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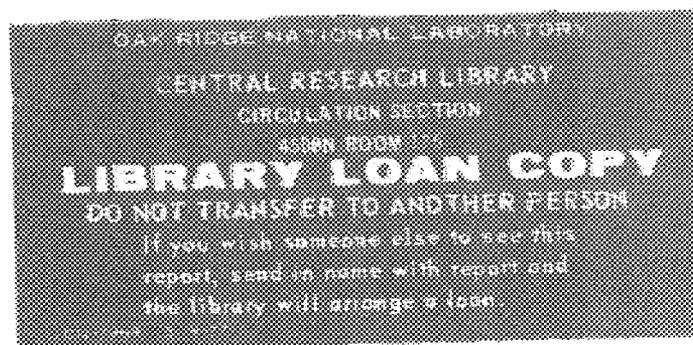
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Behavioral Ecology of Bald Eagles Along the Northwest Coast: A Landscape Perspective

Andrew J. Hansen
M. I. Dyer
H. H. Shugart
E. L. Boeker

Environmental Sciences Division
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ENVIRONMENTAL SCIENCES DIVISION

BEHAVIORAL ECOLOGY OF BALD EAGLES ALONG THE NORTHWEST COAST:
A LANDSCAPE PERSPECTIVE¹

Andrew J. Hansen,² M. I. Dyer, H. H. Shugart,³ and E. L. Boeker⁴

Environmental Sciences Division
Publication No. 2548

¹Submitted as a dissertation by Andrew J. Hansen to the Graduate Council of the University of Tennessee in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

²Present address: Centre for Resource Ecology, Department of Botany, University of the Witwatersrand, 1 Jan Smuts Avenue, Johannesburg 2001, South Africa.

³Present address: Department of Environmental Science, University of Virginia, Charlottesville, VA 22903 USA.

⁴Present address: 8219 West Virginia Avenue, Lakewood, CO 80226 USA.

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ABSTRACT

HANSEN, A. J., M. I. DYER, H. H. SHUGART, and E. L. BOEKER
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northwest coast: a landscape perspective.
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Much of the range of the bald eagle (Haliaeetus leucocephalus) has been subjected to anthropogenic disturbance of greater magnitude than the natural regimes of pre-European settlement times. Consequently, many eagle populations are depauperate. Eagle populations are large and stable, however, along the relatively pristine Pacific Northwest Coast of North America. This study examines (1) the behavior and ecology of bald eagles along the northwest coast, and (2) the effects of environmental disturbance and resource dynamics on the ecology and evolution of eagles.

The ephemeral nature of food supplies along the northwest coast apparently results in eagles being limited primarily by food stress. Studies in the Chilkat Valley, Alaska, from 1979 to 1983 revealed that the number and distribution of eagles correlated with food availability. Also, nonbreeding eagles made migratory movements between food patches. Within the Chilkat Valley in winter, habitat was used preferentially, possibly to minimize the cost of thermoregulation. The use of gravel bars declined and use of streamside trees increased as ambient temperature dropped. During winter storms and at night, eagles sought refuge in dense stands of conifer trees.

The foraging behavior of eagles was analyzed using evolutionary game theory as a theoretical construct. Eagles obtained food by

searching for unclaimed carcasses and by stealing from conspecifics. In a sample of 14 eagles, the rewards (food intake) and costs (incidence of injury) were similar for each tactic. This suggests that eagles hunted and pirated at rates which maximized fitness and that the population was in an evolutionarily stable state. The outcomes of contests for food were influenced by size, hunger level, and possibly position (in the air or on the ground), but not by age. Pirating eagles assessed the size and hunger level of feeders and tried to steal from those who were most likely to retreat without fighting. Hungry birds capitalized on the assessment capabilities of others; they dissuaded attackers by using displays to advertise that they were hungry and willing to fight. A result of assessment was that contests were usually settled without physical fighting. Food availability influenced the foraging behavior of eagles. Frequency of display and escalated fighting increased as food levels decreased. A theoretical model showed that the rates of hunting and stealing across the population may or may not change with fluctuating food levels.

These studies offered new perspectives on information transfer during animal contests. Contrary to current thought, evidence shows that displays may function to signal fighting ability, expected gain in victory, or intentions.

Productivity was found to be variable and generally declining in southeast Alaska. Reproduction was influenced by food abundance and habitat quality but not by chemical contaminants. Food levels in spring influenced if or where eagles nested and when they laid eggs. Active and inactive nests differed in habitat quality. Food supplies during incubation and rearing regulated offspring survival.

Food shortages probably limited eagles over evolutionary time and several adaptations for survival and reproduction are apparent. Eagles maximized energy input for survival by feeding opportunistically, making broad-scale movements to find food patches, locating food within a patch by searching for prey or for conspecifics with prey, assessing prey profitability, acquiring food by hunting and stealing, and by defending food through threat displays or fighting. The light wing-loading of subadults may be an adaptation for making distant flights in search of food. The cryptic plumage of subadults may serve to make them less conspicuous to potential pirates when the subadults are feeding. Eagles conserve energy by minimizing nonessential activities and by maximizing time in habitats that offer favorable microclimates. Injury is minimized by avoiding dangerous prey or dangerous opponents, and by using habitat to maintain a buffer to danger.

Eagles obtain food for reproduction by defending feeding territories and by storing food in their nests. Possible adaptations for nest defense include heavy wing-loading in adults, which may increase flight agility, and bright adult plumage, which may advertise that a territory is occupied.

These strategies and adaptations translate up scale and influence characteristics of the regional population. The mobility and the broad feeding niche of eagles result in the birds being distributed over most of North America. The dispersion of nonbreeding birds reflects the patterning of their food supplies; they are dense where food is abundant and scarce elsewhere. An important consequence of eagles being drawn together at food patches is sociality. Interactions between eagles

in feeding aggregations may be cooperative or competitive. A result of intraspecific competition is that low status individuals may be inhibited from feeding and starve. Thus social behavior in bald eagles is an important factor in the regulation of survival.

Territoriality may also result in endogenous population regulation. Nest site quality in the region is determined primarily by food availability. The best competitors may claim and defend disproportionately large shares of the suitable habitat, and other eagles may be forced to forego breeding that year. A surplus of nonbreeders is probably a natural feature of ephemeral food supplies and territorial behavior. Delayed maturation may be an evolutionary consequence of surpluses of nonbreeders. Young eagles, being poor competitors for nest sites, may maximize lifetime reproduction by avoiding the risks of breeding too early. Another possible consequence of nonbreeder surpluses may be a long-term population cycle resulting from competition for food between breeders and floaters.

The research illustrated some general principles that govern how environmental dynamics influence organisms. Natural disturbance drove the dynamics of the food and habitat resources that limited eagles. Eagles responded at several scales including the organismal, population, and evolutionary levels. These responses were felt at organizational levels ranging from individuals and breeding pairs up to species. This landscape perspective on the nature of environment/animal interactions has important implications for behavioral ecology and conservation biology.

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CHAPTER I

INTRODUCTION

The order Falconiformes includes major five major families and is represented world-wide (Brown and Amadon 1968). The size, beauty, and predatory nature of these birds have fascinated people for centuries. The diurnal birds of prey are also of interest to ecologists because they are stereotypic K-selected organisms (Pianka 1970); most have long spans, delayed maturation, low breeding rates, and small clutches. Such organisms are often difficult to study, but properly designed investigations may provide keen insights into various ecological questions. In this study of bald eagles (Haliaeetus leucocephalus) I explore aspects of evolutionary game theory, environmental determinants of ecology and social behavior, endogenous population regulation, and the adaptive significance of delayed breeding.

POPULATION STATUS: PAST AND PRESENT

Research on bald eagles is critical as many populations may be in disequilibrium with respect to modern environments. The species occurs only in North America, large portions of which have been subjected in recent centuries to disturbance of far greater magnitude than the natural regimes of pre-European settlement times. Consequently, historic landscape changes have been radical. Old growth forests along coasts and rivers are virtually nonexistent in the eastern half of the continent. Extensive deforestation occurred along waterways of southern New England by 1800 (Cronon 1983). Anadromous fishes were

also greatly impacted by man. Stocks of Atlantic salmon (Salmo salar) in New England were severely depleted by the mid 1800's (Netboy 1974). Catches of Pacific salmon (Oncorhynchus sp) in the Sacramento and Columbia Rivers began to decline by 1890 (Hewes 1973, Smith 1979). More recently, chemical toxins such as DDT, PCB's, and dieldrin have been widely introduced in North American ecosystems (Wiemeyer et al. 1984).

