) are treeless and vegetated with a moist tundra community. Lower elevations are dominated by boreal forest, composed predominantly of black (*Picea mariana*) and white spruce (*P. glauca*) with balsam poplar (*Poplar balsamea*), quaking aspen (*P. tremuloides*), and paper birch (*Betula paperifera*) in lower proportions. Eagles nest atop all these tree species except black spruce. Nests are built at elevations between 400 m and 960 m and usually <50 m from water, the only areas where trees grow large enough to support nests.

The weather in this portion of Alaska is changeable, but during the breeding season rainfall is moderate compared to coastal Alaska. One of the most striking physical characteristic of this area is the extended daylight regime from May through August, which approached 24 hours.

Human Use in the Gulkana Basin

The Gulkana is used almost exclusively for wilderness recreation, especially whitewater boating, fishing, and hunting; use of motorized boats is concentrated on a 15-km stretch of the lower Main Stem. Nearly all human use occurs along the river corridor, which exacerbates the conflict between eagles and humans because most pairs nest and forage along the river. Like most wilderness areas in North America (Brockman and Merriam 1979), human use along the Gulkana River has increased over time (Fig. 4.1).

A disproportionately large amount of recreational use takes place within the Gulkana Basin compared to nearby rivers, and several factors contribute to the river's value and popularity as a recreational resource. The Gulkana is one of the few wilderness rivers in Alaska that is accessible by road; it is the largest clear-

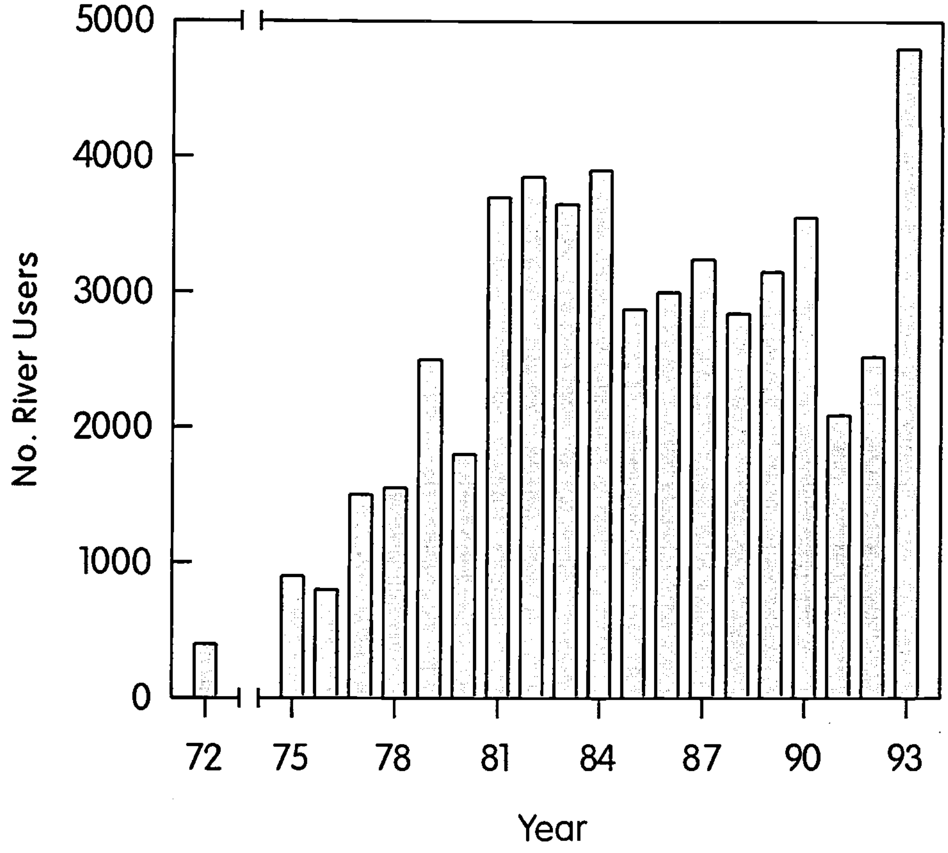

Figure 4.1. The level of human activity within the Gulkana River basin has increased from 1972 to 1993. Note the x-axis is only continuous beginning with 1975. Data from L. Kajdan, U.S. Bureau of Land Management, Glennallen, Alaska (unpublished).

water tributary of the Copper River; it is located less than a 4-hour drive from Fairbanks and Anchorage, the state's largest cities; and it contains abundant populations of sport fish. Lastly, much of the Gulkana Basin is administered by the Bureau of Land Management, which encourages use of the area for wilderness recreation.

Characteristics of the Bald Eagle Population

Bald eagles reach both their highest breeding densities and the northern limit of their geographic range in Alaska, yet throughout the state's vast interior little is known about their breeding ecology. The nesting season is short compared to other latitudes, and eagles face considerable time constraints for nesting. Eagles lay eggs in early May before winter ice breaks up; young begin to fledge by mid-August; and both adults and young begin to leave their nesting territories in early September. The Gulkana Basin supports one of the northernmost nesting populations of bald eagles, which was comprised of 70-80 nesting pairs of bald eagles from 1989-1993. During this period, reproductive success averaged 0.87 young fledged per occupied territory with 59% nest success (***Section 2***). Also, the number of nonbreeding eagles inhabiting the Main Stem corridor sometimes exceeded 250 individuals between June and September.

FIELD METHODS

From 1990 to 1992, a group of 2-3 observers used inflatable rafts to access and observe eagles at nests located along the Gulkana's Main Stem and West Fork. While initially surveying nests in 1989, we observed that recreationists camped near nests represented a serious potential conflict between river users and nesting eagles in this region. Although the vast majority of human-eagle interactions were between people in non-motorized boats and eagles perched in trees along the river, responses of nesting adults to these encounters were brief. Therefore, we designed our study to assess the effects that camping near nests had on the behavioral patterns of nesting adults. While camped, we minimized our activity as much as possible by localizing our movements and restricting the size of our camp to 1 or rarely 2 tents. For inclusion in the study, we chose randomly from those nests whose nest platforms and surrounding areas were observable.

Behavioral Observations

We quantified behavioral patterns of nesting bald eagles during 50 continuous 48-hour observation bouts at 20 nests. Each nest was observed 1-3 times ($\bar{x}$ = 2.5, mode = 3) with at least 3 weeks separating repeated observations at the same nest. Each observation bout consisted of 2 successive 24-hour periods. During one 24-hour period we camped approximately 500 m from nests (control), a distance we believed would have no impact on nesting adults (Fraser et al. 1985), and during the other 24-hour period we camped approximately 100 m from nests (influence). The order of observations (control-influence [52%] or influence-control [48%]) was determined randomly whenever there were useable observation locations both 500 m upstream and downstream of nests (50% of observations). Because of the extended daylight period in Alaska, we were able to record behaviors for an average of 44.4 hours per observation bout (22.2 hrs/day), for a total of 2,215 hours.

We recorded continuously the behaviors, sex, and number of adult eagles on or near nests. We could accurately distinguish between males and females based initially on body size and subsequently using distinguishing plumage characteristics, usually molt patterns. We recorded the amount of time adults performed the following suite of behaviors while at their nests:

Brooding: covering nestlings from low temperatures or weather extremes;

Shading: shielding nestlings, usually from direct sunlight or rain;

Feeding: actively feeding themselves or their young;

Nest Maintenance: repairing or attending to nest or nest contents;

Preening: grooming;

Perching: present on nest but performing no particular behavior;

Sleeping: motionless with head turned and placed into their back;

Dozing: inattentive, with eyes slowly and intermittently opening and closing;

Empty: no adults on nest.

We also recorded continuously the number of times adults vocalized. Repeated vocalizations from the same adult were considered a single vocalization unless they were separated by at least 20 seconds. We ignored vocalization counts from 2 nests because we could not hear acceptably over nearby rushing water. Lastly, we recorded the number of adults perched within 200 m of the nest (= nest area). We chose this distance because when adults were observed $<$500 m from nests they were rarely observed $>$100 m from nests. Further, we believed that adults $>$200 m from their nests were more often foraging rather than performing nest-related activities. Behaviors were recorded to the nearest minute but occasionally to the nearest second.

Quantifying Prey Consumed at Nests

Eagles conspicuously tear off and consume discrete portions of prey ("bites") when feeding themselves or their nestlings. Therefore, we quantified the amount of prey consumed at nests by counting the number of bites consumed by adults and nestlings. Counting bites is an accurate method to quantify prey consumed in field situations because it alleviates biases inherent in other methods. For example, the number of prey deliveries is influenced by prey size and whether the entire prey item is consumed in a single feeding bout. Also, duration of feeding bouts is influenced by the rate (bites/min) at which eagles feed.

When evaluating the number of feeding bouts per day, we excluded those bouts in which $<$5 bites of prey were consumed (n = 38 of 524 bouts, 7%). These feedings consisted mostly of nestlings feebly feeding themselves (29 of 38, 76%), and the mean number of bites for all other feeding bouts was considerably higher ($\bar{x}$ = 57, SE = 2.1, n = 486). Including these small feeding bouts could bias these comparisons by artificially inflating the number of feedings that occurred per day. We did, however, include these smaller feedings when evaluating total prey consumed per day.

During 38 feeding bouts (7%), we were unable to accurately count the number of bites consumed, usually because our view was obstructed by a feeding bird. For these bouts, we estimated the number of bites consumed by adults and nestlings from multiple regression equations based on complete feeding bouts. These equations included duration of the feeding bout, nestling age, age^2, and number of nestlings, all of which were significant regressor variables. We fit separate equations to predict the number of bites consumed per feeding bout by adults and nestlings based on whether nestlings were being fed by adults or feeding themselves ($F > 46.8$, $P < 0.0001$, adjusted $r^2 = 0.32$-0.69 for all regressions).

STATISTICAL ANALYSES

Each nesting behavior was usually performed independently, although brooding was sometimes performed concurrently with nest maintenance, preening, sleeping, or dozing behaviors. In these few instances, we counted both behaviors individually for analyses. As a result, activity budgets sometimes summed to >100% ($\bar{x} = 107\%$, SE = 1.1, $n = 100$).

We quantified nesting behaviors of adults and assessed the effects that our location had on both the duration and frequency of nesting behaviors. For activity budgets, we calculated the percentage of time each behavior was performed based on the total number of hours the nest was observed each visit (n = 50 visits, $\bar{x}$ = 22.2 hrs/observation). We detailed nesting behaviors of bald eagles using only those data collected from control observation locations previously (***Section** 3*).

Most of our analyses examined behavioral patterns on a daily basis (Table 4.1). However, we also considered brooding and feeding behaviors individually so we could examine more thoroughly the relationship of our observation location and several other factors on these behaviors. These factors included the number and age of nestlings (estimated soon after hatching to the nearest 1/2 week), ambient temperature, rain (raining or not), wind (windy or calm), time-of-day (grouped into 6 4-hr blocks), and sex of the attending adult. We developed multiple regression models to describe the relationships between these factors, the duration of brooding bouts, and the amount of prey consumed per feeding bout. We first fit full models that included all parameters, then sequentially eliminated parameters if they did not provide a significant contribution to the model ($P > 0.10$) (Myers 1990:95).

We developed logistic regression models to assess whether our observation location, temperature, rain, wind, and time-of-day affected the likelihood that a particular nesting behavior was initiated. We fit a main effects model for each behavior using variance estimates scaled by model deviance rather than assuming binomial errors (Collett 1991). We then tested for interactive effects of environmental factors using only those subsets of our data where factorial treatment combinations were complete and had ≥5 observations. Because certain environmental conditions never occurred or occurred rarely (e.g., high

Table 4.1. Response parameters measured to compare the effects of human activity on behavior of nesting bald eagles at control (500 m) and influence (100 m) distances from nests on the Gulkana River, Alaska, 1990-1992.

Response parameter	Measures	Sampling scale
Activity budgets at nests	time engaged in brood, doze, empty, feed, maintain nest, perch, preen, shade, and sleep behaviors	% day
Nest attendance	time adults at nest	% day
Nest-area attendance	time adults within 200 m of nest	% day
Brooding behavior	no. brooding bouts	no./day
	duration of brooding bouts	min./bout
Feeding behavior	no. feeding bouts by adults, nestlings	no./day
	prey consumed per day by adults and nestlings	no. bites/day
	prey consumed per feeding bout by adults and nestlings	no. bites/bout
	time elapsed before, and prey consumed at, first feeding	min., no. bites
	rate prey consumed	no. bites/min./bout
Vocalizations	no. vocalizations	no./day

temperatures late at night), we could not simultaneously examine interactions for all factors.

Each of our analyses addressed the null hypothesis that there were no differences in nesting behaviors of bald eagle when humans were camped 500 m (control) versus 100 m (influence) from nests. We used differences between measured behaviors (percentage of time or frequency with which a behavior was performed per day) at control and influence locations (control minus influence) as the response variable for most of our statistical analyses to benefit from the paired (crossover) design of our experiment. We then compared these differences to zero using paired *t*-tests and univariate analysis of variance (ANOVA) and analysis of covariance (ANCOVA), and multivariate analysis of variance (MANOVA). To determine if the regression models developed for brooding and feeding behaviors differed between control and influence locations, we tested the significance of observation location as a model parameter. If location contributed significantly to the model ($P < 0.05$) we concluded that these behaviors changed because of our presence near nests.

We partitioned each 24-hour observation into 6 4-hour time periods to assess whether bald eagles habituated or became sensitized throughout our 24-hour observation bouts. We calculated activity budgets and counted vocalizations for each 4-hour period. Using a multivariate repeated-measures ANOVA blocked on nest, we tested whether differences in these behaviors at control versus influence locations changed throughout the observation period.

Data were transformed when necessary to meet assumptions of statistical tests. We often used natural log transformations for duration of behaviors and square-root transformations for count data. Although some statistical analyses were performed with transformed data, we report arithmetic means ± 1 standard error throughout the paper unless otherwise noted. Eighteen of the 20 nests in our study were observed on more than 1 occasion. Although visits to the same nests were separated by at least 3 weeks, we repeated some statistical tests using only the first visit to each nest ($n = 20$) to avoid any potential problems with repeatedly sampling the same experimental unit (pseudoreplication).

RESULTS

Nesting Activity Budgets

Our presence near nests caused a pronounced change in the way adult eagles apportioned their time among the nesting behaviors in their activity budgets (Table 4.2) (Wilks' $\lambda = 0.58$, $F = 3.4$, $P = 0.0036$). Adults reduced the amount of time they performed maintenance-type behaviors, including feeding themselves and their nestlings, preening, sleeping, and maintaining their nest ($P < 0.04$). In contrast, they increased the amount of time they brooded young, their most protective behavior ($P = 0.0003$). Results from only the first observation at each nest, which took place early in the nestling period ($\bar{x}$ age = 2.9 ± 0.3 weeks, $n = 20$) (Wilks' $\lambda = 0.17$, $F = 5.9$, $P = 0.0037$), were similar to those that included all observations ($\bar{x}$ age = 6.1 ± 0.5 weeks, $n = 50$) (Table 4.2). As a

Table 4.2. Percent change in activity budgets when influenced by the presence of human activity (control versus influence).

	All observations			First observation only[a]	
Behavior	n[b]	% Change[c]	P[d]	% Change[c]	P[d]
Feed	43	-30.0	0.0058	-21.1	0.051
Brood	27	13.8	0.038	11.7	0.046
Preen	36	-52.6	0.0003	-53.2	0.0011
Nest maintenance	36	-49.8	0.0019	-49.1	0.0056
Sleep	24	-55.7	0.028	-57.4	0.081
Doze	32	17.3	0.4	7.7	0.7
Perch	50	-7.8	0.5	-11.8	0.5
Shade	27	1.9	0.9	-7.0	0.7
Nest empty	50	0.7	0.8	2.9	0.9
All behaviors	50		0.0036		0.0037

[a] Includes only the first observation at each nest (n = 20).

[b] Sample sizes represent the number of observations used for calculations, which included only those observations when values from control and influence locations did not both equal zero for univariate tests.

[c] From control to influence observation locations (control-influence ÷ control).

[d] For individual behaviors, P-values are from paired t-tests comparing the difference in the percent time a behavior was performed at control versus influence observation locations; for all behaviors, P-value is from MANOVA.

check of the adequacy of our control locations (500 m), we found that the order in which we performed our observations (control-influence or influence-control) had no overall effect on activity budgets (Wilks' $\lambda = 0.79$, $F = 1.1$, $P = 0.37$).

In addition to changing the percent time they performed most nesting behaviors (Table 4.2), adults also changed the daily frequency with which they performed 6 of 8 nesting behaviors (Table 4.3). Adults significantly reduced the number of times they maintained nests, preened, shaded nestlings, and slept from 47 to 59% from control to influence locations (Table 4.3). Adults also reduced the number of times per day they fed and brooded nestlings (see below). Overall, adults reduced the total number of behaviors performed at nests per day by 27% from control to influence locations (Table 4.3). This reduction in number of behaviors performed by adults at influence locations declined as nestlings aged and adults spent correspondingly less time at nests (slope $= -4.6 \pm 1.3$, $t = 3.6$, $P = 0.0009$) (Fig. 4.2).

