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Author(s): Andrew J. Hansen
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REGULATION OF BALD EAGLE REPRODUCTIVE RATES IN SOUTHEAST ALASKA[1]

ANDREW J. HANSEN[2]
Environmental Sciences Division, Oak Ridge National Laboratory, P.O. Box X, Oak Ridge, Tennessee 37831 USA

Abstract. I examined the influence of food abundance and habitat quality on reproduction of Bald Eagles (*Haliaeetus leucocephalus*) in the Chilkat Valley, Alaska. The proportion of active nests was greatest and the timing of laying earliest in portions of the study area where food was most abundant. Clutch size was not related to food availability. Offspring survival was higher in breeding areas where food was experimentally provided than in control areas. Whether nests were active was also related to 2 of 11 habitat features measured at breeding areas. One habitat variable was associated with nest success. The findings suggest that variable productivity and a surplus of nonbreeders are the norm in the region as a result of high variability of annual food supplies and strong intraspecific competition. The results further suggest that the decline of this species in other parts of North America was at least partially due to alteration of eagle food sources and habitats by humans.

Key words: Bald Eagle; conservation; Haliaeetus leucocephalus; *nonbreeders; population regulation; reproduction; southeast Alaska.*

INTRODUCTION

Many breeding populations of Bald Eagles have declined dramatically over the last century (Coues 1883, Forbush 1927, Sprunt 1969, Sprunt et al. 1973), leading, in part, to the species being declared endangered. Causes of this trend are poorly known; loss of habitat, human disturbance, and shooting were initially suggested (Broley 1958, Howell and Heinzmann 1967, Sprung 1969). More recent evidence strongly implicates biocides (Krantz et al. 1970, Wiemeyer et al. 1972, Wiemeyer et al. 1984). Productivity has increased in some areas since the use of DDT was banned in 1972 (Grier 1982).

In contrast to most of North America, Bald Eagle populations remain large along the relatively pristine Pacific Northwest Coast (PNC) (Vancouver, British Columbia to Kodiak Island, Alaska) (King et al. 1972, Hodges et al. 1979, Hodges et al. 1984). Reproductive levels there have been assumed to be high and stable, but recent studies in southeast Alaska suggest that productivity is variable and generally declining. The proportion of adults in southeast Alaska that failed to breed (or abandoned nests soon after laying) in 1970, 1971, 1972, and 1979 was estimated at 26, 62, 57, and 86%, respectively (Hansen and Hodges 1985). Annual productivity in the Chilkat Valley, southeast Alaska (59°30′ N, 135°30′ W) (Fig. 1) was highly variable, ranging from 0.19 to 0.93 fledglings per active nest during 1980–1983 (Hansen et al. 1986). Along Seymour Canal, a marine bay in southeast Alaska (57°45′ N, 134° W), there has been a significant drop in the total number of offspring in nests in June during 1972–1986, even when the regression model controls for variation in the number of nests sampled ($F = 4.2$; df = 2, 12; $P < .05$) (data from: Hodges 1982; J. I. Hodges, *personal communication*; M. Jacobson, *personal communication*) (Fig. 2).

These patterns raise questions about the factors that regulate reproduction of Bald Eagles under natural conditions. It is unlikely that biocides are involved along the PNC because a sample of eagle carcasses and eggs from the region harbored no abnormal levels of contaminants (see Hansen and Hodges 1985). Herein, I report on tests of two additional hypotheses involving habitat quality and food abundance. Correlations between habitat attributes and productivity have been found in some regions but not in others (Grubb 1976, McEwan and Hirth 1979, Hodges and Robards 1982). If habitat limits breeding, habitat characteristics should differ between active and inactive nests and between successful and unsuccessful nests. Food shortage is seldom suggested as a factor limiting reproduction in Bald Eagles, but in some other raptors breeding rate, clutch size, and fledging rate correlate with food levels (Southern 1970, Smith et al. 1981, Janes 1984). Timing of laying is also influenced by food supplies in several birds (see Ewald and Rohwer 1982). The food limitation hypothesis predicts that surpluses of food during the breeding period will increase breeding density and clutch size, advance laying date, and improve offspring survival.

The results from tests of these predictions offer im-

[1] Manuscript received 28 March 1986; revised and accepted 17 December 1986.
[2] Present address: C.N.R.S., Route de Mende, B.P. 5051, 34033 Montpellier Cedex, France.