These landscape changes have had a substantial impact on bald eagles. DDE contamination inhibited eagle reproduction in many regions during the 1960's and 1970's (Grier 1982, Wiemeyer et al., 1984). The population reductions of that time were attributed to this loss of productivity (Evans 1982). Anecdotal evidence suggests that many bald eagle populations were depauperate even prior to the occurrence of chemical toxins. Coues (1883) noted that bald eagles in New England, though still common in 1883, were less abundant than in earlier times. Just 43 years later, Forbush (1927) declared that breeding eagles were nearly extirpated from southern New England. Such reductions were presumably due to the decimation of food and habitat described above.

Eagle populations remain large, however, in those regions least altered by anthropogenic disturbances. The relatively pristine coastlines of British Columbia and southeast Alaska support over 16,000 eagles (Hodges et al. 1979, Hodges 1984). The apparent inverse relationship between landscape changes by man and bald eagle abundance suggests that in many regions anthropogenic disturbance causes the species to be maladapted to modern environments. This situation presents some difficulty to studies of bald eagle adaptations. More

importantly, the situation raises the more general question of the role of disturbance in ecosystems and its influence on organisms and populations.

DISTURBANCE, LANDSCAPE DYNAMICS, AND BIOTIC RESPONSE

Advancement of ecology has been hampered by a pervasive assumption that biological systems remain in steady state except during infrequent instances of catastrophic perturbation. This notion may have stemmed from (1) the Clementsian view (1936) that vegetative succession tends toward equilibrium (climax) communities and (2) the fact that many mathematical models used in ecology require equilibrium assumptions to be tractable (Karr and Freemark 1984). Recent work has shown that disturbance is a regular feature of many ecosystems (White 1979) and that perturbed systems may be maintained in either equilibrium or disequilibrium depending upon their disturbance regimes. For example, dramatic climatic fluctuations in eastern North America over the last 20,000 years resulted in disequilibrium of forest composition between 40 and 50 degrees N. Lat. (Figure 1-1) (Delcourt and Delcourt 1983). In contrast, the equilibrium of Kirtland warbler (Dendroica kirtlandii) populations is dependant upon frequent fires to produce the young jack pine stands (Pinus banksiana) the birds require (Welty 1975). The role of disturbance in driving ecosystem dynamics, the subsequent responses of organisms, and the resulting biotic patterns over the landscape are now actively under study (Delcourt et al. 1983, Pickett and White 1984, Shugart 1984).

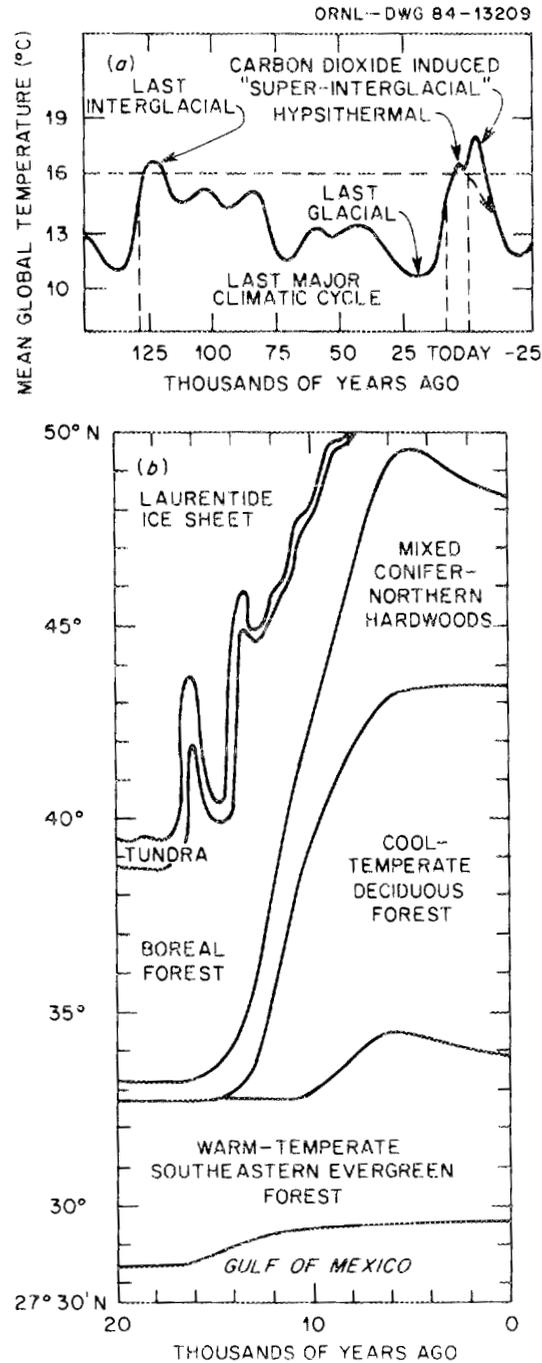


Figure 1-1. (a) Past variation in global climate for the last glacial-interglacial cycle and future changes in climate projected for the next 25,000 years (modified from Delcourt et al. 1983). (b) Change in vegetation patterns on a transect along 85°W longitude in eastern North America over the last 20,000 years (modified from Delcourt and Delcourt 1983).

The concept of limiting factors is central to consideration of the effects of disturbance on animal and plant populations. In a finite world, biotic populations increase in size until environmental resistance halts growth at carrying capacity (Pianka 1974). Environmental constraints include both resource limitations and factors which directly disrupt physiological processes (e.g., predation, injury, disease). The latter can be considered a type of disturbance (White 1979). Across a landscape, resources are spatially and temporally dynamic. For example, food of bald eagles in southeast Alaska varies with the distribution of spawning salmon across the region and with season of the year. A landscape can, in fact, be viewed as a dynamic mosaic of resource patches that are driven by disturbance. Heterogeneous resource patterns result from differential disturbance regimes, created by discontinuities in topography, soil type, vegetation, and other environmental features. Living organisms are influenced by disturbance either directly through physiological disruption or indirectly by way of resource dynamics.

The magnitude of response by plants and animals is dependent upon the scale of the disturbance (Delcourt et al. 1983). A brief, local rain shower may raise stream turbidity and temporarily inhibit feeding by visually-orienting fish. At the other extreme, long-term increase in stream turbidity throughout a region, perhaps due to inundation by meltwater carrying glacial silt, may select for fish with food-detection mechanisms other than sight. Such biotic responses to disturbance and resource dynamics are expressed at differing organizational levels. Response to the rain shower would causally influence a deme for a

short time; the response to glacial processes would shape the evolution of a species.

Bald eagles have evolved in environments subjected to frequent natural disturbance. To understand the behavior and ecology of bald eagles, it is necessary to understand the landscape dynamics that shaped their evolution.

STUDY OBJECTIVES

The goals of my research are two-fold. The first goal is to explore the behavior and ecology of bald eagles in southeast Alaska where anthropogenic disturbance has been minimal and the birds probably remain well-adapted to their environment. Specific objectives are to: (1) identify the factors limiting bald eagles; (2) elucidate strategies and adaptations for survival and reproduction; and (3) describe the population attributes resulting from these adaptations. The second goal is to explore the interrelationships between environmental disturbance, resource dynamics, and the ecology of a vertebrate. This includes: (1) describing the distribution of limiting resources through time and space and the role of disturbance in shaping that distribution; (2) considering, at various scales, the responses of eagles to resource dynamics and disturbance; and (3) depicting the resulting patterns of eagle dispersion and behavior.

Herein, I examine the behavioral ecology of bald eagles in the Chilkat and Chilkoot River valleys in southeast Alaska. The study area is described in Chapter II. In Chapter III the population dynamics, habitat use, daily activities, food sources, movements and

reproduction of the population are examined. Intraspecific competition for food and implications for evolutionary game theory are explored in Chapter IV. CHAPTER V examines the factors regulating reproduction. In Chapter VI all results are integrated into a conceptual model of the adaptations of bald eagles for survival and reproduction. The model is used to interpret the population level characteristics of eagles. Finally, this work and information gleaned from paleoecological literature are used in CHAPTER VII to describe the relationships between disturbance, resource dynamics, and bald eagles along the northwest coast of North America.

CHAPTER II

PACIFIC NORTHWEST COAST OF NORTH AMERICA

CONTEMPORARY CONDITIONS

Southeast Alaska

Southeast Alaska lies along the Pacific Northwest Coast just west of northern British Columbia (Figure 2-1). Sheer mountains and massive ice fields abut on the Pacific Ocean there to create a stunningly dramatic landscape. The region includes three physiographic subzones (Kerr 1936). The ice mantled Coast Mountains in the east have average summit elevations of 1500-1800 m above sea level and the tallest peaks exceed 3,000 m. Glaciers have sculpted the mountains cutting high cirques and deep U-shaped valleys. To the west are the Insular Mountains (1200 m elevation) of the Alexander Archipelago. Between the two is the island-studded Coastal Trough. The southeast to northwest trending Coastal Trough is composed of a network of glacier-scoured fiords and low islands.