Nest and Nest-Area Attendance.—Although the percent time that nearly all nesting behaviors were performed per day changed in the presence of nearby human activity, the percent time that adults attended nests did not differ between control and influence observation locations (Table 4.4). However, the percent time the nest area (within 200 m of nests) was left unattended increased significantly when humans were camped near nests, with a corresponding decrease in the percent time the nest area was attended by 1 or both adults (Table 4.5).

Table 4.3. The frequency that behaviors were performed per day with observers at influence versus control locations. *P*-values from paired *t*-tests comparing the difference between control and influence observation locations for only those days (*n*) when behaviors occurred at least once.

		Control		Influence			
Behavior	*n*	$\bar{x}$	SE	$\bar{x}$	SE	% Change	*P*
Doze	32	7.6	1.5	7.9	1.3	4.6	0.85
Maintain nest	36	10.9	1.6	5.7	1.0	-48.2	<0.0001
Perch	50	15.6	1.8	14.5	1.8	-7.3	0.43
Preen	36	11.9	1.7	6.3	1.2	-47.4	0.0006
Shade	27	11.0	2.3	8.0	1.9	-27.2	0.047
Sleep	24	7.8	1.3	3.2	0.8	-59.0	0.009
All behaviors	50	55.7	7.7	40.9	5.7	-26.6	0.002

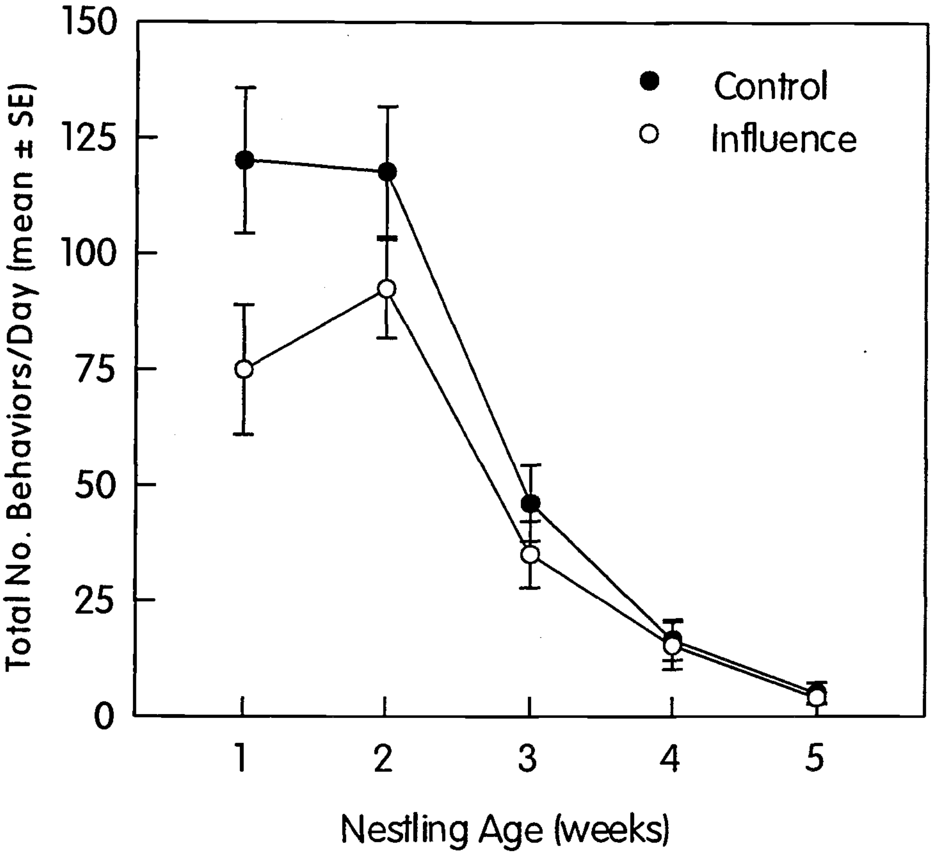

Figure 4.2. The total number of behaviors performed per day ($\bar{x}$ ± SE) by adult bald eagles were reduced when humans were near versus far from nests and declined as nestlings aged. Data are grouped by week.

Table 4.4. Adults did not change the percent time on nests at control versus influence observation locations (n = 49).

	Control		Influence		
No. adults on nest	$\bar{x}$	SE	$\bar{x}$	SE	P
0	60.2	5.5	60.5	5.5	0.91
1	39.3	5.5	39.2	5.4	0.93
2	0.5	0.1	0.4	0.1	0.28

Table 4.5. Adults reduced the percent time spent near nests (within 200 m) at control versus influence observation locations (n = 49).

	Control		Influence			
No. adults near nest	$\bar{x}$	SE	$\bar{x}$	SE	% Change	P
0	27.3	3.8	34.0	4.2	24.5	0.013
1	59.2	3.2	54.3	3.6	-8.3	0.085
2	13.5	1.9	11.6	2.0	-14.1	0.35

Brooding Behavior

In addition to the increased amount of time they brooded nestlings with observers at influence locations (Table 4.2), adults also reduced the number of brooding bouts per day (6.0 ± 1.0) versus control locations (8.1 ± 1.6) (difference = 2.1 ± 1.0, $t = 2.2$, $P = 0.038$). This reduction in brooding bouts reflected a change in behavior by females (control-influence difference = 2.1 ± 0.8, $t = 2.6$, $P = 0.016$) but not males (-0.04 ± 0.42, $t = 0.1$, $P > 0.9$). The reduction in number of brooding bouts but overall increase in time spent brooding resulted because adults increased the duration of brooding bouts at influence (geometric $\bar{x} = 39.3$ min) versus control (26.0 min) locations ($t = 3.2$, $P = 0.0015$).

We investigated whether our observation location (control or influence) affected the duration (min) of brooding bouts after considering the influence of nestling age, ambient temperature, sex of the brooding adult, rain, wind, and time-of-day. Brooding bouts increased in duration as temperature decreased ($P < 0.0001$, Fig. 3.6), were longer when it was raining ($P < 0.0001$) or windy ($P = 0.039$) than not, and varied by time-of-day ($P = 0.022$, Fig. 4.3). Further, the duration of brooding bouts was affected by the interaction between observation location and sex of the brooding adult ($P = 0.025$), indicating that our observation location affected duration of brooding bouts differently for males and females. Both sexes increased the duration of their brooding bouts at influence locations, but males increased theirs to a greater extent (control = 18.7 min, influence = 39.3, a 28% increase) than females (control = 27.7, influence =38.1, a 10%

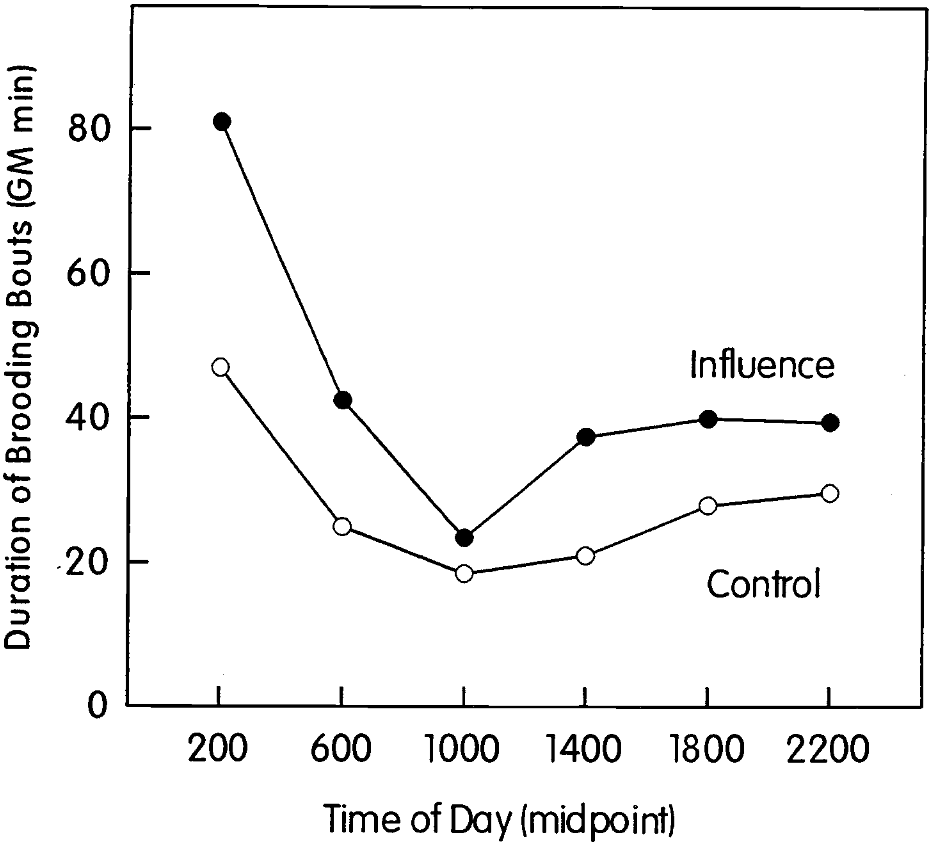

Figure 4.3. Duration of brooding bouts (geometric $\bar{x}$) by bald eagles was longer when humans were near versus far from nests and varied by time-of-day.

increase). In summary, females responded to nearby human activity by decreasing the number of times they brooded per day and increasing the duration of these bouts, whereas males responded only by increasing the duration of their brooding bouts. Nestling age had no apparent effect on brooding bout duration ($P > 0.6$).

Feeding Behavior

In addition to the reduced amount of time adults fed nestlings (Table 4.2), many other facets of bald eagle feeding behavior were adversely influenced by our presence near nests. The total number of feeding bouts per day (by both adults and nestlings) decreased by 20% at influence versus control locations, as did the number of feeding bouts performed by adults alone (-19%) (Table 4.6). The frequency with which nestlings fed themselves per day also decreased at influence locations (-23%), but not significantly. We then examined if nestlings better compensated for the fewer times they were fed by adults when we were camped at influence locations as they matured and their ability to feed themselves improved. Were this true, then the difference in number of feeding bouts at control versus influence locations would decrease as nestlings aged. This difference, however, did not vary with nestling age ($t = 0.6$, $P = 0.5$). This suggests that the reduced number of feedings that resulted when we were camped near nests were from a reduced amount of prey delivered by adults; presumably, nestlings would have fed themselves were prey available.

Unlike the increase in duration of brooding bouts at influence locations, adults did not increase the amount of prey they consumed themselves or fed their

Table 4.6. Number of feedings at bald eagle nests per day was reduced with observers at influence versus control locations. *P*-values from paired *t*-tests comparing the difference at control-influence observation locations; sample size is the number of days in which each type of feeding occurred.

		Control		Influence		%	
Performed feeding	*n*	$\bar{x}$	SE	$\bar{x}$	SE	Change	*P*
Adults	43	4.3	0.5	3.5	0.6	-18.6	0.053
Nestlings	25	3.5	0.6	2.7	0.5	-22.9	0.20
Total (adults+nestlings)	49	5.5	0.4	4.4	0.4	-20.0	0.0025

Table 4.7. The amount of prey consumed per day (bites) was reduced with observers at influence versus control locations. *P*-values from paired *t*-tests comparing the difference at control-influence observation locations ($n = 49$).

	Control		Influence		%	
Prey consumed	$\bar{x}$	SE	$\bar{x}$	SE	Change	*P*
Adult fed to nestlings	269	19	191	18	-29.0	0.0027
Adults fed to themselves	59	9	44	9	-25.4	0.84
Total (adults+nestlings)	329	23	235	23	-28.5	0.0016

nestlings per feeding bout at influence locations relative to control locations ($P > 0.15$), after considering the effects of brood size, nestling age, and sex of the feeding adult (see ***Section 3***). Therefore, because the number of feeding bouts per day was higher at control locations, all measures of the amount of prey consumed per day were lower during influence versus control observations (Table 4.7). These changes represent reductions of 25-29% in the amount of prey consumed per day at nests at influence locations.

The amount of time elapsed (min) from our arrival at each observation location until the time adults first fed nestlings was significantly longer at influence (396 ± 59) versus control (231 ± 44) locations ($t = 2.4$, $P = 0.022$). Adults did not compensate for the delayed time-to-first-feeding in the presence of human activity, because the amount of prey consumed during this first feeding was less at influence locations (57 ± 6 bites) than control locations (72 ± 9), although the difference was not significant ($t = 1.3$, $P = 0.19$).

There were no apparent changes in the rate (bites/min) at which adults fed at control versus influence locations, including the rate at which adults fed nestlings (5.4 ± 0.4, 5.6 ± 0.4, respectively, $t = 0.5$, $P = 0.6$, $n = 35$) or fed themselves (1.5 ± 0.2, 1.3 ± 0.1, respectively, $t = 1.4$, $P = 0.2$). Further, the percentage of feeding bouts performed by each sex did not differ significantly between control (females = 69%, males = 28%, both = 3%) and influence locations (females = 65%, males = 33%, both = 2%) ($\chi^2 = 1.1$, $P = 0.6$). Therefore, when adults did feed nestlings, they fed similarly with observers at control and influence locations; however, with human activity nearby, they delivered less prey which ultimately resulted in fewer feeding bouts and significantly less prey being consumed.

Vocalizations

If eagles vocalized when alarmed as we believed, then our presence near nests was an obvious disturbance. Adults vocalized 307% more per day at influence (geometric $\bar{x} = 48.4$) versus control (11.9) locations ($t = 4.0$, $P = 0.0002$, $n = 48$). This difference was consistent between sexes; males vocalized 347% more at influence (7.6) versus control (1.7) locations ($t = 4.9$, $P < 0.0001$) and females vocalized 433% more at influence (28.8) versus control (5.4) locations ($t = 8.1$, $P < 0.0001$).

Weather and Time-of-Day

We examined changes in eagle responses to ambient temperature, wind, rain, and time-of-day between control and influence observation locations. After accounting for the influence of these environmental parameters (see ***Section 3***), we examined if the likelihood with which adults initiated a particular nesting behavior changed between observation locations. We combined behaviors from influence ($n = 2{,}035$) and control locations ($n = 2, 753$), fitted a model that included observation location and environmental factors, then tested the importance of the observation location parameter. Nearby human activity affected the way in which eagles responded to these environmental parameters for nest maintenance, dozing, preening, sleeping, and perching behaviors ($P < 0.006$), but not for brooding, feeding, or shading behaviors ($P > 0.53$) (Table 4.8). Eagles did not adjust their response to environmental parameters for those behaviors that are probably most important energetically or most likely to affect survival of their offspring (feeding, brooding, shading).

Did Eagles Habituate to Human Activity?

We examined if the changes in nesting behavior at control versus influence observation locations were consistent throughout the 24-hour period we were camped at nests. To examine our data for evidence of habituation we investigated 3 questions: Were there any temporal trends in the behavioral differences between control and influence locations within 24-hour observation periods? If so, what were the shapes of those trends? Were those trends similar for all pairs? We hypothesized that if eagles habituated to human activity then the differences observed in nesting behavior at control versus influence locations would diminish (approach zero) throughout the 24-hour observation period.

There were significant temporal trends in eagle responses to human activity for almost all nesting behaviors, suggesting that responses to nearby human activity changed throughout the 24-hour observation period (Table 4.9). For most behaviors these relationships varied among nesting pairs (Table 4.9). Considering responses of all pairs, differences in nesting behaviors between control and influence locations decreased as observation bouts progressed (Fig. 4.4), suggesting that eagles habituated to human activity near nests.

Table 4.8. Relative odds of a particular nesting behavior being initiated in response to a fixed set of environmental conditions with observers at influence versus control locations (relative odds = 1).

Behavior	Relative odds	χ^2	P
Brood	1.05	0.2	0.65
Doze	0.70	7.8	0.0052
Feed	0.93	0.4	0.53
Maintain nest	1.50	18.5	<0.0001
Perch	0.68	20.7	<0.0001
Preen	1.44	14.1	<0.0001
Shade	0.99	0.1	0.95
Sleep	2.08	17.1	<0.0001

Table 4.9. Results of tests for whether nesting behaviors changed as the amount of time eagles were exposed to human activity increased. *P*-values are from multivariate repeated-measures analyses of within-subject effects (time) and within-subject x between-subject interaction (time x pair), and were reported only if $P < 0.10$.