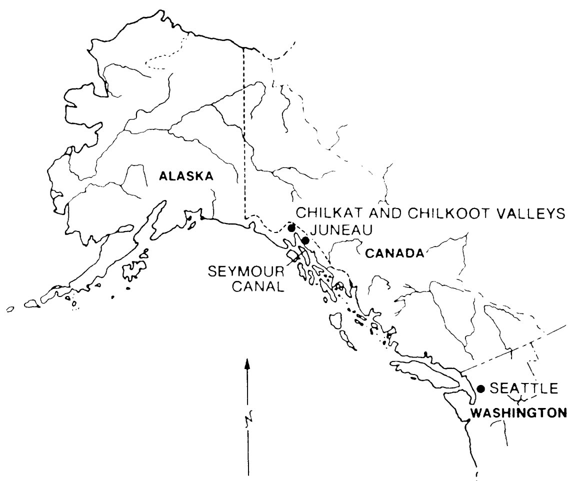

FIG. 1. Map of the Pacific Northwest coast of North America, showing locations of study areas.

portant new insights into the population dynamics of Bald Eagles in natural habitats and into the factors contributing to the decline of eagles in the contiguous United States.

METHODS

Field studies were done in the riverine habitats of the Chilkat Valley during 1980–1983. Approximately 89 Bald Eagle breeding areas (mean density: 0.38 areas/km of shoreline) were located in old-growth stands of black cottonwood (*Populus trichocarpa*), Sitka spruce (*Picea sitchensis*), and western hemlock (*Tsuga heterophylla*). Breeding eagles fed primarily on Pacific salmon (*Oncorhynchus* sp.), euchalon (*Thaleichthys pacificus*), and Dolly Varden (*Salvelinus malma*).

The status of breeding areas was determined by two airplane surveys each year. One was made soon after the start of incubation in early May. The other was conducted just prior to fledging in late August. Terminology on breeding was defined as follows: active nests: those in which an adult was seen in an incubating posture (I assumed eggs were present in such nests); breeding area: a site containing one or more nests, any of which might be used by a particular breeding pair but not by other pairs; breeding density: number of active nests per unit length of shoreline; nonbreeders: eagles of any age that do not contribute to egg production in a given year; successful nests: nests still containing eaglets ≈2 wk prior to the average fledging date.

Eleven habitat characteristics were measured at breeding sites to determine if breeding patterns of eagles were related to habitat quality. Two of the habitat variables described the breeding area: timber type (old-growth, second-growth, or old-growth tree left in logged area); and degree of human activity (none: no activity within 400 m of the nest; low: occasional activity 200–400 m from the nest; moderate: occasional activity between 50–200 m from the nest; high: occasional activity within 50 m of the nest). The remaining nine variables described the nest tree: relative age (immature, mature, or decadent); height class (canopy height, super-canopy height); condition (live, normal; live, broken or dead top; dead); species (black cottonwood, Sitka spruce); height; diameter at breast height; distance to water; base elevation above water; and nest height. These variables were measured once at 41 breeding areas and assumed to remain unchanged throughout the study. The relationships between habitat characteristics of breeding sites, nest activity, and nest success were examined with ANOVA models for the numeric variables and with chi-square tests for the categorical variables.

A fortuitous "natural experiment" allowed me to examine the effects of spring food supplies on proportion of adults breeding, laying date, and clutch size. In spring 1982 and 1983, carcasses of salmon (that had spawned in winter) thawed from river ice and created a concentrated food patch along 2 km of the Chilkat River. In 1982, the food patch was large enough to attract 200–300 eagles for a 2–3 wk period in March, but was not quantified further. In 1983, counts revealed that ≈900 carcasses were available daily for 5 wk in late March and April; ≈250 eagles gathered there during that time. No food patches were present in the study area in spring 1980 and 1981. Comparisons of eagle breeding density under the different food regimes were made both between river sections and between years. Also, laying dates were compared between river sections in 1983.