The cool wet climate of southeast Alaska is controlled by sub-tropical ocean currents and prevailing westerly winds (Heusser 1960). Moist, mild Pacific airmasses generally maintain equitable conditions. Occasionally temperature extremes result when continental air spills westward over the Coast Range. Average temperatures at sea level are about -1°C in January and 13°C in July. Extremes range from -28 to 35°C . Most precipitation falls in autumn and winter; annual averages range between 1500 and 3800 mm (Heusser 1960).

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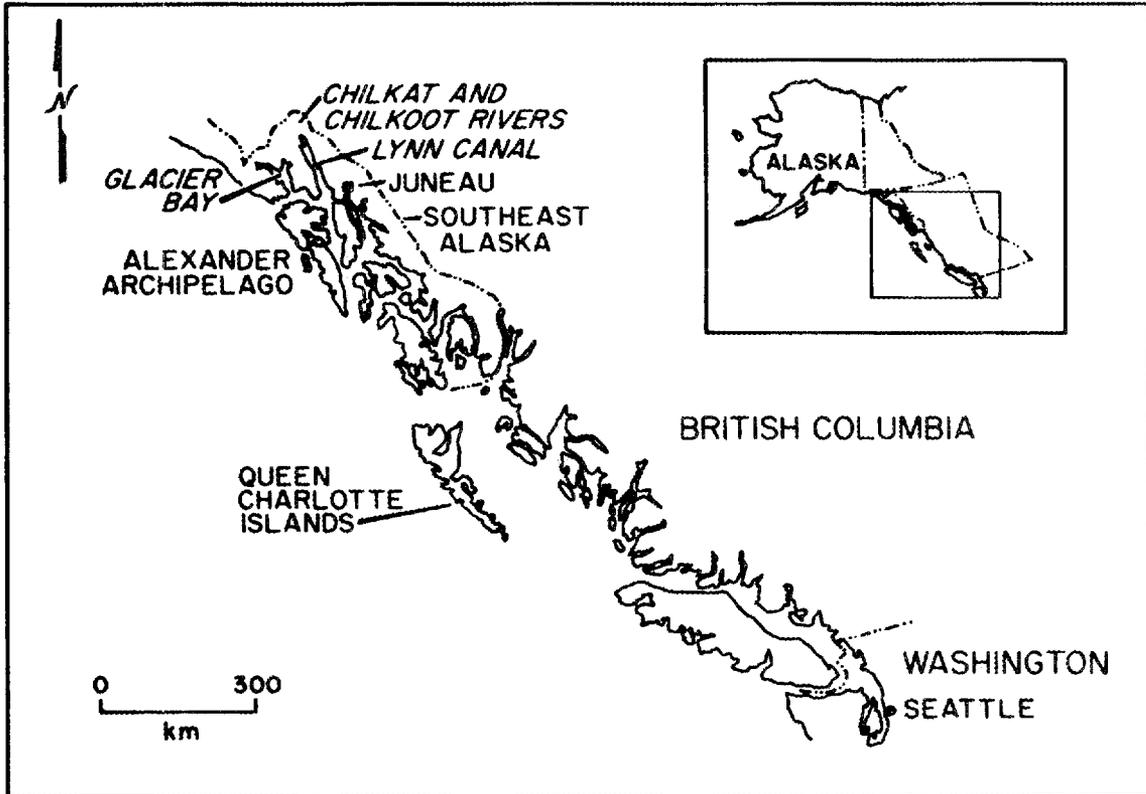


Figure 2-1. Map of the northwest coast of North America.

Vegetation below the 600-m tree line is primarily Pacific Coastal Forest and muskeg (Heusser 1960). Western hemlock (Tsuga heterophylla) and Sitka spruce (Picea sitchensis) comprise over 90% of low-elevation forests (Taylor 1932). Mountain hemlock (T. mertensiana) is more abundant near timber line. The open, sphagnum (Sphagnum sp.)-dominated muskeg is prevalent where surface-water drainage is poor (Lawrence 1958). Black cottonwood (Populus trichocarpa) grows on well drained alluvium of active flood plains while muskeg occurs at wetter alluvial sites.

The marine environment of the northwest coast is among the most productive in the world. Extensive upwellings bring nutrient-rich deep water to the ocean surface where the nutrients are maintained by estuary-like circulation patterns (Rietze 1971). Productivity is further enhanced by mineral sediments introduced from glacially-fed rivers. These nutrients are harvested by plankton which are, in turn, eaten by shrimp and other primary consumers. Higher on the food chain in coastal waters are Pacific herring (Clupea herengus pallasii), eulachon (Thaleichthys pacificus), several species of cod (Gadus sp.) and various flatfishes. Tertiary consumers include Pacific halibut (Hippoglossus stenolepis), Pacific salmon, and marine mammals such as harbor seals (Phoca vitulina), northern sea lion (Eumetopias jubatus), killer whale (Orcinus orca), and humpback whale (Megaptera novaeangliae). Salmon and eulachon are anadromous; mature adults ascend rivers to spawn and then die. After hatching, smolts remain in freshwater for a period of a few months up to two years before migrating to sea. Freshwater residents include trouts (Salmo sp.) and dolly varden (Salvelinus malma).

Anadromous fish can be viewed as nutrient pumps. They consume nutrients throughout oceans and transport the nutrients in the form of their body tissue to freshwater systems. The spawned-out carcasses of these fish provide pulses of food to several vertebrates including bald eagles, crows (Corvus), ravens (C. corax), magpies (Pica pica), gulls (Larus sp.), waterfowl, river otter (Lutra canadensis), coyotes (Canus lantrans), wolves (C. lupus), black bear (Ursus americanus), and brown bear (Ursus middendorff). Even the survival of aboriginal man in the region was dependent upon anadromous fish (Fladmark 1975).

Presently, it is man that controls the fish. Commercial harvest of salmon has been intensive in southeast Alaska. Prudent management, however, has allowed most salmon populations to remain healthy. Timber is another resource exploited by man. Logging has been widespread, but primeval forests still remain along most sections of shoreline. Most other human development in the region is concentrated in the villages and towns which are widely spaced along the coast and are not interconnected by roads. Thus, most of southeast Alaska remains in a condition similar to that of pre-settlement times.

Chilkat and Chilkoot Valleys

The Chilkat and Chilkoot river valleys lie in the Coast Range in northern southeast Alaska (Figure 2-1). Situated near the town of Haines and 128 km north of Juneau, the valley is bordered by Glacier Bay to the southwest, Lynn Canal to the south, and British Columbia to the north. The Klehini and Tsirku Rivers are major tributaries of the Chilkat (Figure 2-2). The Chilkat and Chilkoot valleys experience