			Polynomial[a]	
Behavior	time x pair	time	degree	*P*
Brood		0.0001	2	<0.0001
Doze	0.0002	0.0052	2	0.0027
Empty	0.0002		3	0.040
Feed	0.0058		2	0.075
Maintain nest	0.065		2	0.0076
Perch	0.010	0.014	3	0.034
Preen				
Shade	0.0002	0.0001	3	0.027
Sleep		0.0016	2	0.002

[a] Polynomial is the highest degree polynomial contrast (and associated *P*-value) for which the time effect was significant, and describes the shape of how the differences in percent time that adults performed behaviors at control versus influence observation locations (the response variable) varied with time.

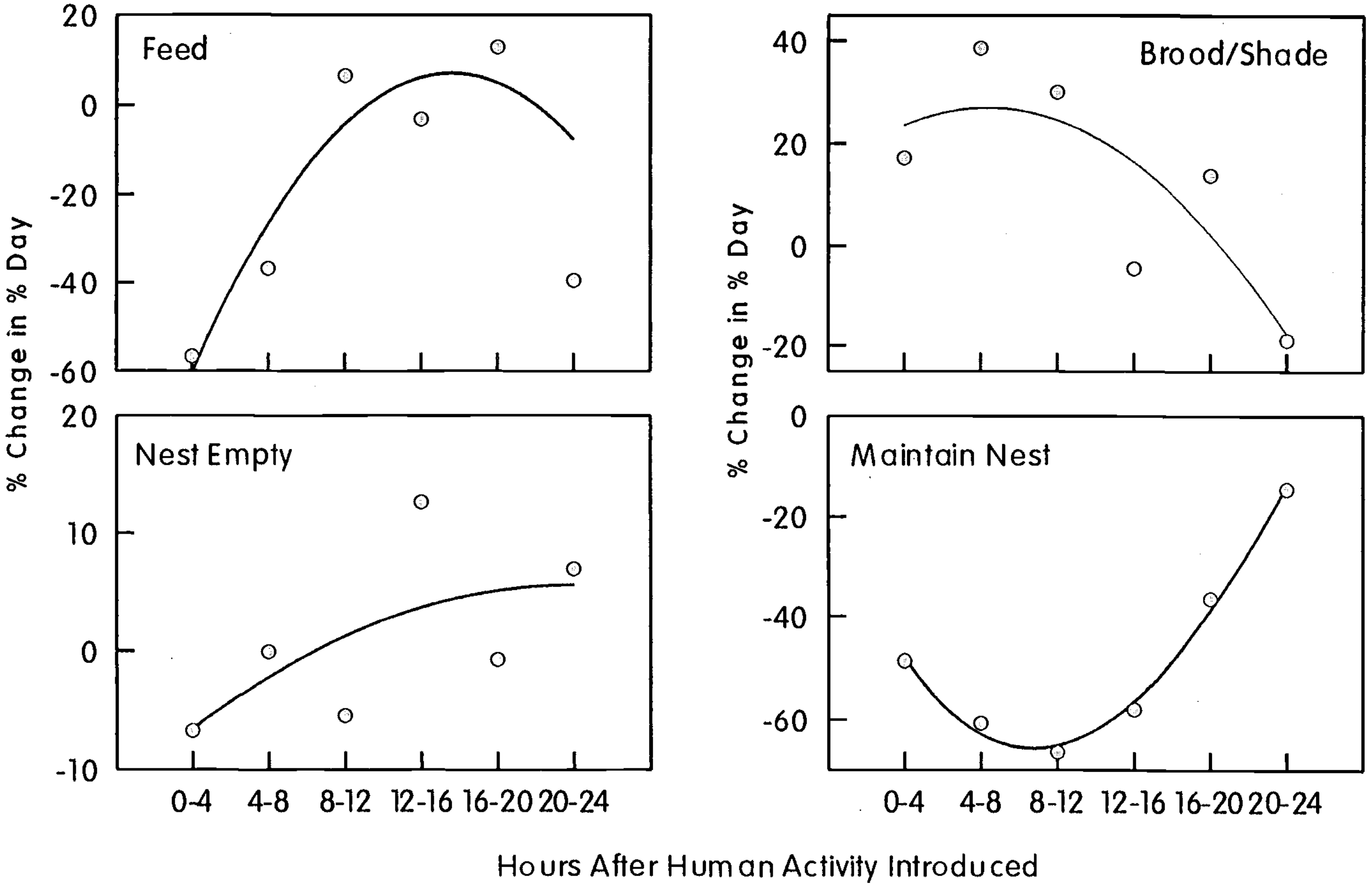

Figure 4.4. Changes in bald eagle nesting behaviors as the amount of time they were exposed to human activity increased. Lines represent the polynomials that best describe the relationship (see Table 4.8).

We performed a similar analysis for the number of adult vocalizations. As with nesting behaviors, the difference in number of vocalizations (square-root transformed) between observation locations varied temporally through the 24-hr observation period but varied differently for some nesting pairs (time x pair interaction: $P = 0.0009$). Unlike the temporal changes in difference of nesting behaviors that tended toward zero as observation bouts progressed (Fig. 4.4), the difference in number of vocalizations for all pairs decreased much more slowly (Fig. 4.5). During the last 4 hours of observation bouts, the number of vocalizations by adults at influence locations was still double (100%) that of adults at control locations (Fig. 4.5).

Lastly, we examined whether the effects of our experiment differed for eagles that nested in areas of relatively high human-use (16 of 50 observations, 32%) compared to those in areas of low human-use (68%). Responses (measured as differences in overall activity budgets between control and influence locations) did not differ strongly between these groups (Wilks' $\lambda = 0.71$, $F = 1.8$, $P = 0.11$). This suggests that in the long term, either eagles in areas of relatively high human use did not habituate to human activity, or that the amount of activity in these areas was not substantial enough to compel eagles to habituate.

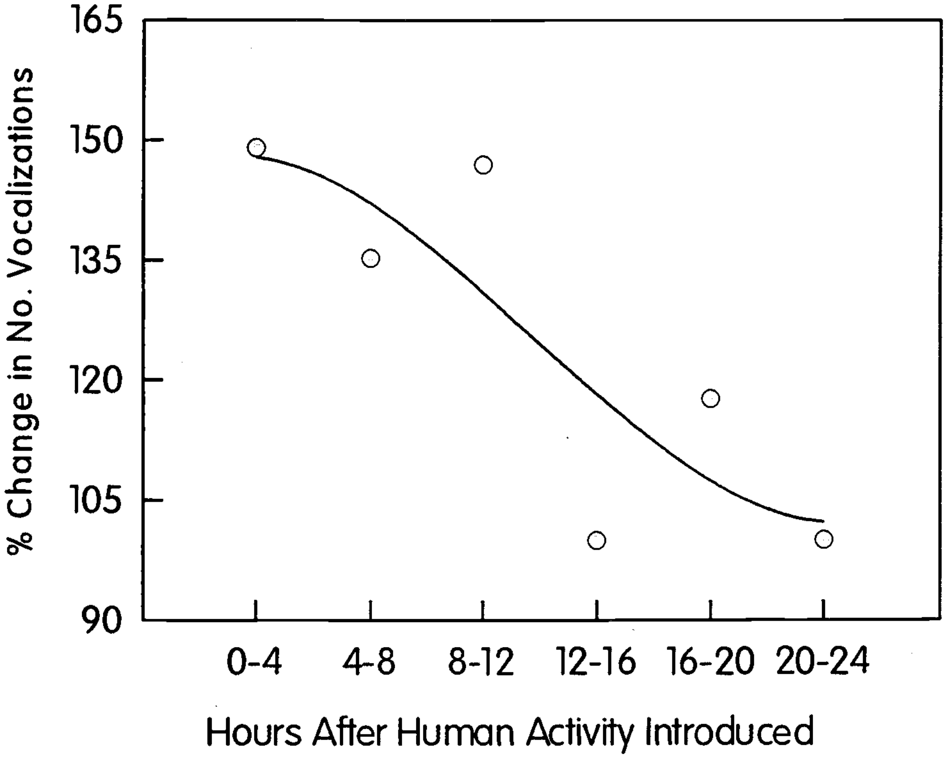

Figure 4.5. Changes in number of vocalizations as the amount of time bald eagles were exposed to human activity increased.

DISCUSSION

Nesting Behavior

We found that human activity near active bald eagle nests affected virtually all aspects of adult behavior. These effects included changes in the duration and frequency of most behaviors, in the types of behaviors performed, and in the way eagles responded to particular sets of environmental conditions. Previous research has shown that breeding raptors responded to different relatively short-duration disturbances in other ways. For example, activity budgets of prairie falcons (*Falco mexicanus*) nesting in areas exposed to blasting differed from those in control areas during incubation and brood-rearing periods (Holthuijzen et al. 1990). Further, although bald eagles have successfully completed nesting after having been disturbed, they may be more likely to change their nesting location the following year (Hancock 1966). Three studies that examined rates of nest-changing the year following a disturbance all found a higher rate in disturbed than control territories (Grier 1969, Fraser et al. 1985, Anthony et al. In press). This type of delayed response to human disturbance has not been limited to bald eagles, but also has been observed in gyrfalcons (*Falco rusticolus*) (Platt 1977), peregrine falcons (*Falco peregrinus*) (Ratcliffe 1980), and ferruginous hawks (*Buteo regalis*) (White and Thurow 1985).

Although it may seem both logical and somewhat reassuring that adult eagles spent more time protecting their nestlings (brooding) in the presence of human activity, this change in activity budgets could have energetic consequences on eagle reproduction. For example, the amount of prey consumed at nests decreased by an average of 29% in the presence of human activity, while the number of feeding bouts per day decreased by an average of 20%. Therefore, nestlings probably suffered the highest energetic costs because of their complete dependence on adults for food.

The energetic costs associated with human disturbance may be ultimately manifested in an several ways. Growth rates of nestling bald eagles have been correlated with the mass of prey delivered to nests by adults (Bortolotti 1989). Therefore, reduced amounts of prey provided to nestlings, as we observed, could retard growth rates which would either lengthen the nestling period and prolong fledging dates or result in lower mass at fledging, which has been shown to influence survival in some species (Perrins et al. 1973, Jarvis 1974). In northern regions such as Alaska, migratory birds are under considerable time constraints to complete nesting activities because of the brief summer and are therefore particularly vulnerable to this prospect (e.g., Henson and Grant 1991). Later fledging dates could force juveniles to migrate prematurely which may reduce first year survival. Nestling growth rates were found positively correlated with postfledgling survival and recruitment in black-legged kittiwakes (*Rissa tridactyla*) (Coulson and Porter 1985).

Habituation

Within our 24-hour observations, we observed a general decrease in the behavioral responses of eagles to human activity as the observation period progressed. This decreasing trend suggests that the greatest effects on eagle behavior occurred during the initial hours of disturbance (Figs. 4.4 and 4.5). However, even after 24 hours of continuous disturbance, eagles were still vocalizing at twice their typical rate (Fig. 4.5). We suggest that although their patterns of nesting behavior were approaching normal levels (Fig. 4.4), eagles were still considerably stressed.

Frequent, short-duration disturbances within the same breeding territory could have cumulative effects on adults and important energetic consequences to developing young. Alternatively, habituation to human activity could continue across repeated disturbances if habituation does not wane as intervals between disturbances increase. Our observations of between-disturbance intervals of 3-4 weeks indicate that the tendency for eagles to habituate was not cumulative—rather, each subsequent disturbance was effectively independent of the last. Adults at nests visited on more than 1 occasion did not respond differently than those visited only once (Table 4.2). Unless disturbances were more frequent, we believe long-term habituation to nearby human activity will not occur, at least within a single breeding season. Responses of prairie falcons exposed to repeated blasting waned within a given day but showed no long-term response through the entire nesting period (Holthuijzen et al. 1990).

A Synthesis of Human Impacts on Breeding Bald Eagles

Eagle responses to human activity are extremely variable and depend on a variety of factors at many temporal and spatial scales. Much of the variability in responses, however, can be attributed to a few factors that could interact to affect behavior in complex ways. The timing, type, duration, and novelty of a particular disturbance, as well as the previous level (amount) at which it existed within a breeding area influence how disturbance affects breeding raptors. Developing an understanding of these factors is essential before management strategies are devised to ameliorate the effects of human disturbances. Although we will not review all research on human impacts to breeding eagles, we will formulate some general principles that have emerged from this and previous studies.

Timing of disturbances.—Breeding eagles are differentially vulnerable to human activity during different periods of their nesting cycle and are probably most susceptible during egg laying, incubation, and the early nestling period. We studied effects of human activity only throughout the nestling period, which is the period when breeding bald eagles in the Gulkana Basin are exposed to human disturbance. The changes that resulted from our disturbances were limited to alterations in behavioral patterns. Our activities did not cause nesting failure, as only 1 of 20 nests that we observed ultimately failed to fledge young. Other evidence also suggests that eagles are not most sensitive to human activity during the nestling period. Climbing to nests both throughout (Bortolotti et al. 1983) and once during the nestling period (Grier 1969, Anthony et al. In press) had no apparent effects on reproductive success that year. In contrast, climbing to nests during incubation and early in the nesting period has caused profound effects in other northern populations. For example, 3 of 4 nests with eggs or young <1 week old were abandoned by adults after being climbed to install cameras, whereas nests climbed with older young >3 weeks old (n = 3) were not abandoned (Cain 1985). Further, when adults do not abandon nests after being climbed during incubation their productivity may still be reduced (see Bortolotti et al. 1983). During the nestling period breeding eagles are also vulnerable to human activity near nests (this study) and in foraging areas (McGarigal et al. 1991) when the energetic demands of nestlings are high and adults increase their foraging intensity. In summary, the degree and spatial scale at which eagles are vulnerable to human disturbance changes throughout the nestling period.

Type and duration of disturbances.—Responses of eagles to human activities also depend on the type of disturbance. Pedestrians tend to have the most extreme effects on breeding eagles when compared to boats, vehicles, short-duration noises, or aircraft; however, effects caused by all disturbance types become more acute as an eagle's distance to the disturbance decreases (Grubb and King 1991, McGarigal et al. 1991, ***Section 5***). Therefore, eagles that breed and forage along rivers are likely to be more vulnerable to most human disturbances because the encounter distance tends to be shorter than along open-water systems. Bortolotti et al. (1983) suggested that the duration of time researchers spent near the nest determined the severity of a disturbance.

Existing amount of disturbance.—Breeding eagles respond to human activity by choosing nest sites (Fraser et al. 1985) and foraging sites (McGarigal et al. 1991) in areas with relatively low levels of human activity, and by selecting habitats within their home ranges that receive proportionally low levels of human use (Garrett et al. 1993). Wintering (Russell 1980) and breeding bald eagles (***Section 5***), as well as breeding prairie falcons (Holthuijzen et al. 1990) inhabiting areas with low levels of human activity, showed greater responses to introduced disturbances than birds inhabiting areas where the particular disturbance had occurred previously. This evidence suggests that raptors can habituate to particular types and levels of human activity (probably under some threshold level) but will respond adversely to a change in disturbance type or amount. When raptors accustomed to a particular disturbance context were exposed to either a novel disturbance type or to the same disturbance in a new area, their responses became more intense and increased in likelihood (Stalmaster and Newman 1978, White and Thurow 1985).

Lastly, the impacts of human activity on breeding raptors can interact with other environmental factors, such as inclement weather or levels of prey abundance. For example, the effects of human activity on both ferruginous hawks and European kestrels (*Falco tinnunculus*) were exacerbated during periods of food stress (Van der Zande and Verstrael 1985, White and Thurow 1985).

MANAGEMENT RECOMMENDATIONS

The behavioral changes of bald eagles to nearby human activity that we observed unequivocally demonstrate the potential adverse effects of human activity near nests. However, using behavioral measures as response variables leaves at least 2 questions for resource managers and researchers to address: (1) which eagle behaviors do they consider most important? and (2) at what level is an eagle sufficiently "disturbed" to merit management action? If an experiment mimicking the relevant disturbance context in an area results in a behavioral change beyond some preestablished threshold level, then protective guidelines need to be implemented. With these 2 questions in mind, we make the following recommendations.

Within the framework of this study and the low existing levels of human activity on the Gulkana River, we recommend posting signs at river put-in points warning of the potential effects caused to bald eagles by remaining near nests. Further, we suggest that camping be prohibited from within 500 m of active nests. One management alternative would be to designate particular locations along the river corridor as permanent camping areas. If eagles indeed show a propensity to habituate to stationary human activities, then this strategy could reduce the adverse effects of humans on eagle nesting behaviors. We stress, however, that accurate counts of river users need to be obtained to detect increases in use levels. If use levels increase, as they likely will, the probability of disturbing eagles either at nests or in foraging areas will also increase. When use increases beyond some threshold level of human use established by managers, more restrictive management practices to reduce impacts on eagles should be enacted (see *Section 6*).