Offspring in 36 nests were counted from a helicopter on 7 June 1983, ≈4–6 wk after eggs were laid. At that

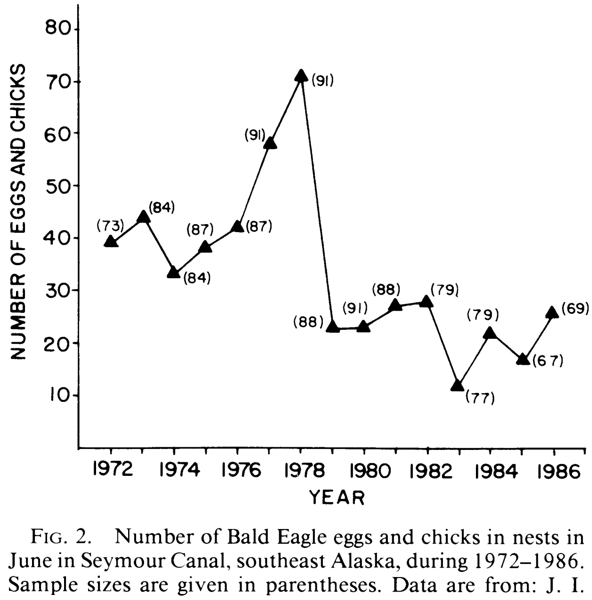

FIG. 2. Number of Bald Eagle eggs and chicks in nests in June in Seymour Canal, southeast Alaska, during 1972–1986. Sample sizes are given in parentheses. Data are from: J. I. Hodges 1982 and (*personal communication*), M. Jacobson (*personal communication*).

TABLE 1. Status of Bald Eagle breeding areas in the Chilkat Valley, Alaska, during years of high or low food availability.

Treatments	Nest active		Nest inactive		
	n	%	*n*	%	Total *n*
Low food availability					
1980	25	32	53	68	78
1981	30	45	37	55	67
High food availability					
1982	40	58	29	42	69
1983	47	61	30	39	77

time, 56% of the offspring had hatched. Mean clutch sizes within 3 km of the food patch and >3 km from the food were determined. Some eggs or young perished prior to the helicopter survey; 16% of the offspring in 9 nests for which there are data are known to have been lost between 7 May and 7 June 1983. Comparison of clutch sizes, despite the late survey date, seems valid because food abundance and predation rates appeared to be similar throughout the study area during the incubation period. Thus the offspring in each river section were probably equally susceptible to mortality.

An artificial feeding experiment was initiated in May 1983 after floods removed all remaining salmon carcasses. Food was provided at nine active breeding areas that were randomly selected from those that were accessible. Approximately 500 g of salmon carrion was provided per family member per day. This was equivalent to the average daily energy requirement of adult Bald Eagles in winter (Stalmaster and Gessaman 1984). The food was placed three times weekly on gravel bars within each breeding area so that it was visible from the nest. Two pairs refused to take the supplemental food and were omitted from the experiment. The experiment continued until 9 July 1983 when the chicks were recounted from an airplane. Three separate flights were made over some nests to ensure accuracy. Survival rates of offspring and nest success were compared between the helicopter flight of 7 June 1983 and the airplane survey of 9 July 1983 for the 7 experimental and 29 control nests.

RESULTS

Habitat quality

Two of the 11 habitat variables differed between active and inactive nests: elevation of nest tree above water ($\bar{X}$ for inactive nests = 4.1 m, $\bar{X}$ for active nests = 11.4 m, $n = 142$, $F = 5.4$, $P < .02$) and height class of nest tree ($\chi^2 = 4.5$, df = 1, $P < .05$). Seventy percent of the nests in trees that extended above the canopy were active ($n = 27$) while 46% of the nests in canopy-level trees were active ($n = 112$). The habitat attributes of successful and unsuccessful breeding areas differed only in nest tree species ($\chi^2 = 5.7$, df = 1, $P < .02$). Thirty-six percent of the nests in Sitka spruce trees ($n = 14$) were successful and 12% of the nests in black cottonwoods ($n = 124$) were successful.

Food limitations

A greater percentage of nests were found to be active during 1983, when major food patches existed, than in either 1980 ($\chi^2 = 13.1$, df = 1, $P < .001$) or 1981 ($\chi^2 = 3.8$, df = 1, $P < .05$) (Table 1). A smaller food patch was present in 1982 and a greater percentage of nests was active that year than in 1980 ($\chi^2 = 10.0$, df = 1, $P < .01$), but the difference between 1981 and 1982 was not significant ($\chi^2 = 2.4$, df = 1, $P > .05$). Moreover, in 1983 the proportion of active nests was higher within 6 km of the food patch than farther away ($\chi^2 = 4.1$, df = 1, $P < .05$) (Table 2). However, no such pattern existed in the years when the food distribution was not clumped (1980: $\chi^2 = 1.0$, df = 1, $P > .30$) (1981: $\chi^2 = 3.0$, df = 1, $P > .05$) (Table 2). The pattern was not significant in 1982 ($\chi^2 = 2.2$, df = 1, $P > .10$), even though food was concentrated in a section of the river.