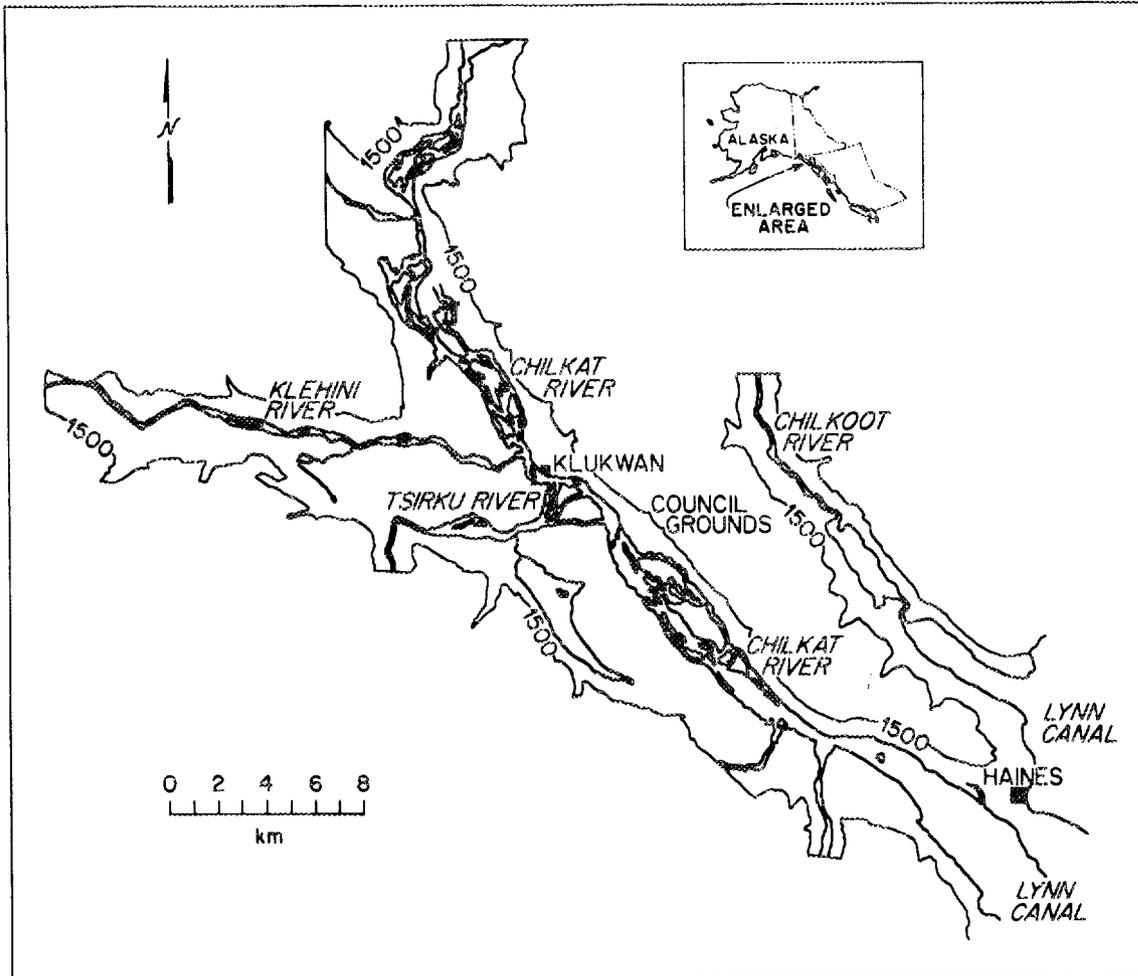


Figure 2.2. Map of the Chilkat and Chilkoot valleys.

greater temperature extremes than is typical for southeast Alaska. Extended periods of subzero temperatures are common in winter.

An unusual hydrological condition occurs along a 5 km stretch of the Chilkat at its confluence with the Tsirku River. Strong flows of ground water at temperatures of 4-6°C percolate up through the river bed. This clear, relatively warm water offers superb spawning habitat. Consequently, a very large and uniquely late run of chum salmon (O. keta) congregate there each fall and winter. The spawned-out carcasses of these fish attract thousands of bald eagles, hence people of the Tlingit tribe call this place "Council Grounds of the Eagle". Four other species of anadromous fish spawn in the Chilkat and Chilkoot drainages providing eagles with food during much of the year (Table 2-1).

LANDSCAPE DYNAMICS

Although the northwest coast has not undergone extensive change at the hand of man, it has not been static. A hierarchy of natural disturbance regimes generate cycles of landscape dynamics at various temporal and spatial scales (Figure 2-3). Presented below is an array of landscape cycles of differing scale which may have shaped the ecology and evolution of northwest coast bald eagles.

Global Climatic and Glacial Cycles

The broadest scale disturbance of interest is the long-term fluctuation in solar radiation striking earth due to systematic changes in the orbital geometry between earth and the sun. This variation in solar radiation results in global climatic cycles of glacial cooling

Table 2-1. Anadromous fish runs in the Chilkat and Chilkoot valleys which are major food sources for bald eagles.

Fish species	Spawning period	Location of spawning grounds	Approximate size of run ¹ (numbers of individuals)
Eulachon (<u>Thaleichthys pacificus</u>)	May	Chilkat River Estuary Chilkoot River Estuary	Unknown Unknown
Sockeye salmon (<u>O. nerka</u>)	July-Dec	Chilkat Lake	60,000-90,000
	July-Dec	Chilkoot Lake and River	70,000-100,000
Pink salmon (<u>O. gorbuscha</u>)	July-Aug	Chilkat River	25,000-35,000
	July-Aug	Chilkoot River	25,000-35,000
Chum salmon (<u>O. keta</u>)	Sept-Oct	Klehini River	10,000-60,000
	Oct-Jan	Chilkat River	100,000-500,000
Coho salmon (<u>O. kisutch</u>)	Dec-Jan	Chilkat River	Unknown
	Dec-Jan	Chilkat Lake	Unknown

¹Estimates provided by Ray Staska, Alaska Department of Fish and Game.

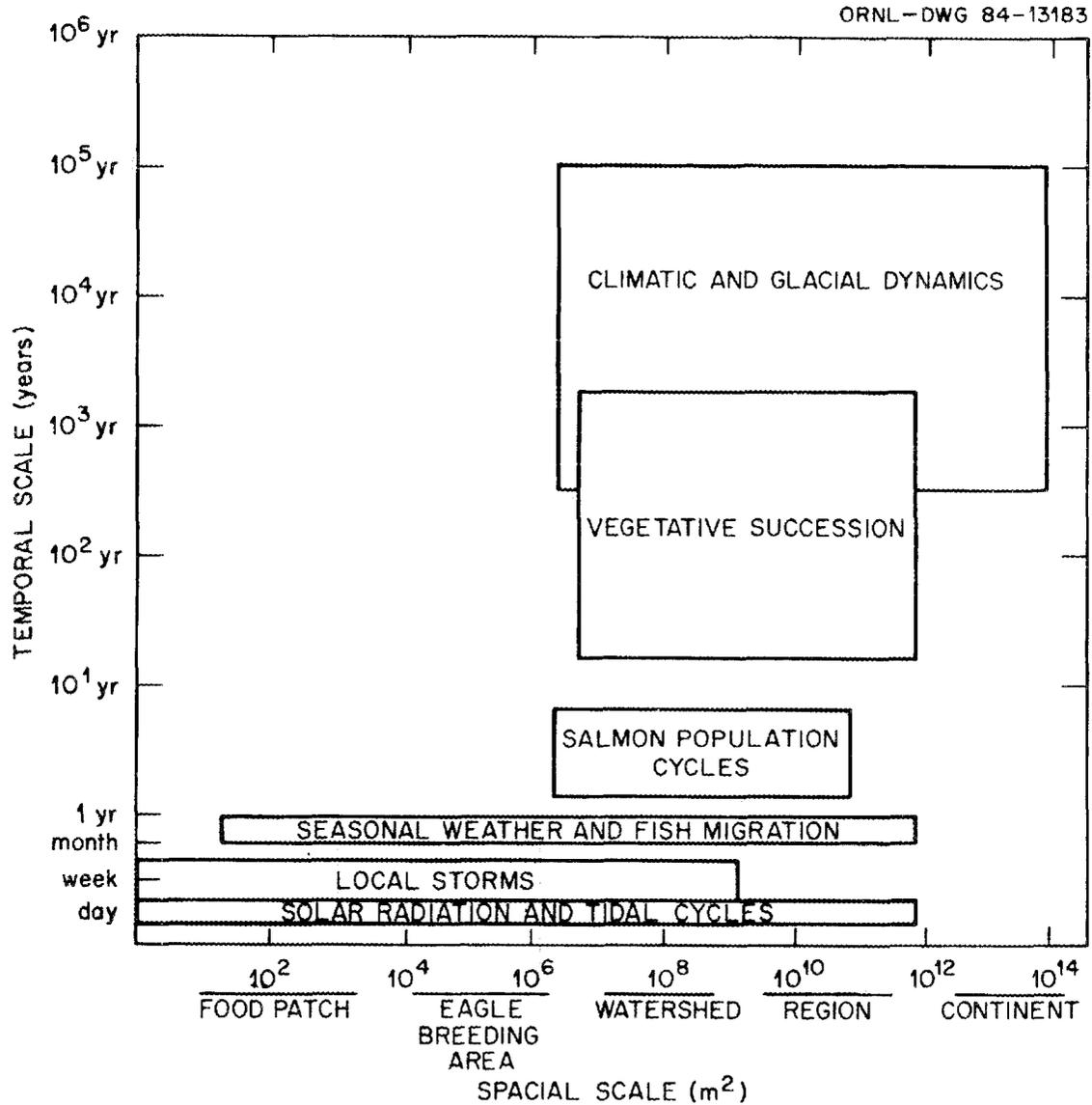


Figure 2-3. The time and space domains of natural disturbances and cycles that influence resources required by bald eagles. The rectangles show only the relative positions of the factors. The actual shapes of the domains may not be rectangular.

and interglacial warming with discrete periodicities of 100,000, 41,000, and 23,000 years (Delcourt et al. 1983). Such glacial cycles prevailed in the Pacific Northwest throughout the Pleistocene (Pewe 1976). However, patterns of glacial movement are well-known, only for the most recent of major ice advances, the Fraser Glaciation, because it obscured signs of earlier glaciations. Evidence from sites not inundated by continental ice documents a relatively warm period (interstadial) that persisted from 45,000 to 25,000 BP (years before present). Conditions in the Queen Charlotte Islands, British Columbia then were 1-2°C cooler and wetter than at present (Warner et al. 1984). In western Washington, this interstadial was interrupted during 39,000-30,000 BP when cooler temperatures caused alpine glaciers to readvance (Heusser 1977) (Figure 2-4).