RESEARCH RECOMMENDATIONS

Scope and Applicability.—The scope of inference for our study is, of course, limited to bald eagles nesting within the Gulkana Basin. This population inhabits an area with very low existing levels of human activity and is therefore representative of populations nesting in wilderness areas. The population is only exposed to human activity during the nestling period, which corresponds to the period when the river is free of ice and therefore, accessible for most recreational uses. However, the level and intensity of human activity can be relatively high ($\geq$20 groups/day) during salmon fishing season (late June and July) (***Section 6***).

Future Research.—To expand the breadth of understanding of the effects of indirect human activity on bald eagles and other species, we encourage others to replicate our experimental approach and modify the design to reflect the disturbance contexts to which species are exposed. A series of similar studies on eagles and other species in areas with different existing levels and types of human activities will allow us to generalize about indirect human impacts on behavior, and eventually, to broaden our management and research focus from individual species to species assemblages (Anthony et al. 1994).

For example, in 1993 a similar study was performed on golden eagles (*Aquila chrysaetos*) in Wrangell-St. Elias National Park, Alaska (K. Kozie, Natl. Park Serv., Copper Center, AK, unpublished data). The design was identical to ours except that control observations were established approximately 1,000 m and influence observations approximately 400 m from nest cliffs to better reflect the disturbance context in these treeless, mountainous habitats. Although the magnitudes of responses by adult golden eagles to nearby human activity differed somewhat from bald eagles, the responses were strikingly similar. Adults decreased the percent time they performed feeding (-28%), nest maintenance (-72%), and preening (-71%) behaviors from control to influence observation locations and performed significantly fewer feeding bouts per day with observers at influence ($\bar{x} = 2.3$) versus control locations ($\bar{x} = 5.0$) ($t = 3.22$, $P = 0.049$). Further, the amount of prey consumed at nests declined by 39% for nestlings ($t = 3.3$, $P = 0.046$) and by 67% for adults ($t = 2.5$, $P = 0.087$). The similar findings between this study and ours suggests that avian responses to human disturbance may be consistent within taxonomically similar groups.

Although we observed a tendency for pairs to habituate to human activity, we need to better understand how frequent repeated disturbances of varying duration affect eagle responses as well as their tendency to habituate. We also only examined the effect of human activity at 1 influence distance (100 m). Because responses varied considerably among pairs (Table 4.9) and nesting behavior changed greatly as nestlings aged (Figs. 3.1*a* and *b*), we are unable to specify a minimum distance at which all pairs in all populations will be free from the effects of human disturbance during the entire nesting period. Contrasting responses of pairs exposed to human activity at different distances from nests and at different times of the breeding cycle will be necessary to develop more general management strategies to protect birds from the effects of human activity.

Assessing the non-immediate effects of recreational activity on animals and their behavioral patterns is more difficult and inherently more time consuming than assessing effects on reproductive success. We believe, however, that behavior is a more appropriate measure by which to gauge wildlife responses to human disturbance because it is often a more sensitive response parameter, and because potentially serious effects on reproductive fitness can be recognized and managed for preemptively, before long-term consequences from indirect disturbances result. We believe there is no better measure to aid our understanding of human impacts on wildlife and for devising mitigative strategies to protect wildlife populations. We suggest that the presence of humans near nesting bald eagles has significant impacts on their breeding behavior, and that even a low-level human presence, if sustained, could ultimately result in population-level impacts through reductions in reproductive success or survival of fledglings.

5: RESPONSES OF BALD EAGLES TO HUMAN ACTIVITY DURING THE SUMMER IN INTERIOR ALASKA

INTRODUCTION

The effects of human activity on wildlife populations are both complex and highly variable. Many types of non-consumptive activities adversely affect wildlife in a multitude of ways, including altering nesting activity budgets (***Section 4***), foraging patterns (Skagen 1980), distribution and habitat use (Stalmaster and Newman 1978, Knight et al. 1991); reducing reproductive success (White and Thurow 1985) and foraging efficiency (Knight and Knight 1986, Knight et al. 1991, Skagen et al. 1991); and increasing energetic expenditures (Stalmaster 1983) and stress (Fernandez and Azkona 1993). In contrast, management strategies used to decrease the effects of human activity on populations of sensitive wildlife species such as bald eagles (*Haliaeetus leucocephalus*) tend to be simplistic and typically consist of spatial or temporal restrictions (or both) on the amount of human use in critical habitats (Anthony et al. 1994).

Because they are classified as endangered or threatened in the 48 conterminous states, bald eagles often have been studied to understand and reduce the effects of human activity on their populations. Most management strategies developed have used a buffer-zone approach (Mathisen et al. 1977) within which human use is restricted near nest sites, communal roosts, or winter concentrations (Anthony et al. 1994). However, restricting human use along narrow river systems with any buffer zone effectively eliminates the entire river corridor from use. On these systems, therefore, other management strategies are necessary if eagles and humans are to coexist successfully.

During the summers of 1990 to 1992 we studied the responses of bald eagles to recreational boating activity in the Gulkana River basin of Interior Alaska. This area and eagle population are particularly interesting because (1) similar to many wintering eagle populations, large numbers of nonbreeding eagles are attracted to the area because both chinook (*Oncorhynchus tshawytscha*) and sockeye salmon (*O. nerka*) spawn throughout the basin during the summer; (2) the basin also supports more than 70 pairs of nesting eagles, allowing comparisons of disturbance responses between breeding and nonbreeding eagles; and (3) the river reaches within the basin are impacted differentially by recreational activity, allowing comparisons between reaches with different levels of human use.

METHODS

Field Techniques

From early June until mid-September 1990-1992, we used inflatable rafts to navigate the Main Stem and West Fork of the Gulkana River. We floated the main river course and recorded whether an eagle flushed in response to our approach and the distance at which it flushed. To duplicate the activity of river users, we did not intentionally flush perched eagles. We also recorded 13 potentially relevant factors to characterize the context in which each disturbance occurred (Table 5.1). We measured all distances to perched eagles with a

Table 5.1. Factors examined to assess the influence of human activity on flush response and flush distance of bald eagles on the Gulkana River, Alaska, 1990-1993.

		Examined for[a]		
Factor	Variable type	Breeding adults	All adults	All ages (non-breeding)
Eagle age	Categorical	no	no	yes
River reach	Categorical	yes	yes	yes
Distance disturbance first visible (m)	Continuous	yes	yes	yes
Distance perched from river's edge (m)	Continuous	yes	yes	yes
Perch height (m)	Continuous	yes	yes	yes
Number of eagles within 50 m	Continuous	no	yes	yes
Perched within 1,000 m of nest?	Categorical[b]	yes	yes	no
Perched within 500 m of a salmon carcass?	Categorical	no	yes	yes
Ambient temperature (°C)	Continuous	yes	yes	yes
Raining?	Categorical	yes	yes	yes
Hour of day	Continuous	yes	yes	yes
Date (Julian)	Continuous	yes	yes	yes
Year	Continuous	yes	yes	yes

[a] yes = examined to determine its effect of flush response and distance; no = not examined.

[b] Used as a continuous variable for analyses on nesting adults.

rangefinder, except perch height, which we estimated. All factors were measured up to a distance of 500 m, except distance to nest, which we measured to 1,000 m.

We classified eagles into 5 distinguishable age/plumage classes (McCollough et al. 1986) and excluded data for eagles we could not accurately classify (<3%). We combined age classes of subadults that were not distinguishable in the field. Eagles with completely white heads and tails were classified as adults (≥5 yrs old). Those with nearly complete adult plumage except some brown feathering in their heads or tails were classified as near-adults (≥4 yrs). Those with a predominantly brown breast, a moderate amount of white feathering in their heads, and a predominantly yellow cere and beak were classified as older subadults (≈ 3-4 yrs). Those with heavily mottled white and brown feathering on their breasts and dark ceres, beaks, and irises were classified as younger subadults (≈ 1-2 yrs). Those with almost uniformly brown plumage, cere, beaks, and eyes were classified as juveniles (≈ 1-4 weeks after fledging). We recorded data on juveniles, which were usually perched ≤1 km from a nest, only after they fledged.

Adults perched ≤1 km from a nest were classified as breeding and all others as nonbreeding, because breeding eagles in the Gulkana Basin spent most ($\bar{x}$ = 66%) of the day perched <100 m from their nests (*Section 3*). We used this classification to minimize the likelihood of misclassifying nonbreeders as breeders; however, we probably misclassified some breeders as nonbreeders when they perched >1 km from nests.

We divided our study area into 4 river reaches based on the relative amounts and types of human use (*Section 6*). Three reaches were segments of the

Main Stem of the Gulkana River and the other a major tributary of the Main Stem, the West Fork (Fig. 5.1). The Upper Main Stem reach (from the outlet of Paxson Lake) received moderate levels of human use, almost exclusively by non-motorized crafts (rafts, canoes, kayaks). Nearest the headwaters, the river channel in the Upper reach was narrow (20-60 m). The Middle Main Stem reach received the highest levels of human use, including all the non-motorized crafts that used the Upper reach, plus motorized crafts that accessed the river where it meets the Richardson highway. The river channel here was more wide and open, and had more expansive gravel bars than the Upper reach (60-70 m). The Lower Main Stem reach received intermediate levels of non-motorized use and occasional motorized use, and was accessible from several points along the highway. The river channel here was relatively wide (70-100 m) and surrounded by many tall bluffs (>80 m) and expansive gravel bars. Lastly, the West Fork reach (from Fish Lake) received almost no human use because it was only accessible by float plane. The river channel here was narrow (30-50 m) and meandering.

Disturbance Context

When a human approaches an eagle, the eagle must choose whether to respond the disturbance, and if so, the distance at which to respond. Whether an eagle responds to a disturbance is likely to depend on a suite of variables that we defined as the disturbance context. For example, eagle responses to humans depend on factors such as how high it is perched above the ground. To understand how the disturbance context influenced flush rate and flush distance,

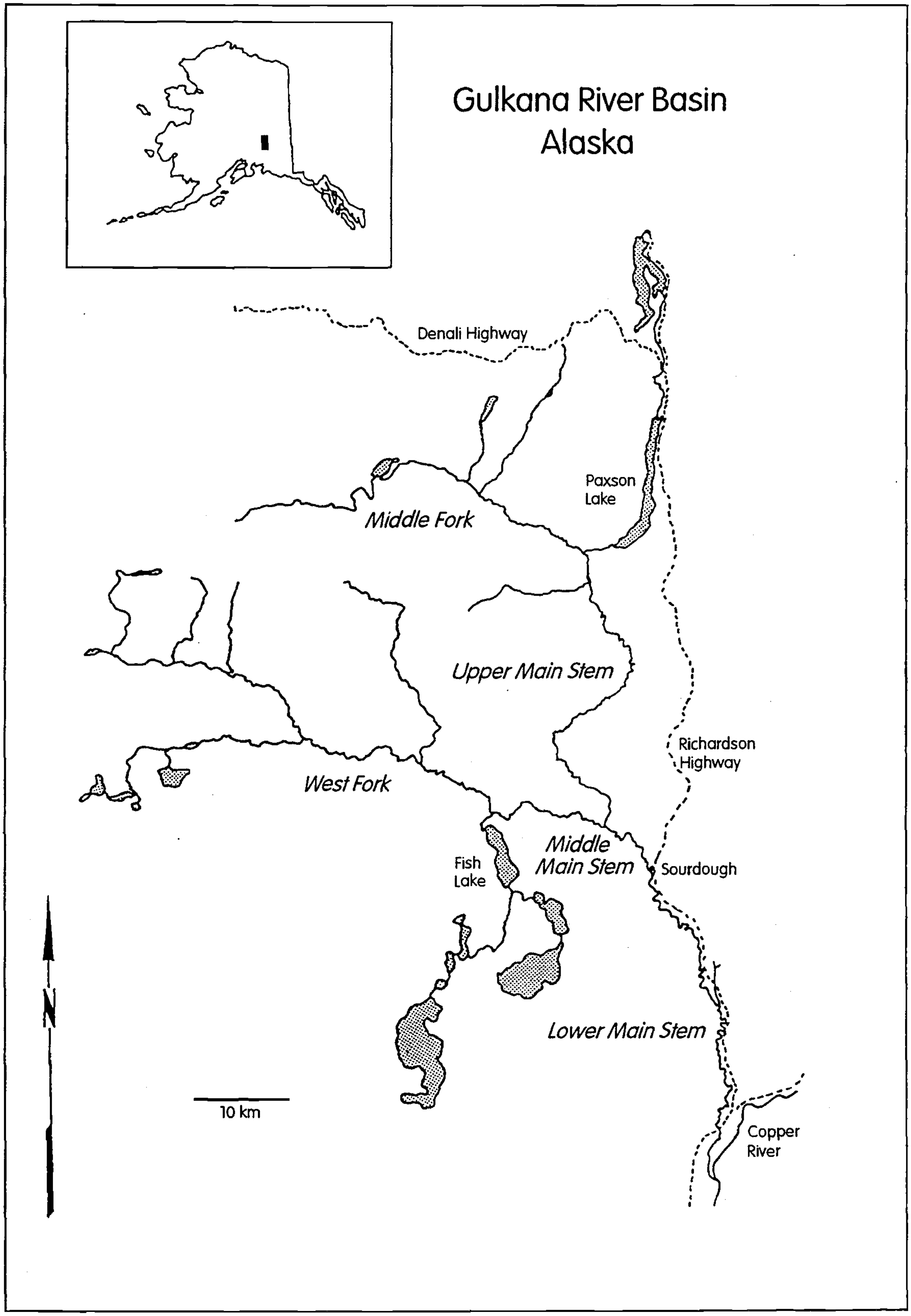

Figure 5.1. The Gulkana River basin, Alaska.

we assessed the effects of 13 different variables on eagle response (Table 5.1). Our analyses simultaneously considered all these potentially influential variables.

Statistical Analyses

We developed 2 types of models to describe how the disturbance context affected responses of eagles to an approaching disturbance: (1) whether an eagle flushed when approached (flush response), and (2) the distance at which it flushed (flush distance). To identify those factors that influenced flush response and flush distance, we used logistic and multiple linear regression, respectively. To identify which model parameters were influential, we first fit full models consisting of all regressor variables (Table 5.1), then systematically eliminated variables with little explanatory power ($P > 0.10$). We used drop-in-deviance tests and extra sums-of-squares F-tests for logistic and multiple regressions, respectively (Myers 1990:95, 315), to assess the explanatory power of variables.

We developed flush response and flush distance models for 4 non-exclusive groups of eagles: (1) breeding adults, (2) all adults (both breeding and nonbreeding), (3) nonbreeding eagles of all age-classes, and (4) nonbreeding eagles flushed on more than 1 occasion. The first 3 model sets were developed using only our first approach to individual eagles (n = 1,164); the last set used repeat approaches to the same eagle (n = 1,467). We report complete results of models (1) and (3) and report only instructive differences derived from models (2) and (4).

Throughout the duration of our study we undoubtedly approached some of the same eagles more than once. To minimize problems associated with lack of sample independence, we separated repeat trips on each river reach by at least 3 weeks. Therefore, we treated all first approaches to an eagle as independent observations. We usually had no difficulty following flight paths of birds that flushed and believe that we misclassified few if any repeat approaches to the same bird as the first approach. Lastly, we transformed variables when necessary to better meet assumptions of parametric statistical tests. However, we report arithmetic means ± 1 SE rather than retransformed values to maintain consistency and facilitate comparisons with previous studies.

RESULTS

Responses of Adults

Breeding Adults.—Only 23% (42 of 184) of breeding adults flushed in response to our approaching raft although we passed ≤ 80 m ($\bar{x} = 62.5 \pm 3.6$ m) from 80% of the birds that did not flush. When adults were on nests they were even less likely to flush. Only 8% (2 of 26) of adults on nests flushed compared to 25% (24 of 118) of all other breeding adults ($\chi^2 = 3.9$, $P = 0.047$). Flush response also increased as an eagle's distance from its nest increased, decreased as perch height and the distance perched from the river's edge increased, and was higher for birds nesting in the remote West Fork reach (43%) than other reaches (22%) (Table 5.2).

Flush distance ($\bar{x} \pm$ SE) of breeding eagles averaged 87.5 ± 10.2 m ($n = 42$) and increased as an eagle's distance from its nest increased, decreased somewhat as

Table 5.2. Factors that significantly influenced ($P < 0.10$) flush response rate of breeding bald eagles on the Gulkana River, Alaska, 1990-1993 ($n = 184$).

Factor	Odds ratio[a]	χ^2	P
Distance perched from river (ln)	0.58	5.9	0.015
Distance perched from nest (ln)	1.08	9.4	0.0022
Perch height (square root)	0.62	3.9	0.047
Nesting along West Fork reach	13.2	6.8	0.0091
Year	0.60	4.0	0.046
Full model (-2 log L statistic)		59.5	<0.0001

[a] Odds ratio for a "typical" flush response = 1; odds ratios >1 indicate that a given factor increased the likelihood of a flush response by the odds ratio when increased by 1 unit when all other factors were held constant; odds ratios <1 indicate the opposite effect.

ambient temperature increased, and varied by river reach (Table 5.3). Flush distance of breeding eagles was greater in the remote West Fork (110.6 ± 12.8 m) and the Lower Main Stem reaches (94.8 ± 15.3 m) compared to other reaches (80.5 ± 14.9 m) (Table 5.3).