Laying date was influenced by proximity to spring food supplies. Pairs nesting within 3 km of food patches laid eggs earlier than those nesting farther from food clumps ($\chi^2 = 10$, df = 1, $P < .01$) (Table 3). Mean clutch size, however, was not significantly larger within 3 km of food supplies ($\bar{X}$ + SD = 1.94 ± 0.56) than elsewhere in the Chilkat Valley (1.71 ± 0.47) (Mann-Whitney U test, $n_1 = 17$, $n_2 = 14$, $U = 96$, $P > .05$). Lastly, nest success during June was higher at breeding areas where food was provided than at control areas (Exact Probability Test, $n = 36$, $P < .04$). In experimental nests 4 of 12 offspring survived, while 2 of 48 survived in control nests (Table 4).

DISCUSSION

Evaluation of hypotheses

Breeding activity.—The results show that breeding activity was related to food abundance and to habitat quality. More nests were active in the Chilkat Valley in 1983 when food was plentiful than in 1980 or 1981 when food was sparse. The trend was also significant between 1982 and 1980, but not between 1982 and 1981. Furthermore, in 1983 the proportion of nests

TABLE 2. Status of Bald Eagle nests within two portions of the Chilkat Valley, Alaska, in 1980–1983.

Year	River section 1				River section 2				Total
	Active		Inactive		Active		Inactive		
	n	%	*n*	%	*n*	%	*n*	%	*n*
Food abundance: section 1 and 2: low									
1980	9	35	17	65	6	22	21	78	53
1981	12	52	11	48	8	29	20	71	51
Food abundance: section 1: high; section 2: low									
1982	15	65	8	35	13	45	16	55	52
1983	20	71	8	29	13	45	16	55	57

TABLE 3. Effect of nest proximity to food patches on laying date of Bald Eagles in the Chilkat Valley, Alaska in 1983.

Nearness of nests to food patches	Eggs laid			
	Before 26 April		After 26 April	
	n	%	*n*	%
<3 km	11	58	8	42
>3 km	2	10	18	90

active was higher in river sections where food patches existed than in other river sections. However, there was no difference in nest activity between the river sections in years when no food patches occurred. Food was concentrated in a portion of the Chilkat Valley in 1982, but this did not significantly alter the proportion of active nests between river sections that year. The food patch was possibly too small in size or occurred too early in the year ($\approx$1 mo earlier than in 1983) to influence strongly the number of eagles that laid eggs that year.

Two habitat variables differed significantly between active and inactive nests. Height class and base elevation of nest tree were important, possibly because eagles with nests positioned high above feeding grounds and above the surrounding canopy were better able to locate prey.

Laying date and clutch size.—Laying date was advanced where food was abundant. This is probably advantageous to Bald Eagles because juveniles fledging earliest have more time to acquire the skills required for enduring harsh weather and unpredictable food supplies in winter.

Clutch size is known to be influenced by feeding conditions in some bird species (Drent and Daan 1980). The absence of this effect in Chilkat eagles may indicate (1) that clutch size does not change with food abundance in this species, or (2) that my sample size was too small to detect an actual relationship between food and number of eggs laid.

Nest success.—Offspring survival was significantly improved by supplemental feeding. This is, to my knowledge, the first published experimental evidence that food supplies influence egg and chick survival of a diurnal raptor. (Newton 1979:135, mentions unpublished experimental results. Circumstantial evidence is given by Newton 1979 and Simmons et al., *in press*.) The high rate of failure in control nests probably occurred because abundant food in spring allowed high breeding rates but subsequent food shortages caused widespread starvation among eaglets. The loss of some offspring from experimental nests may have been due to itinerant eagles taking some of the supplemental food.

The significant association between nest success and only one of 11 habitat variables (nest tree species) suggests that there was, at best, a weak relationship between nesting habitat characteristics and nest success.