The Fraser Glaciation began about 25,000 BP when mountain glaciers coalesced to form the Cordilleran Ice Sheet. The Cordilleran Ice Sheet extended 3760 km from the Aleutian Islands, Alaska, southward to Washington and reached from the Pacific coast eastward to the Rocky Mountains (Heusser 1960). Most of southeast Alaska was overridden with a mantle of glacial ice up to 1800 m thick. The westernmost portion of the Alexander Archipelago and much of the Queen Charlotte Islands probably remained ice free (Fladmark 1975, Warner et al. 1984).

With climatic amelioration, the Cordilleran began to recede by 14,000 BP (Hamilton and Thorson 1983) and the ice reached its present location by about 10,000 BP. The warming trend continued into the Holocene and between 8,000 to 6,000 BP leveled off at temperatures slightly warmer than those of today. Between 3000 and 300 BP,

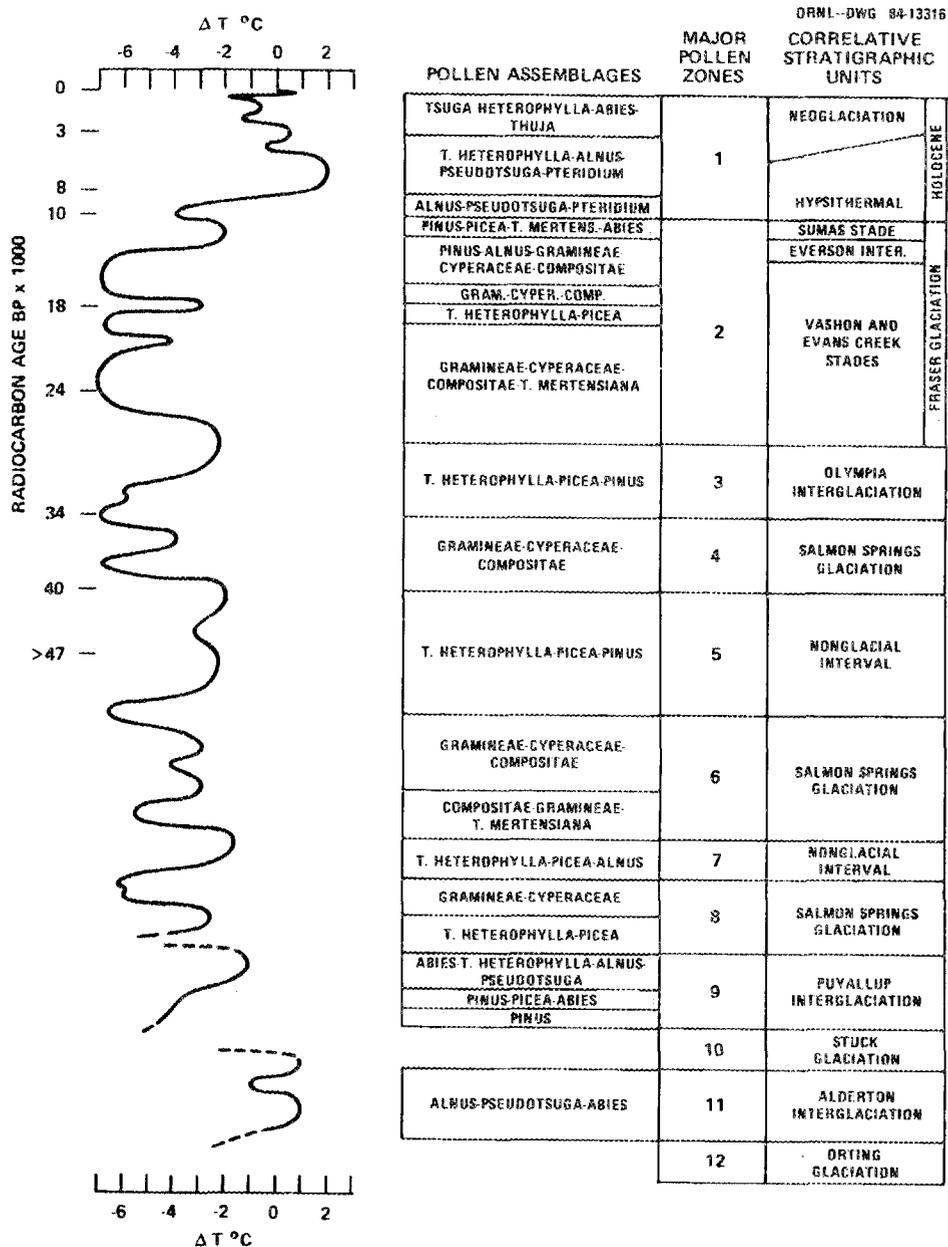


Figure 2-4. Correlation of reconstructed temperature changes, pollen assemblages, major pollen zones, and stratigraphic units on the Pacific slope. Temperature changes are amounts above or below the present mean for July. Assemblages designated through Zone 8 pertain to the Hoh-Kalaloch pollen stratigraphy. Note that the record below 40,000 yr BP is not on the same scale as the portion above this time plane (modified from Heusser 1977).

deteriorating climate caused mountain glaciers to readvance (Miller 1976). During this "Little Ice Age", Glacier Bay completely filled with ice although few ice fields further south reached tidewater. Subsequently, glaciers began to subside and the retreat continues today.

Vegetative Response to Glaciation

These climatic and glacial cycles exerted great influence over vegetation. During the interstadial prior to the Fraser advance, a coniferous forest of mountain hemlock, western hemlock, and Sitka spruce dominated portions of the Queen Charlotte Islands (Warner et al. 1984) and similar stands probably persisted in southeast Alaska. The advancing Cordilleran destroyed all of the coastal vegetation except that which survived in refugial areas along the northwest coast and south of the ice sheet. Just beyond the southernmost ice lobe grew forests of Douglas fir (Pseudotsuga menziesii), mountain hemlock and lodgepole pine (Pinus contora) (Heusser 1983). Beringia, the vast region of central and western Alaska that remained unglaciated, supported grasslands with scattered clumps of black cottonwood and alder (Alnus sp.) trees and shrubs (Hopkins et al. 1981). After the Cordilleran subsided, plants quickly recolonized the coast and developed communities similar to those of today (Ager 1983).

Effects of Glaciation on Salmon

Pacific salmon are also very sensitive to environmental conditions and thus they are greatly affected by climatic and glacial cycles. Successful reproduction can occur only in aquatic environments which offer suitable water temperature, and oxygen concentration, and minimal

turbidity (Wickett 1958). Glaciers can influence salmon directly by overrunning spawning habitats or indirectly by altering stream conditions through meltwater runoff.

Neave (1958) argued that glacial dynamics and corresponding sea level changes during the mid to early Pleistocene are responsible for the evolution of Pacific salmon. He suggested that trout from North America penetrated the North Pacific and became trapped in shallow embayments when glaciers formed and sea levels fell. Divergence occurred there and rising sea level allowed the ancestral salmon to escape and colonize the North Pacific.

Glacial dynamics also influenced distribution of salmon. Presently, Pacific salmon range in North America from California to the Arctic Ocean. Although fossil evidence of salmon from the late Pleistocene is sparse, it is reasonable to assume that their range during the previous interstadial was similar to that of today as conditions then and now are comparable. During the Fraser Glaciation when most of the coast was shrouded with ice, North American salmon stocks probably survived both south of the ice sheet and in Beringia (McPhail and Lindsey 1970). As the Cordilleran retreated, stocks of salmon from the southern refugium probably repopulated most of the northwest coast while those from Beringia expanded into Asia (McPhail and Lindsey 1970).

Thus, it appears that global climate cycles with 100,000 year periodicities triggered glaciations that controlled vegetation patterns and influenced the evolution and distribution of Pacific salmon. The distribution and abundance of bald eagles probably fluctuated with their

food supplies and habitat. During the previous interstadial the eagle population along the northwest coast was probably similar to that of today. However, during the Fraser Glaciation bald eagles may have survived both to the north and to the south of the Cordilleran. It is possible that during that time gene flow between the two demes was low enough for genetic divergence to occur. The two demes surely merged after the ice receded. Undoubtedly though, the glacial cycles of the Pleistocene and their subsequent effects on salmon and vegetation elicited various evolutionary responses in bald eagles (Chapter VII).