All Adults.—We compared flush rates and flush distances of breeding adults to all other adults (those >1 km from a nest). After adjusting for other significant model effects, we found that breeding adults were less likely to flush in response to our approaching boat (23%, $n = 184$, odds ratio = 0.32) than other adults (57%, $n = 442$, odds ratio = 1.0) ($P < 0.0001$). Breeding adults also flushed at shorter distances (87.5 ± 10.2 m, $n = 42$) than nonbreeding adults (113.0 ± 4.5 m, $n = 253$) ($P = 0.023$).

Responses of Nonbreeding Eagles

Overall, 58% ($n = 1{,}164$) of all nonbreeding eagles flushed in response to our approaching raft but only 23% flushed at distances >100 m (Fig. 5.2*b*). For eagles that flushed ($n = 684$), most (52%) did so between 25 and 100 m from the approaching disturbance (Fig. 5.2*a*). However, whether an eagle flushed was a complex response that was influenced by many factors (Table 5.4). Flush rate increased as the distance the disturbance was first visible to an eagle decreased (Fig. 5.3*a*); i.e., the farther an eagle could observe an approaching disturbance, the less likely it was to flush (Table 5.4). The location of an eagle's perch clearly influenced response rate, which decreased as perch height (Fig. 5.3*b*) and distance from the river's edge increased (Fig. 5.3*d*). Flush response rate also increased with

Table 5.3. Factors that significantly influenced ($P < 0.10$) the distance at which breeding bald eagles flushed in response to our approaching boat on the Gulkana River, Alaska, 1990-1993. Results are from multiple linear regression model ($n = 34$).

Factor	Parameter estimate	SE	t	P
Distance perched from nest (ln)	0.039	0.014	2.8	0.0082
Nesting along river reach				
West Fork	1.10	0.47	2.4	0.025
Lower Main Stem	0.47	0.25	1.8	0.075
Ambient temperature	-0.072	0.038	1.9	0.070
Intercept	4.17	0.056	7.5	<0.0001
Full model (F-statistic)			2.9	0.037

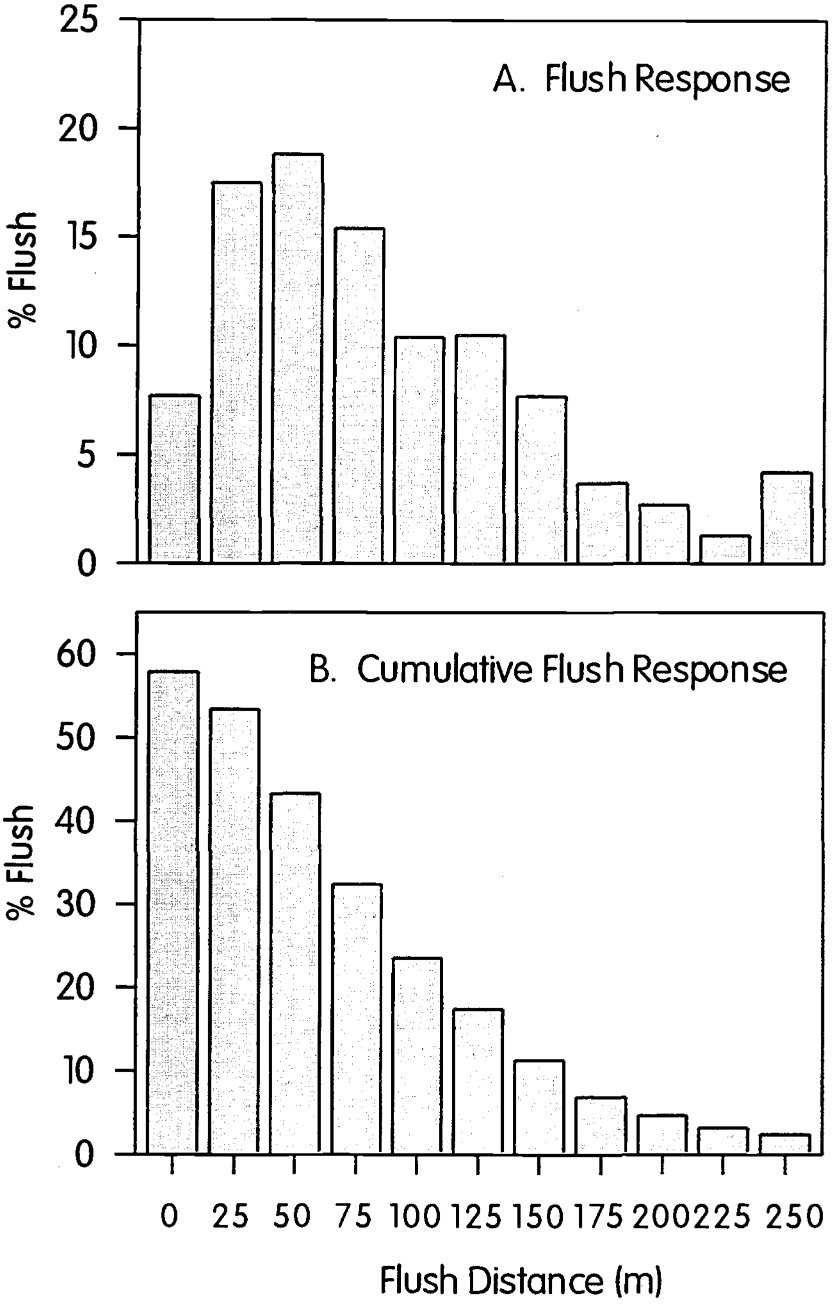

Figure 5.2. (A) Flush response distances of nonbreeding bald eagles in response to human activity and (B) cumulative flush response distances (the percentage of eagles flushing at or beyond a given distance) in the Gulkana Basin, Alaska, 1990-1993.

Table 5.4. Factors that significantly ($P < 0.10$) influenced flush response rate of nonbreeding bald eagles on the Gulkana River, Alaska, 1990-1993. Results are from a logistic regression model ($n = 776$).

Factor	Odds ratio	χ^2	P
Distance perched from river (ln)	0.56	52.9	<0.0001
Distance disturbance first visible to eagle (ln)	0.99	3.4	0.067
Perch height (square root)	0.77	20.0	<0.0001
Perched along river reach[a]			
Upper Main Stem	1.83	7.24	0.0071
Lower Main Stem	2.23	17.2	<0.0001
West Fork	4.91	6.5	0.011
Age class[b]			
Juvenile	0.07	29.1	<0.0001
Older subadult	0.56	5.1	0.023
Year	0.85	2.9	0.090
Julian date	1.02	14.7	<0.0001
Number of eagles in group	1.48	30.9	<0.0001
Ambient temperature	1.05	3.6	0.059
Full model (-2 log L statistic)		275.7	<0.0001

[a] Compared to middle Main Stem (odds ratio = 1.0).

[b] Compared to adult age class.

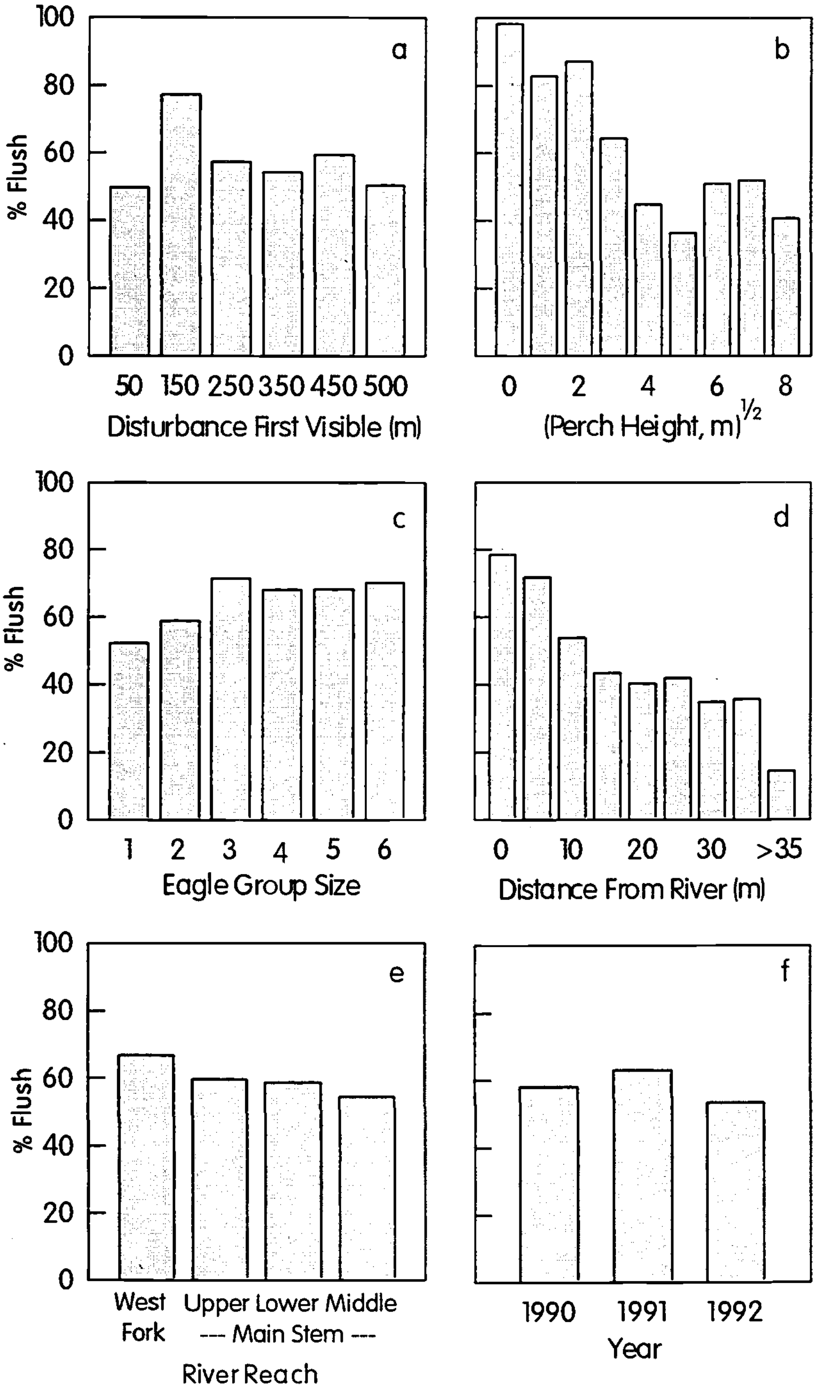

Figure 5.3. Influence of (a) distance at which disturbance was first visible, (b) perch height, (c) group size, (d) distance from river, (e) river reach, and (f) year on flush response rates of nonbreeding bald eagles to human activity in the Gulkana Basin, Alaska, 1990-1993.

eagle group-size (Fig. 5.3*c*) but varied little among eagles aged ≥ 1 year; only older subadults differed from adults (Fig. 5.4). However, juveniles flushed less frequently than all other age classes (Fig. 5.4).

The existing level of human use varied among river reaches and may have been responsible for the differences we observed in flush response rate among reaches (Table 5.4). Response rates were highest for eagles perched along the West Fork, a reach that received little human use, and were lowest along the Middle Main Stem, the reach that received the highest level of human use (Fig. 5.3*e*).

Flush distance was influenced by many of the same factors that influenced flush response rate (Table 5.5, Fig. 5.5). Four factors had particularly noteworthy effects. First, in contrast to flush response, flush distance increased as the distance the disturbance was first visible to an eagle increased (Fig. 5.5*a*). This illustrates how the visibility of a disturbance governed flush distance. If a disturbance was first visible only 50 m from a perched eagle then flush distance was constrained within a 50 m limit. Second, flush distance was influenced by perch height, which was related to perch substrate (Fig. 5.5*b*). When perched on or near the ground ($<$2 m), eagles flushed at relatively far distances. When perched in trees ($\approx$ 2-20 m), flush distance steadily decreased as perch height increased. When perched on river bluffs ($>$20-80 m), however, flush distance steadily increased as perch height increased. Flush distance increased as perch height increased on bluffs because these high perches were near the river's edge and eagles were almost directly above the approaching disturbance when flushed. Because of the perch's height, eagles were still a relatively great distance from the disturbance. Further,

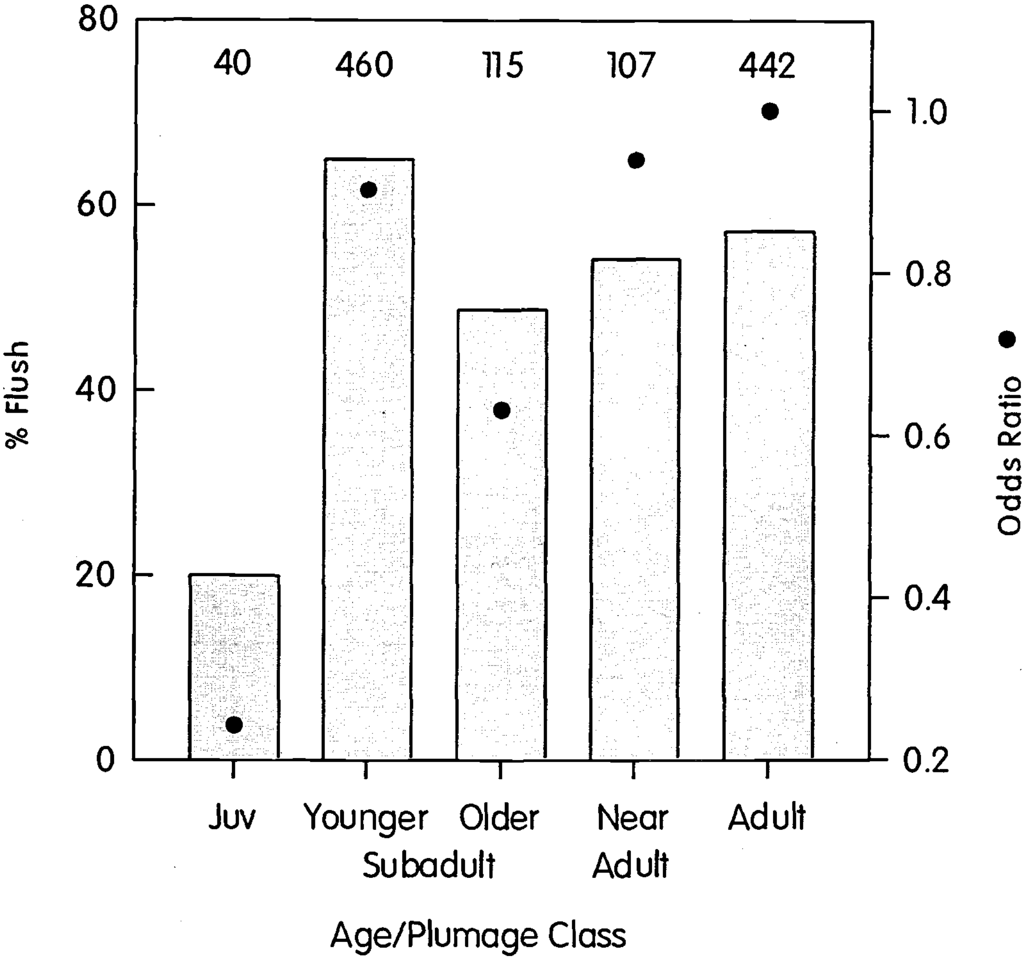

Figure 5.4. Influence of eagle age on flush response rates of nonbreeding bald eagles in the Gulkana Basin, Alaska, 1990-1993. Odds ratios are adjusted for other significant model effects (Table 4.2). Numbers at top of figure are sample sizes for each group.