Implications for Northwest coast eagles

Population regulation.—These findings demonstrate that the variation in fledging rates of Bald Eagles in the Chilkat Valley is probably due to fluctuations in food supplies. Hunting conditions for eagles are relatively unpredictable in this glacier-fed river because river level and turbidity vary with rates of glacial melting. Most Bald Eagles in the PNC nest along marine waters where hunting conditions are variable, but probably less variable than in glacier-fed rivers.

Why did so many adults fail to breed in southeast Alaska in some years? The ephemeral food supplies of the PNC (Hansen et al. 1986) may allow more eagles to survive than can reproduce. Nonbreeding eagles can wander extensively and utilize dispersed food patches (Hodges et al., *in press*), but breeders must forage close to their nests. The nest may be abandoned if food cannot be obtained for as little as a few weeks. The results suggest that there is a shortage of breeding areas that provide a reliable food supply during the entire nesting season. The best comeptitors may claim these areas, forcing other eagles to nest in marginal habitat or forego breeding that year (see Brown 1969). Thus, nonbreeding adults are probably typical in the region and are a result of naturally ephemeral food supplies and strong territoriality of adults in favorable breeding areas.

The results from the riverine habitats of the Chilkat Valley further suggest that the negative trend in productivity in the marine habitats of Seymour Canal is due to reduced food available to breeders. Habitat quality is unlikely to be a factor in Seymour Canal because the old-growth forests there appear to have changed little since the nest surveys were started. No effort has been made to quantify the abundance of prey species of Bald Eagles in Seymour Canal. However, it is plausible that prey abundance there has declined due either to natural causes or human activity such as overfishing or destruction of spawning habitat. A persistent reduction in food supplies would probably cause an eventual decline in the size of the eagle population.

Alternatively, food abundance may have remained stable in Seymour Canal, but an increasing share of the

TABLE 4. Effect of supplemental feeding of breeding Bald Eagles in the Chilkat Valley, Alaska on nest success and offspring survival between 7 May and 7 June 1983.

	Nest status				Offspring survival			
	Successful		Unsuccessful		Survived		Died	
Treatments	*n*	%	*n*	%	*n*	%	*n*	%
Food provided	3	43	4	57	4	33	8	67
Control	2	8	27	93	2	4	46	96

food may have been taken by nonbreeding eagles. Brown (1969) reviews data indicating that competition between breeders and nonbreeders may reduce reproduction. It is theoretically possible that the regular presence of nonbreeding Bald Eagles has resulted in an endogenous long-term population cycle in southeast Alaska. An initial population may increase in size until breeding habitat is saturated and nonbreeders become so numerous that they compete with breeders for food and thereby decrease productivity. Recruitment into the nonbreeding population may then drop, permitting productivity of breeders to increase, initiating the cycle anew. The important implication of this hypothesis is that eagle productivity may fluctuate considerably in natural habitats, with periods of reduced productivity balanced by recovery periods.

Implications for eagle populations elsewhere in North America

The results of this study allow speculation that eagles were as abundant in some other locations in North America during presettlement times as they are along the PNC today. Anadromous fish such as Atlantic salmon (*Salmo salar*), alewives (*Alosa pseudoharengus*), and American shad (*A. sapidissima*) were profuse along the northeast coast (Netboy 1974) and Pacific salmon spawned as far south as the Sacramento River, California (Hewes 1973). Overfishing, however, led to decimation of these fish populations, and logging caused the disappearance of old-growth coastal forests in many places soon after European settlement (Smith 1979, Cronon 1983). This destruction of the food and habitat of Bald Eagles may have depressed productivity and, along with shooting, contributed to the population declines of the 19th and early 20th centuries. This decline was further exacerbated by the introduction of DDT in 1942.

Now that DDT is banned, eagle populations are increasing in parts of North America. If this trend continues, wildlife managers should not be surprised if the dynamics of these populations come to resemble those in southeast Alaska. The proportion of nonbreeding adults may increase if these expanding populations eventually saturate available habitat.

This study makes clear that restoring viable populations in the former range of the species will require the maintenance and enhancement of the food supplies and habitat on which eagles depend. Management strategies can be no less stringent along the PNC. Efforts are needed to determine if the significant decline in Bald Eagles in Seymour Canal is due to natural causes or human activity.

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