Vegetative Succession

Plant succession is an intermediate-scale phenomenon which affects bald eagles along the northwest coast (Figure 2-3). Disturbance such as glaciation, windthrow, and insect infestation initiate either primary or secondary succession. Recovery, in the absence of further disturbance, can take several hundred years. Newly deglaciated till, for example, is first colonized by a herb/shrub community of Dryas (Dryas drummondii), fireweed (Epilobium sp.), and willow (Salix sp.) (Lawrence 1958). An alder thicket stage follows. Black cottonwood and Sitka spruce eventually emerge through the alder canopy. Western hemlock and Sitka spruce become dominant about 200 years after ice recession and continue to replace themselves on well-drained sites. Muskeg becomes the climax community on poorly-drained locations. In river valleys, periodic flooding often maintains a mid-successional black cottonwood/alder stage.

Salmon Reproductive Cycles

Salmon populations cycle with a periodicity equivalent to their age at reproduction which is 2 to 6 years depending on species (McPhail and Lindsey 1970). Because Pacific salmon generally reproduce only once in a lifetime, different age cohorts are reproductively isolated from each other. Consequently, the size of spawning runs can vary greatly between years. For example, pink salmon mature at two years of age and many streams have large spawning runs only in alternate years.

Seasonal, Monthly and Daily Cycles

On a seasonal scale, weather fluctuations alter food available to eagles. Glacial melting in summer increases river and lake turbidity such that aquatic prey are masked from view. In winter, surface ice blocks eagles access to freshwater fish. Local storms with approximately monthly periodicities cause eagles to adjust their use of habitat within watersheds. On the daily level, day/night cycles and tidal cycles influence prey availability and hunting conditions for eagles.

Landscape Dynamics and Responses of Eagles

The northwest coast, then, is a dynamic landscape where natural disturbances occurs at a hierarchy of scales (Figure 2-3). The time and space domains of the disturbances range from those influencing areas smaller than watersheds on a daily basis to those of continental scale with 100,000 year periodicities. Each level of disturbance differentially influences the food and habitat resources on which

eagles depend. Eagles, in turn, respond to resource dynamics at the individual, population, and evolutionary levels. In Chapter VII, the relationships between environmental dynamics and the ecology and behavior of bald eagles is covered in more detail.

CHAPTER III

GENERAL ECOLOGY

Several descriptive studies have focused on bald eagles and much is known about the natural history of the species. The adaptive significance of most traits, however, remains poorly understood. This chapter lays the groundwork for later discussions of the evolutionary ecology of eagles. First, the general ecology of bald eagles is briefly summarized. Results are presented for descriptive studies of Chilkat eagles and are followed by a discussion of the factors regulating their survival.

SUMMARY OF PRESENT KNOWLEDGE

The bald eagle is a member of the genus Haliaeetus (sea eagles) which is represented by eight species on five continents (Brown and Amadon 1968). The sea eagles are large raptors which inhabit shoreline habitats and forage primarily on fish. Haliaeetus is in the hawk family Accipitridae which is one of five major families of diurnal birds of prey (Order Falconiformes).

The sea eagles are believed to be most closely related to the kites and both may be linked to the Old World vultures (Murphy 1979). Neither the routes by which bald eagles (or their ancestors) emigrated to North America nor the time of arrival are known. Fossil remains indicate, however, that the species was on the continent at least since the late Pleistocene (Howard 1932).

The sea eagles are notable for their size. Adult female bald eagles in southeast Alaska average 5.3 kg and adult males 4.1 kg; wing spans average 223 and 210 cm respectively (Imler 1941). Subadults are slightly lighter in weight than adults (Imler 1941) but have longer feathers; the lengths of the eighth primary, first secondary, and tail feathers are inversely related to age (Bortolotti 1984). The function of reversed sexual size dimorphism in this species is unknown, as are the functions of varying proportions in body weight and feather size.

Bald eagles are striking in coloration. Adults have yellow beaks, brilliant white heads and tails, and chocolate brown bodies and wings. Subadults, in contrast, are drab and variable in color. Plumage types of subadults are probably related to age (Servheen 1975), but rates of plumage maturation are known to vary (Bortolotti 1984). The adult plumage is generally attained at 3-5 years of age. Age when sexual maturity is reached is not clear. Eagles in subadult plumage seldom breed, although cases are known of subadults pairing with an adult and producing eggs (S. Postupalsky pers. comm.). The adaptive significance of plumage variation and delayed maturation remains a mystery.

Bald eagles nest along waterways throughout North America in ecosystems ranging from tundra to desert although their highest densities are in forests. Breeding rates may vary between regions. Sherrod et al. (1977) found virtually all adults on Amchitka Island in western Alaska attempted to breed each year. In contrast, non-breeding adults comprised 16-86% of the adult population throughout southeast Alaska during four years of study (Hansen and Hodges, in press).

Breeding pairs lay 1-3 eggs on a large nest platform, usually built of sticks and lined with grass or moss (Herrick 1934). The incubation period is about 35 d and nestling phase about 12 wk (Herrick 1934). Mean number of young fledging from successful nests ranges from 1.0 to 1.7 (Sprunt et al. 1973). During the nesting season, the birds take many types of live prey and carrion including fish, birds, mammals, reptiles, and crustaceans (Imler 1941, McEwan and Hirth 1980, Grubb and Hensel 1978). Eagles repel intruding conspecifics at nest sites and sometimes defend feeding territories (Mahaffy 1981).

The location and behavior of non-breeding adults and subadults during the breeding season are seldom mentioned in the literature. Gerrard et al. (1978) found that color-marked subadults returned to their natal areas and interspersed among breeding territories. In southeast Alaska during summer, non-breeding eagles either disperse along the coastline or aggregate at food patches (Hansen and Hodges, in press).

Following the breeding season, eagles of all ages move to sites offering good food supplies. These concentrations in fall and winter range from just a few birds up to a maximum of 500-600 eagles observed at Glacier National Park, Montana (McClelland et al. 1982) and the Klamath Basin Oregon (Keister 1981). The types of "food patches" (concentrated food supplies) that attract the birds are diverse. They include salmon spawning grounds (Servheen 1975, Stalmaster et al. 1979, McClelland et al. 1982), waterfowl refuges (Keister 1981), dam sites where fish kills are common (Southern 1963, Steenhof 1976), and areas with high densities of small mammals (Platt 1976). Intraspecific

interactions over food in winter are complex. Food is attained by hunting prey items or stealing from conspecifics. Stalmaster (1981) found pirating is the favored strategy even when food is abundant. He suggested that pirating is adaptive only when food is scarce and is suboptimal at other times. When not feeding, wintering eagles typically either rest at perchs or soar high on thermal air currents. Knight and Knight (1983) proposed that eagles locate potential feeding sites while soaring. At night, the birds often roost communally in stands of dense trees (Swisher 1964, Lish and Lewis 1975). Roosting in forests provides a favorable microclimate (Hansen et al. 1980, Stalmaster 1981) and roosting in groups may result in transfer of information on location of food between eagles (Hansen et al. 1980, Knight and Knight 1983). Radio telemetry studies in the vicinity of the Rocky Mountains have revealed that eagles generally migrate southward to large food patches in winter, and that they return to breeding habitats in early spring (Young 1983).

The factors regulating survival and reproduction in this species are poorly known. Shooting is the leading cause of death of recovered carcasses (Evans 1982) although Stalmaster (1981) and Sherrod et al. (1977) suggested survival is limited primarily by starvation. Chemical toxins and destruction of nesting habitat are thought to limit reproduction (Grier 1982, Evans 1982).

The ecology of bald eagles in the Chilkat and Chilkoot valleys, Alaska was examined from 1979-1983. This work may offer new insights into eagle ecology because (a) the full annual cycle of a population in pristine habitats was studied and (b) birds leaving the Chilkat Valley were tracked so that migratory movements throughout the region were

determined. These studies were sponsored by the National Audubon Society and U.S. Fish and Wildlife Service. The research team included E. L. Boeker, J. I. Hodges, and myself. The migratory movement studies were led by Hodges and their results were reported in more detail in Hodges et al. (ms).