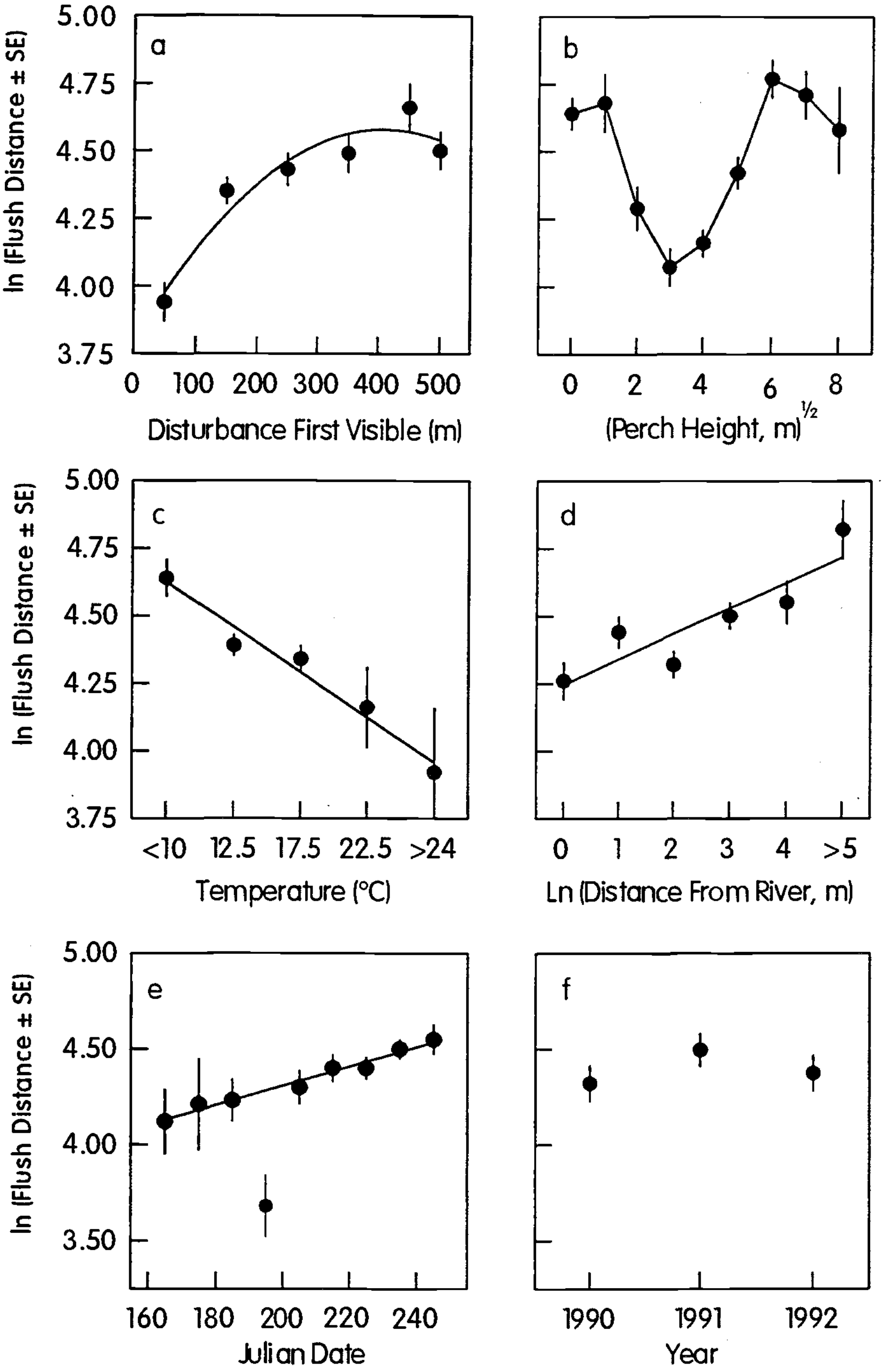

Figure 5.5. Influence of (a) distance at which disturbance was first visible, (b) perch height, (c) ambient temperature, (d) distance from river, (e) julian date, and (f) year on flush distances of nonbreeding bald eagles to human activity in the Gulkana Basin, Alaska, 1990-1993.

Table 5.5. Factors that significantly influenced ($P < 0.10$) the distance at which nonbreeding bald eagles flushed in response to our approaching boat on the Gulkana River, Alaska, 1990-1993. Results are from multiple linear regression model ($n = 580$).

Factor	Parameter estimate	SE	*t*	*P*
Distance perched from river (ln)	0.095	0.031	3.1	0.0021
Distance disturbance first visible to eagle[a]	0.0049	0.0010	5.1	< 0.0001
Perch height (square root)	-0.354	0.040	8.9	< 0.0001
Perch height	0.046	0.006	8.0	< 0.0001
Perched along Upper Main Stem reach	-0.175	0.063	2.8	0.0059
Age class[b]				
Juvenile	-1.624	0.238	6.8	< 0.0001
Young subadult	-0.127	0.058	2.2	0.028
Older subadult	-0.228	0.097	2.4	0.019
Near adult	-0.222	0.095	2.3	0.019
Year	0.058	0.032	1.8	0.071
Julian date	0.0042	0.0015	2.9	0.0040
Ambient temperature	-0.017	0.008	2.1	0.038
Intercept	-1.79	2.92	0.6	0.54
Full model (F-statistic)			17.1	< 0.0001

[a] This distance factor also had a significant quadratic component ($P < 0.0001$) (see Fig. 5.7*a*) but its value was so small as to be negligible (-6.8×10^{-6}).

[b] Compared to adult age class.

the tallest perches afforded the highest visibility which increased flush distances (Table 5.5).

Third, unlike flush response rate, age strongly influenced flush distance (Table 5.5, Fig. 5.6). Adults flushed at significantly greater distances (113.0 ± 4.5 m, $n = 253$) than subadults of all age classes (95.3 ± 3.2 m, $n = 412$) ($P < 0.03$ for all comparisons). Flush distances of subadults, however, did not differ from one another ($P > 0.3$), but flush distances of juveniles were far lower than that of all other age classes (24.8 m, $n = 8$) (Fig. 5.6). Fourth, contrary to what we expected, flush distance increased as distance to the river channel increased (Fig. 5.5*d*), which suggests that increased distance to the river channel did not provide an increased level of security to an eagle. This result probably reflects that eagles perched farther from the river channel were merely perched farther from the disturbance when flushed.

Effects of Repeat Disturbances

We examined how eagles responded to repeated approaches. Flush response rate of eagles approached a second time (47%, $n = 126$) decreased compared to when first approached (58%, $n = 1{,}164$) ($\chi^2 = 10.9$, $P < 0.0001$). Flush rate of eagles approached a third time (54%, $n = 29$) did not differ from those approached the first or second time ($\chi^2 < 0.85$, $P > 0.36$). However, after adjusting for the different disturbance contexts of each approach, the number of times an eagle was approached had no effect on flush response ($\chi^2 = 10.9$, $P = 0.18$). Therefore, eagles in similar disturbance contexts flushed at the same rate regardless of the

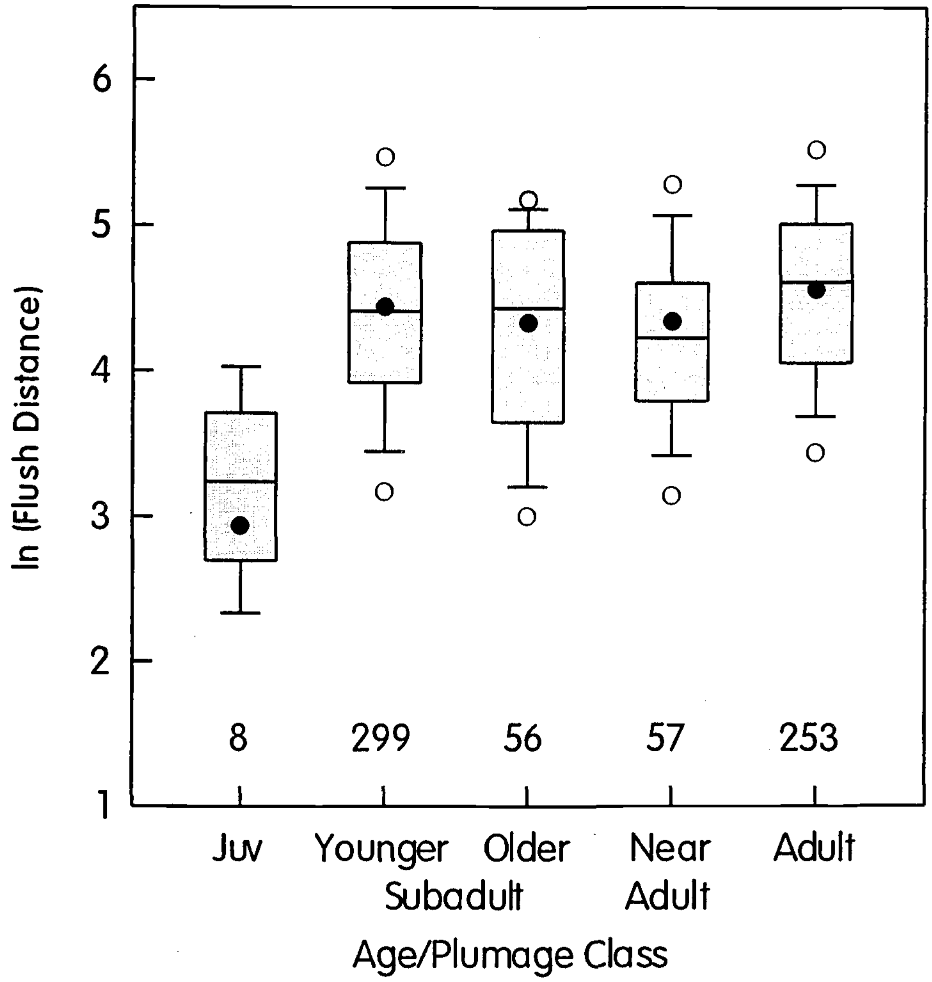

Figure 5.6. Influence of eagle age on flush distance (m) of nonbreeding bald eagles in the Gulkana Basin, Alaska, 1990-1993. The lower and upper boundaries of each box represent the 25th and 75th percentile, respectively, the line through the box represents the 50th percentile (median), the capped bars represent the 10th and 90th percentile, and the open points represent the 5th and 95th percentiles of flush distances for each age class. The solid points represent means after they were adjusted for other significant model parameters (Table 4.5), and the numbers at the bottom of the figure are sample sizes for each age class.

number of times they were flushed previously. This illustrates the misleading results obtained by comparing flush response without considering the disturbance context.

Flush response was not affected by the number of approaches because eagles perched in less vulnerable locations after being flushed. Both the height they perched above the river (slope = 0.32 ± 0.09, $P = 0.0002$; based on square-root transformed data) and the distance they perched from the river (slope = 0.18 ± 0.06, $P = 0.0046$; based on $\log_e$ transformed data) increased with the number of times they were approached ($n = 1{,}487$).

Although the number of times eagles were approached did not affect flush response rate, the average distance at which they flushed declined after they were initially flushed ($t = 2.6$, $P = 0.0097$). Flush distance ($\bar{x} \pm$ SE) for eagles approached the first time was farther (101.0 ± 2.6 m, $n = 674$) than when approached a second (73.6 ± 4.4, $n = 126$) and third time (79.6 ± 9.7, $n = 29$).

Avoidance Flights.—Avoidance flights of those eagles that did not fly out of the area after being flushed (≤ 500 m) averaged 151.2 ± 5.7 m ($n = 317$) and did not change as the number of times an eagle was flushed increased ($t = 0.01$, $P > 0.9$). The percentage of eagles responding to the disturbance by flying out of the area (>500 m) also did not change with the number of times they were flushed ($\chi^2 = 0.4$, $P > 0.8$) (overall = 18%, $n = 386$).

DISCUSSION

Flush responses and flush distances of bald eagles were variable and complex responses governed by the context within which each human-eagle interaction occurred. Eagle responses were probably influenced by additional factors that are difficult to investigate, such as an eagle's previous experience, habituation to humans, levels of stress or hunger. Generalizing from previous research is complicated because the disturbance contexts, disturbance types, and other ecological circumstances varied among studies, all of which probably influence eagle responses. However, some factors have consistently influenced flush responses across studies and these are most useful for generalizing eagle response to human activities. Other factors that have been found to only occasionally influence responses are those that need to be examined in particular populations before developing site-specific management criteria.

The distance a disturbance is first visible to an eagle is the fundamental factor controlling flush response, although its influence on bald eagles has seldom been examined. This distance governed flush distance (Table 5.5) by establishing the upper limit at which an eagle could flush. Accordingly, we found that flush distance increased as distance first visible increased (Table 5.5). This factor is likely responsible for the lower observed flush distances of eagles when approached from vegetated areas as compared to open areas (Stalmaster and Newman 1978). Disturbance visibility also could explain the tendency for flush distances to be lower for populations inhabiting riverine habitats versus more open estuaries or lakes (Table 5.6). One must account for the distance a disturbance is first visible to an eagle before the effects of other factors on *flush distance* be interpreted. Similarly, only after accounting for the effect of approach distance can *flush response* be compared among populations.

Flush response rate of a given population depends on the distance at which disturbances approach eagles. For example, if all eagles are purposely approached until they flush, then flush response rate would be 100%. In open systems, such as lakes or estuaries, distances that recreational disturbances approach eagles range greatly, and flush response rates logically increase with decreasing encounter distance (e.g., McGarigal et al. 1991). However, along relatively narrow river systems crafts usually approach very close to perched eagles. On the Gulkana, for example, virtually all eagles (94%, n = 1,164) were approached within 100 m, unless they flushed previously. Therefore, while it is crucial to consider approach distance when interpreting flush response rate, in the Gulkana Basin approach distance was relatively consistent; nearly all eagles could have been approached within 100 m.

The distance an eagle allows a disturbance to approach can be considered the inverse of tolerance: the lower the approach distance, the higher an eagle's tolerance. However, approach distance cannot be considered when modeling flush response and distance because (1) approach distance is identical to flush distance for birds that flush, and (2) birds that do not flush often allow the disturbance to approach closer than birds that do. For example, we approached as close as 6 m to eagles that did not flush, and closer than 100 m to >86% of these birds (Fig. 5.7).

Table 5.6. Flush distances of nonbreeding bald eagles of all age classes from 6 different populations approached by boats.

Flush Distance (m)	*n*	Habitat	Season	Source
101	674	River	Summer	This study
167[a]	195	River	Winter	Knight and Knight 1984
176	42	Estuary	Summer	Buehler et al. 1991
197[b]	40	Estuary	Summer	McGarigal et al. 1991
225[a]	49	River	Winter	Knight and Knight 1984
265	34	Estuary	Winter	Buehler et al. 1991

[a] Weighted average of eagles perched in trees and on ground reported separately.

[b] Also includes breeding eagles; value would likely be lower if breeders were excluded.

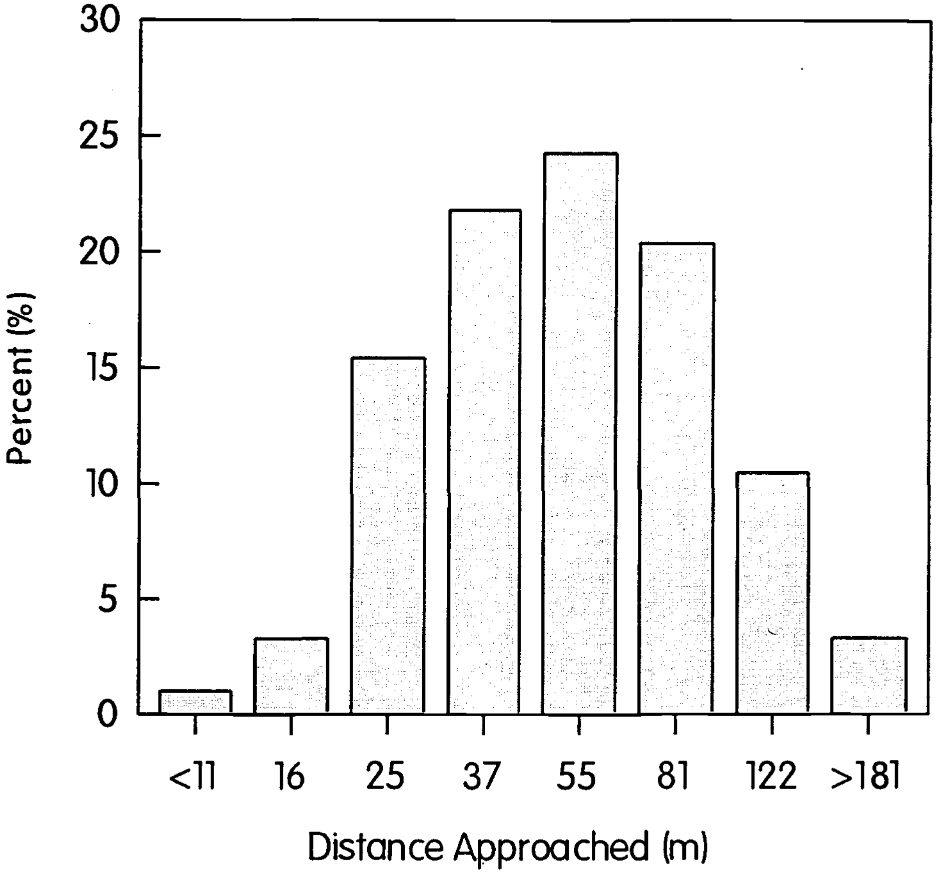

Figure 5.7. Distribution of distance we approached nonbreeding bald eagles that did not flush in the Gulkana Basin, Alaska, 1990-1993. Values along x-axis had been retransformed from original ln transformation.