METHODS

Population Dynamics

The numbers and distributions of bald eagles were estimated by ground and aerial surveys. Accessible river sections were surveyed by auto (Figure 3-1). Eagles were counted from 21 observations points spaced such that 90% or more of the river along the survey route could be seen. A much smaller proportion of the mid-Chilkat section was examined, however, because of its inaccessibility. Counts were conducted in mornings at seven day intervals. Observers drove sequentially to each census point and scanned the river. Location by river mile and age class were recorded for each eagle sighted. Birds with predominately white heads and tails were considered adults and all others subadults. Censuses were performed within the following periods: 10/4/79 - 1/26/80; 5/2/80 - 2/8/81; 6/27/81 - 1/23/82; 6/25/82 - 8/5/83. Total eagle use days (EUD) in fall and winter were calculated as follows:

$$EUD = \sum_{i=1}^{n-1} d_i \left(\frac{c_i + c_{i+1}}{2} \right)$$

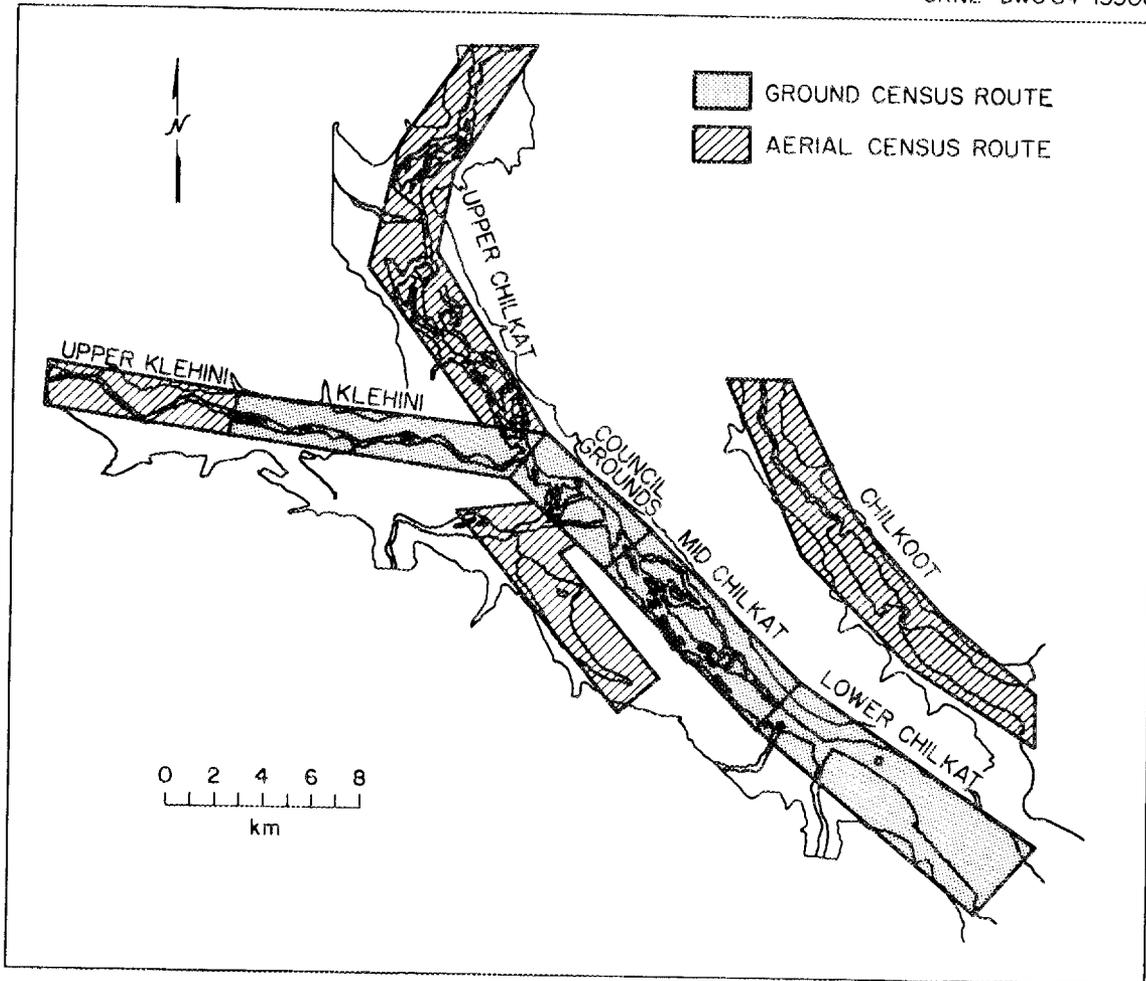


Figure 3-1. Portions of the Chilkat and Chilkoot valleys where eagles were censused from the air or ground.

where d = number of days between count i and $i + 1$; i = count number; n = number of counts; and c = number of eagles seen on a given count (from McClelland et al. 1982).

River sections outside the ground census route were examined from the air in late fall and early winter. When weather permitted, biweekly counts were conducted by two observers flying in a fixed wing aircraft.

To determine the environmental factors influencing population dynamics, wind speed, morning temperature, snow depth, ice coverage of river, precipitation type and amount, and cloud cover were recorded daily in the Council Grounds in fall and winter. Wind speed and temperature were measured with an anemometer and thermograph that were continuously recording. Depth of snow was measured with a meter stick and ice coverage, precipitation, and cloud cover were subjectively determined.

Food abundance was also measured in the Council Grounds in fall and winter. Survey teams walked all river shores in the Council Grounds along which salmon spawned and counted fish judged as available to eagles. Judgment criteria were developed based on observations of feeding eagles. Fish were considered available if they were healthy and in less than 7 cm of water, or were either weakened or dead and in less than 13 cm of water. Carcasses that were frozen and inedible were not tallied. Fourteen fish surveys were done during 12/12/80 - 12/24/80, 11/10/81 - 12/21/81, and 11/10/82 - 02/04/83.

The extent to which eagle numbers varied with environmental conditions and food availability was analyzed with multiple regression.

Habitat Use

Diurnal and nocturnal use of habitat was studied in the Council Grounds during fall and winter. The Council Grounds was subdivided into 53 units which were vegetatively or geographically distinct and less than 2.5 km² in area. The units comprised six habitat types: cottonwood river, cottonwood delta, conifer, gravel bar river, gravel bar delta, and mixed conifer/hardwood (Figure 3-2). The cottonwood type consisted of nearby pure stands of mature black cottonwood trees. The "river" units were located on both shores of the Chilkat River and "delta" units rimmed the western and southern edges of the Tsirku River delta. The silt and gravel islands in the active flood plain that were inundated by river water frequently enough to inhibit the establishment of shrubs or trees were designated gravel bar. "River" units were in the Chilkat River flood plain and "delta" units comprised the expansive Tsirku River delta. Conifer habitats were located on mountain slopes and were dominated by mature Sitka spruce and western hemlock. Stands of paper birch (Betula papyrifera), black cottonwood, Sitka spruce, and western hemlock growing on steep, rocky slopes were designated as mixed habitat type.

The number of eagles in each of the 53 habitat units was counted in the morning at 7-10 d intervals during two periods: 10/15/79 - 02/18/80 and 10/27/80 - 02/09/81. A total of 30 counts were made. These data were analyzed by comparing the relative density of eagles in each habitat type on each survey day. The relative density of birds in each unit was determined by dividing the proportion of each survey