Both flush response and flush distance have been consistently affected by the location and height of an eagle's perch. Eagles perched on the ground were more likely to flush and flushed at greater distances than those in elevated perches (Stalmaster and Newman 1978, Knight and Knight 1984, McGarigal et al. 1991, this study). This makes populations of eagles that feed principally on spawned salmon and other carrion particularly vulnerable to the effects of human activity.

Another factor that has consistently affected eagle responses is the existing level of human activity in an area. We found that both flush response and distance of breeders and nonbreeders were highest in areas with the lowest existing levels of human activity. This phenomenon has been observed in studies of bald eagles in winter (Russell 1980, Knight and Knight 1984) and summer (Buehler et al. 1991). This suggests that either (1) eagles inhabiting areas with higher levels of human activity habituate to common disturbance types, or (2) eagles that are more sensitive to human activity relocate to areas with lower levels of human activity (Russell 1980).

Comparing eagle responses at larger geographic scale suggests that patterns governing responses differ across spatial scales. If patterns observed *within* regions (highest response rates and distances in areas of lowest human activity) were similarly manifested *across* regions we would expect areas of low human activity to have the lowest flush responses. This, however, was not the case. Levels of human activity on our remote study area in interior Alaska (*Section 6*) are probably substantially lower than other areas previously studied, thus we expected greater flush distances. In contrast, however, flush distances of our study population were well below those reported from other areas (Table 5.6). Note that only flush distance and not flush responses are comparable across populations because approach distances vary among regions.

Breeding eagles were less likely to flush and flushed at shorter distances than nonbreeding adults (Tables 5.2 and 5.3). McGarigal et al. (1991) found similar results for flush response (but not for flush distance) and suggested that breeding adults on their territories were more secure than migratory transients. In addition, we believe that breeding adults (1) probably are more willing to tolerate disturbances because of their reproductive investment in offspring, and (2) are much more likely than transients to be habituated to local disturbance types.

Lastly, studies that have examined the effect of eagle age on flush response and distance have reported mixed results. Except for juveniles, we found that age strongly influenced flush distance (Table 5.4) but marginally influenced flush response (Table 5.5). Others have found that age influenced (Stalmaster and Newman 1978) or did not influence flush distance or flush response (Knight and Knight 1984, McGarigal et al. 1991, Buehler et al. 1991). We believe that age does influence eagle flush responses to human disturbance and studies failing to find this effect suffered either from small samples sizes, low precision of measurements, or may not have adequately accounted for other influential variables within the disturbance context.

MANAGEMENT RECOMMENDATIONS

Flush responses have been used to establish buffer zones to protect eagles populations (e.g., Stalmaster and Newman 1978, Knight and Knight 1984). One approach is to establish a buffer-zone width at the distance at which 95% of eagles flush (Anthony et al. 1994). For breeding and nonbreeding eagles in the Gulkana Basin these distances were 200 m and 220 m, respectively. Even at its widest point, the Gulkana River is <125 m wide, therefore this strategy would effectively eliminate the entire river corridor from human use. Given the current low levels of human use in the basin, we think this would be an unnecessary restriction. With a dramatic increase in human use, however, we believe a reasonable management alternative would be to limit the number of users on the river rather than the areas they can use. Therefore, we suggest that the best strategy for management on this and similar narrow wilderness rivers is to maintain accurate counts of human users and establish use thresholds. When these thresholds are exceeded then restrictive management actions could be instituted.

From 1989-1992, an average of 183 groups used the Upper Main Stem per year (***Section 6***). Because most human use is of short duration at a particular location (e.g., rafting), one method to establish use thresholds is to calculate the average number of groups that would pass a given point on the river each day, where they could potentially disturb a nesting pair or a foraging eagle. The period of highest human use in the Gulkana Basin is between 1 June and 11 September, a period of 102 days. During this period in 1989-1992, an average of 1.8 groups per day (183 crafts/102 days) floated the Main Stem. If the use threshold was set at 5 groups per day, for example, restrictive management action should be invoked when the total number of crafts per season reached 510 (groups/season = threshold level x season length). Similarly, if the threshold levels was set at 10 groups per day, then restrictive management action should be invoked when the number of groups reached 1,020 (groups/season = 10 x 102). Management areas that include upstream (motorized) use need to determine additional patterns to calculate use thresholds for these areas, such as the number of times per day that boats travel up and down river, and the average number of days an area is used.

RESEARCH RECOMMENDATIONS

Flush responses and distances of bald eagles are extremely variable, both within and across populations. Therefore, to determine the influence that different factors have on these parameters requires large sample sizes to reduce the likelihood of Type II errors. We recommend that biologists make a preliminary survey to determine the sample sizes necessary to meet some predetermined level of statistical power before initiating a full study of eagle responses for research or management purposes (see Peterman 1990). Further, care must be taken to adequately and precisely measure all components that comprise the disturbance context (Table 5.1) and to simulate the relevant disturbance type. We suspect previous studies that failed to detect the influence of some important factors either neglected to adequately measure and analyze the potentially confounding effects comprising the eagles' disturbance context, or committed Type II errors because of small sample sizes and high variability. Guidelines and research results based on these errors or oversights could result in management strategies that are inappropriate.

6: HUMAN USE AND BALD EAGLE REPRODUCTION ON THE GULKANA NATIONAL WILD RIVER, ALASKA

INTRODUCTION

The number of people recreating in wilderness areas has increased tremendously since the 1950's (Brockman and Merriam 1979, U.S. Department of Interior 1982). Because the amount of wilderness land available for these activities has not increased at the same rate, the intensity with which these lands have been used has also increased. When the amount of human activity on wilderness areas exceeds some threshold then the land's ability to function as wilderness degrades. From the perspective of wilderness recreationists, when the amount of human activity exceeds some "carrying capacity" (Shelby and Heberlein 1986), the quality of the wilderness experience degrades. Additionally, as human use increases so does the potential for adverse effects on wildlife inhabiting these areas (Boyle and Sampson 1985). For areas to maintain a high degree of wilderness character and habitat quality, use-limitations need to be considered when use exceeds these carrying capacities.

The Gulkana National Wild River in interior Alaska receives a disproportionate amount of human use compared to other rivers in the Copper River basin because of its geographic location, accessibility, clear waters, and abundant populations of sport fish. The Gulkana Basin also supports more than 70 pairs of bald eagles, many of which nest within 50 m of the river channel.

Because human, eagle, and other wildlife use is concentrated along the river corridor, the potential for human-wildlife conflict is intensified.

We believe that the Gulkana River provides an opportunity to establish management strategies that satisfy the needs of both humans and wildlife resources. Because strategies to minimize human impacts on resources in wilderness areas require accurate assessments of the amount of human use, we quantified the amount and types of use on the Gulkana River from June to September 1989-1992. Further, we also assessed the association between current use-levels on different river reaches and bald eagle reproductive success.

STUDY AREA

We stratified the Gulkana Basin into 5 river reaches based on accessibility and types of human use (Fig. 5.1). Three reaches were segments of the Main Stem of the Gulkana River plus the West Fork and Middle Fork, the two major tributaries of the Main Stem. The Upper Main Stem (from the outlet of Paxson Lake to the Main Stem's confluence with the West Fork) was used almost exclusively by recreationists in non-motorized crafts. The Middle Main Stem (from the Main Stem's confluence with the West Fork to Sourdough campground) was used predominantly by motorized crafts in addition to the non-motorized crafts that had floated the Upper reach. The Lower Main Stem (from Sourdough campground to the Richardson Highway bridge, 7 km above the Gulkana's confluence with the Copper River) received both motorized and non-motorized use and was accessible from several points along the highway. The West Fork (from the outlet of Fish Lake to its confluence with the Main Stem) and Middle Fork (from the outlet of Dickey Lake to its confluence with the Main Stem) were the most remote areas in the basin because they were accessible only by float plane. Consequently, use on these reaches was limited, although motorized crafts from the Middle Main Stem reach sometimes traveled a few kilometers up the West Fork before being impeded by shallow riffles during most of the summer.

METHODS

From 1989 to 1992, we recorded the amount and types of human use within the Gulkana Basin during float trips from early June to early September, the period of highest use on the Gulkana. Because our trips varied from 1 to 15 days in duration, we assessed human use on a per day basis. We were unable to systematically measure levels of human use on all reaches during the same period each year. Therefore, some annual variability evident in our observations may have been attributable to the temporal and spatial variability in our sampling.

Human use can be quantified by counting the number of user groups, crafts, or people. Although we recorded all 3 measures, most of our analyses focused on the number of groups because groups tended to travel the river together. Also, interactions with groups rather than individual crafts or people constituted the majority of disturbances to eagles.

During the 4 years of our study, we encountered a total of 604 groups (Table 6.1), 15 (2.5%) of which we were unable to determine the number of people. However, because we were able to count the number of crafts in these groups, we estimated the number of people in these groups by using the average number of people for each craft type which we determined from groups that were counted accurately.

Seasonal Estimates of Human Use

We estimated the total number of groups, crafts, and people that used each reach of the Main Stem Gulkana River between 1 June and 11 September (102 days). Using these sample estimates, we constructed smoothed seasonal-use curves using moving averages (Taub 1990). We then estimated the area under these curves to generate our total seasonal estimates of use.

Statistical Analyses

We compared the number of people and crafts per user group between river reaches using analysis of variance and Tukey's studentized range test for separation of means (Tukey 1949). To examine interrelationships between the number of groups, crafts, and people encountered per trip we used Pearson correlations (r) and linear regression. To examine correlations between levels of human use and bald eagle reproduction on each river reach, we used Spearman rank correlations (r_s) because of the wide disparity in use levels among river reaches. Typically, measures of bald eagle reproductive success (young fledged/occupied territory, nest

Table 6.1. Number of float trips and characteristics of groups, crafts, and people we encountered on 4 reaches of the Gulkana River, Alaska, 1989-1993.

Year	Reach	Trips	Days	Groups	Crafts	People
1989	Upper Main Stem	5	22	41	64	146
	Middle Main Stem	4	4	5	3	15
	Lower Main Stem	1	1	0	0	0
	West Fork	1	3	0	0	0
	Total	11	30	46	67	161
1990	Upper Main Stem	12	57	114	172	441
	Middle Main Stem	17	19	62	93	332
	Lower Main Stem	7	18	50	51	258
	West Fork	4	12	3	3	7
	Total	40	111	229	319	1,039
1991	Upper Main Stem	6	28	59	124	341
	Middle Main Stem	9	14	66	92	279
	Lower Main Stem	5	13	31	39	127
	West Fork	3	8	2	2	9
	Total	20	63	158	257	756
1992	Upper Main Stem	8	27	50	78	190
	Middle Main Stem	8	8	42	49	169
	Lower Main Stem	8	22	79	92	354
	West Fork	0	0	0	0	0
	Total	24	57	171	219	713
All Years	Upper Main Stem	31	134	264	438	1,118
	Middle Main Stem	38	45	175	233	784
	Sourdough to Bridge	21	54	160	182	739
	West Fork	8	23	5	5	16
	Total	95	261	604	862	2,669

success) are not adjusted for population density, a factor potentially influenced by human activity. Therefore, we also correlated density of occupied nests (per km of river) with levels of human use. Lastly, we compared eagle productivity between reaches that received high- and low-intensity use with *t*-tests and nest success with contingency tables.

RESULTS

Amount and Types of Human Use

From 1989 to 1992 we encountered an average of 0.6 groups per day on the West Fork, 2.0 groups on the Upper Main Stem, 3.0 groups on the Lower Main Stem, and 3.9 groups on the Middle Main Stem (Table 6.1). These averages, however, are somewhat misleading because use varied markedly throughout the summer, but always peaked early in July (Fig. 6.1). Most annual variability in use occurred during this peak period and probably depended on whether the July 4th holiday (Julian day = 185) was a 3-day weekend (1989, 1991, 1992) or not (1990).

Seasonal-use levels were generally similar among years (Fig. 6.1), so we estimated use-levels by combining data for all years. As with the number of groups encountered, total seasonal use differed among river reaches and was highest on the Middle Main Stem, lowest on the Upper Main Stem, and intermediate on the Lower Main Stem (Table 6.2). Between 1989 and 1992, we estimated that an average of 2,869 people per year used the Wild Sections of the Gulkana Basin, which include the Upper and Middle Main Stem, the West Fork, the Middle Fork,

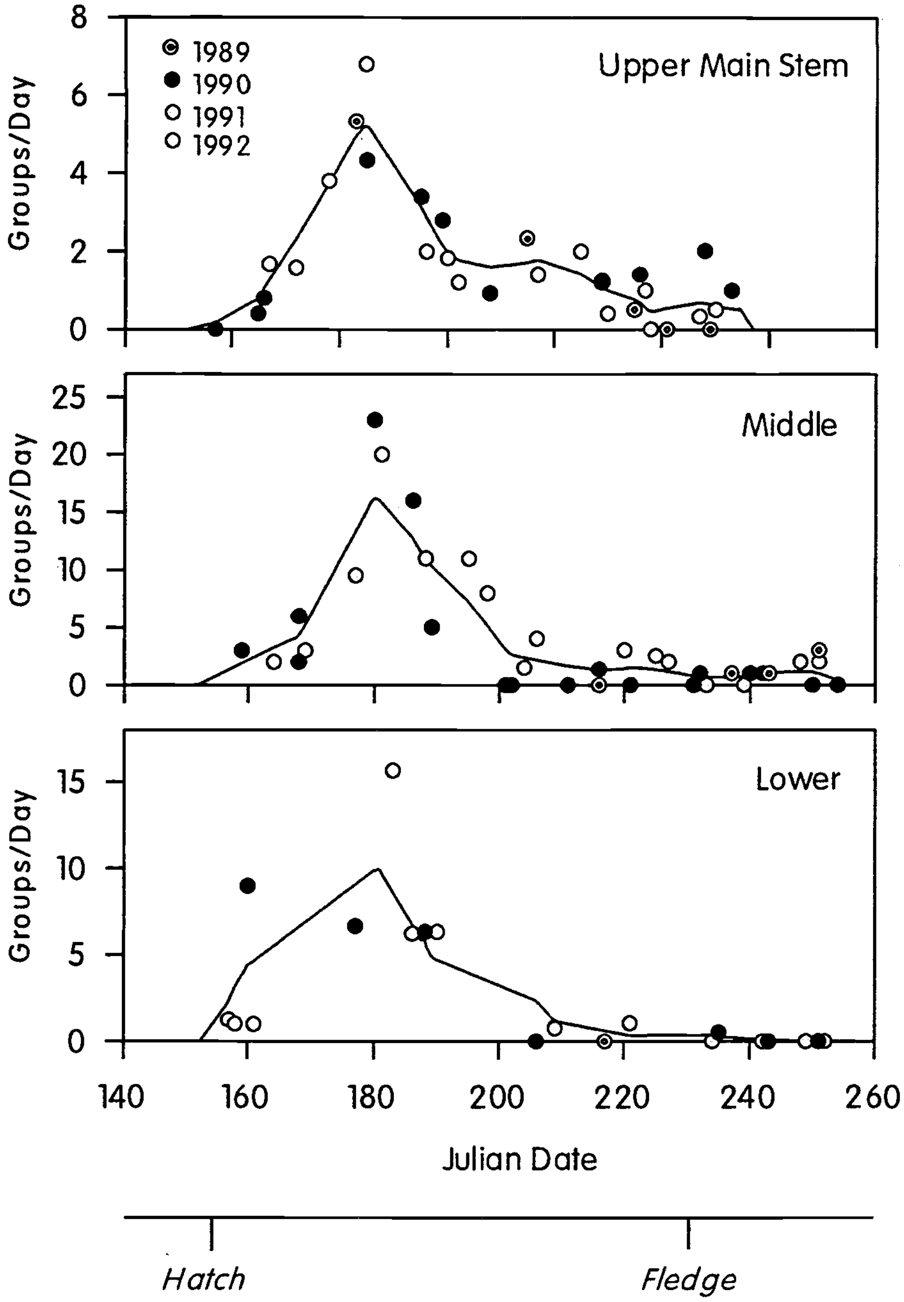

Figure 6.1. Number of groups encountered per day on 3 reaches of the Main Stem Gulkana River, Alaska, 1989-1993. The line represents a moving average generated with data from all 4 years combined. Julian dates 152, 185, and 244 are 1 June, 4 July, and 1 September, respectively. The horizontal below the x-axis is the estimated median hatching and fledging dates for bald eagles nesting in the Gulkana Basin.

Table 6.2. Estimated number of groups, crafts, and people using 3 reaches of the Main Stem Gulkana River, Alaska, between 1 June and 11 September, 1989-1993. Values represent use-level estimates for a single year.

Craft type	Groups	Crafts	People
Upper Main Stem	183	305	764
Middle Main Stem	433	601	2,073
Lower Main Stem	298	329	1,379
All reaches[a]	919	1,243	4,238

[a] Includes estimates of 5 groups, 8 crafts, and 22 people per season on the West Fork, and 2 groups, 4 crafts, and 10 people per season on the Middle Fork.

and exclude the Lower Main Stem. Because use of the West and Middle Forks was so infrequent, we excluded it from comparisons among reaches.

The number of people, crafts, and groups encountered per trip were highly intercorrelated ($r > 0.95$, $P < 0.0001$); therefore, temporal trends in crafts and people were almost identical to those observed for groups (Fig. 6.1). Because of these strong interrelationships, each use-measure can be predicted with reasonable accuracy from any of the others. For example, the number of people encountered per trip can be predicted accurately from the number of crafts encountered (Fig. 6.2).

Most groups travelled the river on rafts (45%); however, the types of crafts used varied by river reach (Table 6.3). The use of motorized crafts was highest on the Middle Main Stem (85%) compared to other Main Stem reaches (2-29%). Although the number of people per group was similar among reaches ($P = 0.88$), the number of crafts per group was significantly higher on the Upper Main Stem compared to other reaches ($F = 6.1$, $P = 0.0024$) (Table 6.4). This difference resulted because (1) more groups on the Upper Main Stem used rafts (61%) compared to groups on other Main Stem reaches (10-51%) (Table 6.3), and (2) the number of crafts per group was higher for groups that used rafts versus most other commonly used crafts (Table 6.5).

Nearly all groups encountered on the Gulkana Basin were recreating, most undertaking multi-day wilderness trips that involved boating, camping, and fishing. Of 604 groups encountered, 56% were observed boating and fishing, 27% were

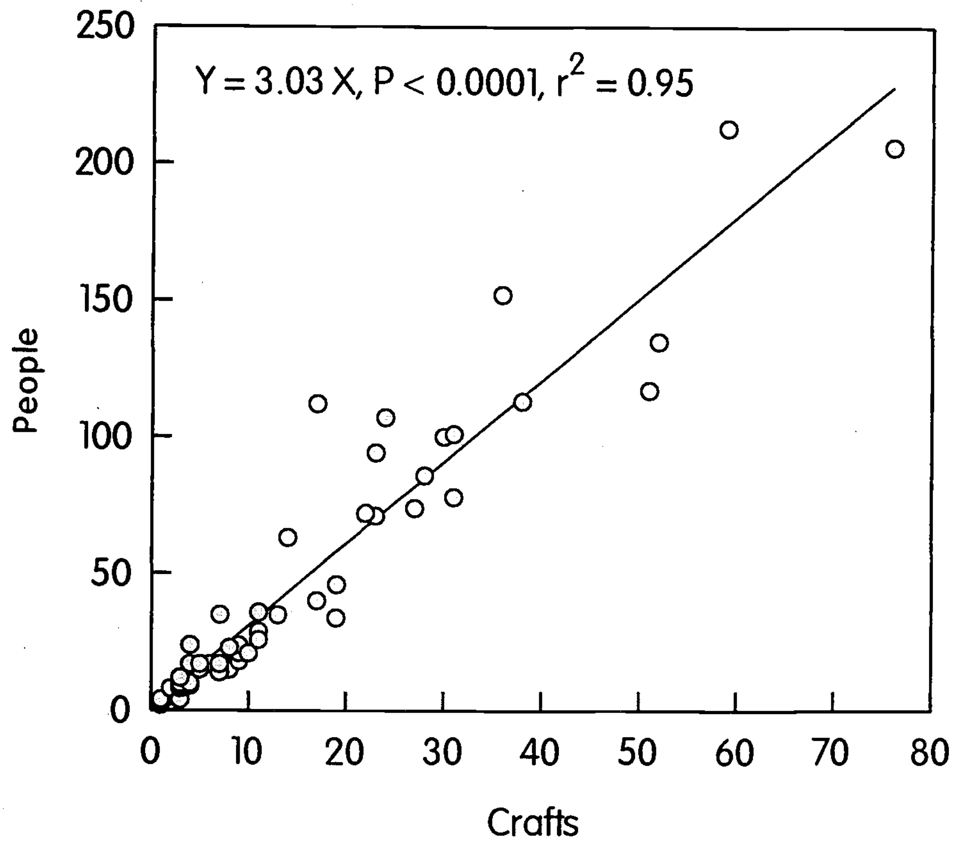

Figure 6.2. Number of people encountered per trip can be predicted with reasonable accuracy by the number of crafts encountered. Data collected from the Gulkana basin, Alaska, 1989-1993.

Table 6.3. Percentage of crafts used by recreationists on 3 reaches of the Main Stem and West Fork Gulkana River, Alaska, 1989-1993.

	River reach				
Craft type	Upper Main Stem	Middle Main Stem	Lower Main Stem	West Fork	All
Raft	61.2	9.7	50.5	20	44.8
Jet boat	1.4	80.2	19.2	60	26.8
Canoe	25.8	4.6	14.3	20	17.6
Raft with transom	1.4	2.1	8.8	0	3.1
Kayak	4.6	0.8	2.2	0	3.0
4x4 ATV	4.6	0	0	0	2.3
Drift boat	0.7	0	4.4	0	1.3
Motorboat	0.2	0.8	0.5	0	0.5
Air boat	0	1.7	0	0	0.5
Helicopter	0.2	0	0	0	0.1
All river crafts[a]					
Non-motorized	98.3	15.2	71.4	20	68.7
Motorized	1.7	84.8	28.6	80	31.3
n	438	237	182	5	862

[a] Excludes 4x4 ATV's and helicopter.

Table 6.4. Number of people and crafts per group on 3 reaches of the Main Stem Gulkana River, Alaska, 1989-1993. Excludes those groups not using crafts.

		People/group		Crafts/group	
Main Stem river reach	n	$\bar{x}$	SE	$\bar{x}$	SE
Upper	260	4.24	0.21	1.66 A[a]	0.07
Middle	134	4.23	0.34	1.32 B	0.10
Lower	159	4.08	0.22	1.35 B	0.06
All reaches	553	4.19	0.15	1.49	0.05

[a] Means followed by the same letters are not significantly different ($P > 0.05$).

Table 6.5. Number of people and crafts per group, and number of people per craft encountered on the Gulkana River, Alaska, 1989-1993. Includes only those groups using one type of craft (561 of 604, 93%).

	People/group			Crafts/group			
Craft type	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	$\bar{x}$ people/craft
Drift boat	7	4.6	0.8	7	1.4	0.3	3.2
Raft	237	4.4	0.2	238	1.4	0.1	3.1
4x4 ATV	7	4.3	0.8	9	2.2	0.3	1.5
Jet boat	166	3.7	0.2	172	1.2	0.1	3.0
Zodiac	18	3.4	0.4	18	1.3	0.1	2.7
Canoe	80	2.8	0.2	82	1.5	0.1	1.8
Motorboat	3	2.0	0.6	4	1.0	0.0	1.5
Air boat	2	2.0	0.0	2	1.0	0.0	2.0
Helicopter	1	2.0	–	1	1.0	0.0	2.0
Kayak	7	1.7	0.3	7	1.7	0.3	1.0
No craft	33	7.3	1.6	–	–	–	–
All crafts[a]	528	3.8	0.1	540	1.4	0.1	2.7

[a] Excludes "no craft" category.

only boating, 7% were encamped, 5% were fishing from river-access points, 2% were boating and hunting, and 2% were electrofishing for fisheries research.

Human Use and Bald Eagle Reproduction

The number of young fledged per occupied nest and nest success were negatively correlated with the rank-level of human use on a river reach between 1989 and 1992 ($r_s = -0.90$, $P = 0.037$ for both), suggesting eagle reproduction was negatively associated with the level of human activity. We found no correlation between use levels and bald eagle nest density or brood size (young fledged per successful nest) ($P > 0.10$) (Table 6.6).

In addition to differing in the amount of human use, reaches also differed in the type of use they received. Therefore, we grouped reaches into two categories: high-intensity use, which we defined as those that received a high level of use (>100 groups/yr) or substantial amounts of use by motorized crafts (Middle and Lower Main Stem) and low-intensity use, which we defined as those that received a low level of use or no use by motorized crafts (West Fork, Middle Fork, Upper Main Stem). We found that three measures of reproductive success differed between these two groups. Productivity ($\bar{x} \pm$ SE) was significantly lower ($t = 3.0$, $P = 0.0031$) along reaches of high-intensity use (0.72 ± 0.12, $n = 43$) versus low-intensity use (1.24 ± 0.12, $n = 54$), as was nest success (53% versus 74%, respectively; $\chi^2 = 4.5$, $P = 0.035$). Because high levels of human use did not occur until after eggs hatched (Fig. 6.1), the differences we observed in nesting success may have been related to some factor other than human disturbance. However, if

Table 6.6. Approximate length, level of human use, and characteristics of bald eagle reproduction on 3 reaches of the Main Stem, West Fork, and Middle Fork Gulkana River, Alaska, 1989-1993.

	River reach					
Characteristic	Upper Main Stem	Middle Main Stem	Lower Main Stem	West Fork	Middle Fork	All
Reach length (km)	52	13	51	25	39	180
No user groups/season (rank)	183 (3)	433 (5)	298 (4)	5 (2)	<5 (1)	924
No. nesting territories	6	2	8	3	4	23
Nest density[a] (rank)	0.115 (2)	0.154 (4)	0.157 (5)	0.120 (3)	0.103 (1)	0.127
% Nest success (rank)	67.9 (3)	66.7 (2)	50.0 (1)	75.0 (4)	85.7 (5)	64.9
Young fledged per occupied territory (rank)	1.18 (3)	0.78 (1)	0.71 (2)	1.25 (4)	1.36 (5)	1.01
Young fledged per successful territory (rank)	1.74 (5)	1.17(1)	1.41 (2)	1.67 (4)	1.58 (3)	1.56

[a] No. per kilometer of river.

we exclude failed nests, most (92%) of which failed during incubation before high levels of human use occurred (Fig. 6.1, ***Section 2***), the number of young fledged per successful nest (brood size) was also significantly lower ($t = 2.3$, $P = 0.025$) in reaches of high-intensity use (1.35 ± 0.10, $n = 23$) than those with low-intensity use (1.68 ± 0.09, $n = 40$). Therefore, nests in areas of high levels of human use tended to have smaller brood sizes after hatching than those with low-intensity use.

DISCUSSION

Because the peak of human use within the Gulkana Basin occurred during the nestling period (Fig. 6.1), the impacts of human activity on breeding eagles were probably less severe than if this peak occurred during egg laying or incubation, when bald eagles seem most vulnerable to human disturbance (Cain 1985). However, energetic demands of rapidly developing nestlings are high during this period, as are the associated demands on adults to provide food. Therefore, the effects of human activity on eagles can still be significant and may have been responsible for the lower productivity, nest success, and brood sizes that we observed in areas of high-intensity human use. Therefore, if levels of human activity were sustained near these critical habitats then there is high potential to adversely affect both adult and nestling eagles (***Section 4***, McGarigal et al. 1991). We caution, however, that correlational analyses such as this cannot establish cause and effect because many factors can affect reproductive rates (***Section 2***).

For the Main Stem Gulkana River, Whittaker (1989) recommended that 10 on-river group encounters per day (non-motorized crafts) be established as a threshold to minimize recreational impacts on the river's wilderness character. Levels of use between 1989 and 1992 were below this level except during late June and early July when use levels peaked (Fig. 6.1). We believe this threshold represents a level compatible for minimizing human impacts on breeding and nonbreeding bald eagles and should be accepted as a use-threshold to protect the eagle population (see ***Section 5***).

However, setting use-thresholds also requires that one differentiate between motorized and non-motorized crafts. Specifically, motorized crafts typically pass a given location on the river repeatedly whereas non-motorized crafts pass each point only once. Each motorized craft, therefore, is likely to be encountered repeatedly by downstream users and will have a greater effect on both the perceived level of use (or wilderness character) and actual physical impacts (such as wake-induced riverbank erosion) than non-motorized crafts. Similarly, motorized crafts also disturb eagles more frequently than non-motorized crafts by repeatedly passing near a nest or foraging area. Eagles flushed more frequently when approaching boats were loud rather than quiet in a study along the lower Columbia River (McGarigal et al. 1991). Hence, the amount of human activity on the Middle Main Stem is even more intense relative to other reaches because most use on this reach is with motorized crafts (Table 6.3).

Managing wilderness areas to minimize human impacts on their ecological systems while simultaneously meeting the expectations of wilderness recreationists can be viewed as conflict resolution. However, in wilderness areas we believe management for all of these interests can be complimentary, and all vulnerable resources should be considered concurrently during planning. Our suggestion to establish use-thresholds for eagles at levels prescribed previously to maintain the river's wilderness character for recreationists is a first step towards such an approach. Carefully outlined management strategies with use-thresholds established to reduce stress on resources would ultimately benefit all wilderness users including humans and wildlife by minimizing disturbances caused by encounters, competition for shared resources such as fish, and other long-term effects of overuse, such as soil compaction and vegetation destruction. We believe that carefully assessed levels of human use within the Gulkana Basin is a high priority if managing agencies are to develop sound strategies that allow balanced and compatible use of all the basin's resources. Our estimate of 2,869 river users per year between 1989 and 1992 on the Wild Sections of the Gulkana River was remarkably similar to the Bureau of Land Management's average estimate of 2,828 (range = 2,089-3,552) during this period (L. Kajdan, B.L.M., Glennallen, AK, personal communication), suggesting that current methodology may be adequate to assess use-levels.

7: SUMMARY AND MANAGEMENT RECOMMENDATIONS

We believe that the levels and types of human use in the Gulkana Basin (*Section 6*) did not severely affect breeding or nonbreeding eagles, except perhaps along the Middle Main Stem reach (from the West Fork Confluence to Sourdough Campground) where use levels were highest. However, the potential to adversely impact eagles exists (*Section 4*), especially in late June and July when most use occurs (*Section 4*), if use levels continue to increase. To assess future levels of human use and potential impacts on bald eagles we suggest the following monitoring strategy.

- Conduct aerial surveys of nest occupancy and reproductive success every year following the methodology described in *Section 2*. Although we believe that there may be superior measures by which to assess human impacts on breeding eagles (*Section 4*), productivity surveys are simple, valuable, and relatively inexpensive to conduct. In addition to data on productivity and nest success, these surveys provide additional information such as population size, density, rates of territory occupancy, and rates of between-year nest changing, all of which can be influenced by human activities.
- Because human activity in nesting territories affects bald eagle breeding behaviors (*Section 4*), educational postings should be placed at river-entry points to make users aware of their potential adverse effects on

nesting eagles. Camping should be prohibited within sight of or within 500 m (whichever is farther) of active eagle nests.

- Managers should consider designating particular locations along the river corridor as permanent camping areas to capitalize on the propensity for nesting eagles to habituate to stationary human activities (*Section 4*).
- Because spatial restrictions on human use along narrow rivers cannot be implemented or enforced easily (*Section 5*), we suggest that a maximum use-threshold be established at an average of 10 groups per day between 1 June and 31 August (920 groups). Current levels of human use on the Gulkana River are below this level (*Section 6*) which has previously been suggested as a threshold necessary to maintain the river's wilderness character (Whittaker 1989).
- Levels of human use must be measured accurately. Estimates based on current methodology seem reasonable (*Section 6*) but could be improved if the relationships used to generate these estimates were quantified. Use levels should be estimated separately for the Middle Main Stem reach because use on this reach is qualitatively different than on other reaches (*Section 6*). For motorized crafts, use should not simply be measured as the number of user days as for non-motorized crafts, but instead the number of user days should be multiplied by a factor that represents the average number of times a motorized craft navigates the river in a day. This would yield a measure that better

represents the impact of motorized crafts on the Gulkana River and its resources.

Future Work

The management strategies suggested above can be improved—especially the accuracy with which use-thresholds are established to provide levels compatible with breeding and nonbreeding eagles—if our knowledge of this bald eagle population were more complete. In particular, more information would allow the development of demographic population models to provide insight to better understand and manage the effects of human activity on the Gulkana Basin's eagle population.

Survival rates may be the most important parameter affecting bald eagle population dynamics (Grier 1980). Data on survival rates, in addition to annual data on reproductive success, are therefore the most critical for these demographic analyses. This information can be gathered by radio-marking a sample of nestlings from different broods prior to fledging. Using radio transmitters capable of being monitored by satellite would facilitate gathering survival and location data because within the first years of life, young eagles often travel great distances from their natal territories. Radio-marking adults, although logistically more difficult, would not only provide information on survival rates, but would also yield information on other important demographic parameters, such as rates of population turnover and individual reproductive success as well as information on migration routes and important wintering areas. Lastly, as mentioned above, it is important to continue collecting data on reproductive success and population size annually, because only long-term reproductive data are acceptable to assess trends of long-lived species such as bald eagles.

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