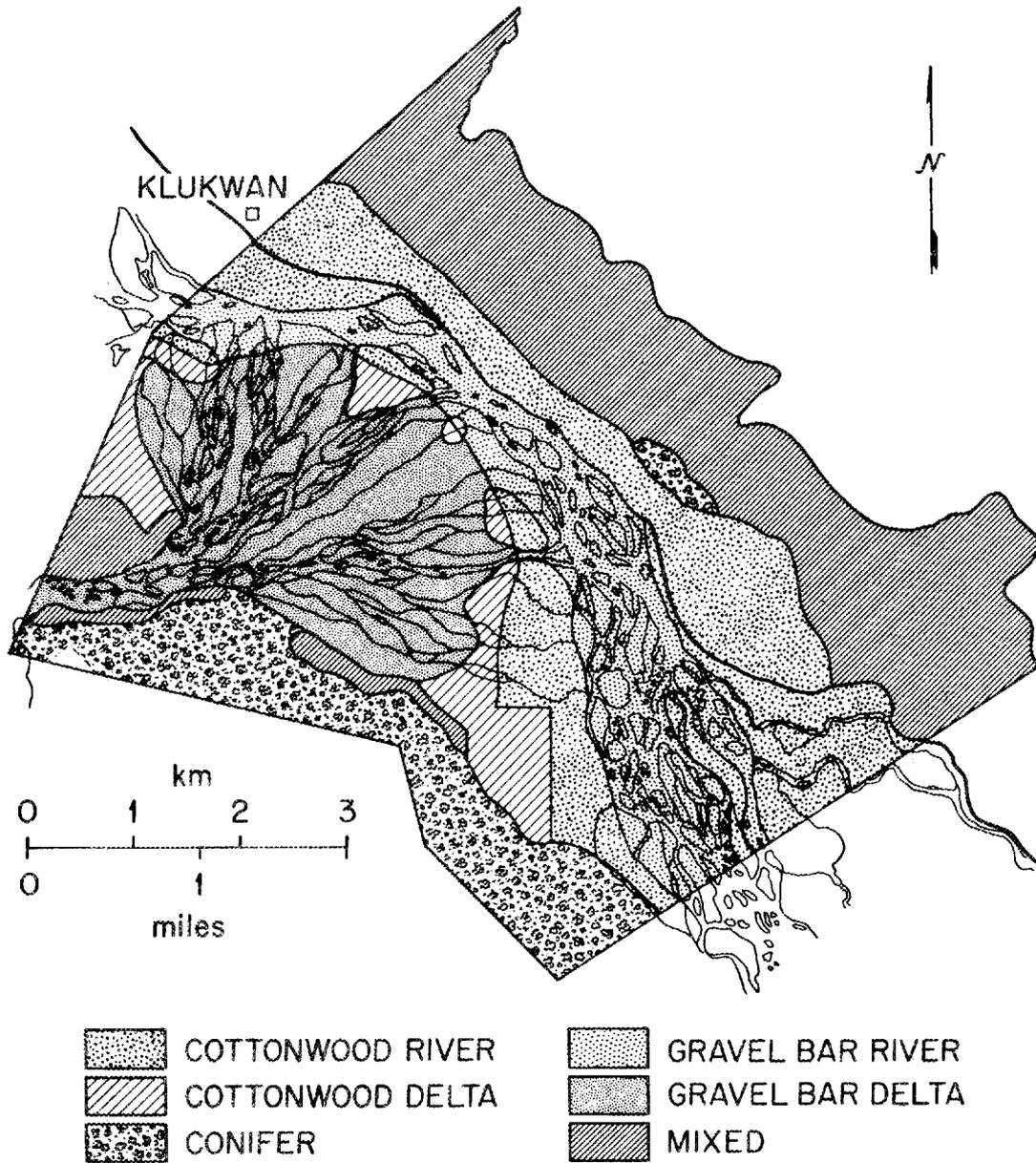


Figure 3-2. Habitat types within the Council Grounds.

total within a unit by the unit's surface area. Relative density was analyzed, rather than absolute density, because the eagle population varied in size by an order of magnitude during fall and winter. Using absolute density would have biased the results toward the habitat use patterns that existed during late November when the eagle population attained maximum size. Relationships between habitat use and environmental conditions were analyzed with multiple regression.

Communal roosts were located by watching the flight patterns of eagles in late afternoon. Once roosts were found, the number of eagles using them was estimated by counting birds entering the roosts at dusk or leaving at dawn. Twelve roost counts were made during fall and winter 1979-80 and 1980-81.

Habitat characteristics of 59 breeding areas were qualified by measuring attributes of nests, nest trees, and the breeding sites. The habitat characteristics of breeding areas along the upper reaches of the Chilkat River were not measured because of their inaccessibility. All breeding areas included in the data set were visually inspected and classified by habitat type (hardwood, conifer, or mixed), timber type (old growth, second growth, or logged area), and land form (riverine, lake-side, intertidal). Degree of human activity at breeding areas was rated as none (no activity within 400 m), low (occasional activity within 200-400 m), moderate (occasional activity within 50-200 m), or high (frequent activity within 50 m). Nest trees were classified by relative age (immature, mature, or decadent), relative tree height (sub-canopy, canopy, or super-canopy), and by species. Nest tree diameter was measured at chest height with a circumference tape. Nest

tree height and nest height were measured with a clinometer. A logger's tape was used to determine the distance from nest tree to the nearest body of water. Finally, the elevation of the base of the nest tree above the nearest body of water was calculated from the distance to water and the slope between the base of the nest tree and the nearest shoreline.

Food Sources

The species and condition of prey consumed by the bird were assessed by (a) identifying food remains collected in nests or on the ground below them, (b) watching eagles eating at nests, and (c) by flushing eagles feeding on river bars and examining the prey left behind.

Productivity

Eagle nests were located and mapped during aerial and ground searches of all likely habitats in the study area. Nest status was determined by surveys from an airplane. Flights were made each year soon after the start of incubation in early May and just prior to fledging in late August. Nests were assigned to breeding areas based on the distribution of breeding eagles over all years of study. Terminology for reproductive parameters follows Postupalsky (1974).

Movements

Twenty-eight bald eagles were captured in the Chilkat Valley and equipped with radio transmitters. The trapping devices included padded

steel traps (Young 1983), perch snares (modified from those described by Robards 1966), and snares attached to floating fish. Three nestlings (10-12 weeks of age) were also fixed with radio transmitters. A sealed transmitter weighing 55 g and having a 10-15 month operational life was fitted to each bird with a backpack harness. A link in the attachment was designed to eventually deteriorate and allow the harness to fall from the bird.

Movements of radio-tagged eagles were monitored within the study area with hand-held receivers. After departing the Chilkat Valley the radio-tagged birds were located by aircraft on monthly reconnaissance flights over southeast Alaska. Once each spring a flight was also made over the coasts of British Columbia and northern Washington. The range of reception of the telemetry gear was about 8 km when the receiver was on the ground and 30-120 km when the receiver was in an airplane at the survey altitude of 2,400 m.

RESULTS

Population Dynamics

The number of eagles in the study area varied greatly between seasons, but annual trends were similar (Figure 3-3). The early spring population of 100-200 birds included both breeders and nonbreeders. Population size typically swelled to about 500 during the run of the smelt-like eulachon in late spring as non-breeders and subadults from elsewhere entered the valley and then remained below 200 throughout summer. Beginning in September and continuing through late autumn, thousands of eagles flew into the Chilkat Valley. Annual population

BALD EAGLE POPULATION SIZE IN THE CHILKAT VALLEY, ALASKA.

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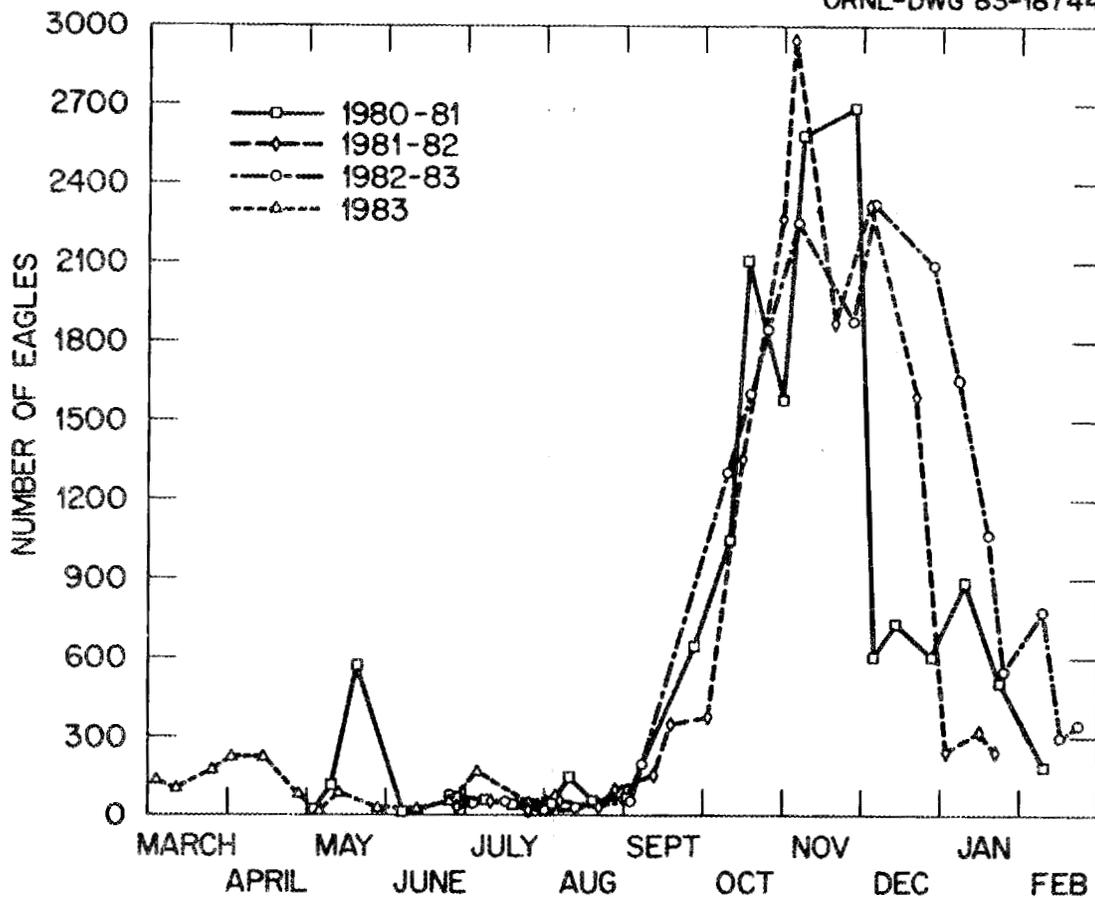


Figure 3-3. Fluctuations in the size of the Chilkat eagle population as determined by ground censuses.

peaks, as determined by combined aerial and ground census results, varied from 3126 to 3664 birds (Table 3-1). Eagle numbers rapidly declined in December when frigid temperatures and ice formation caused food to become less available. Generally, 300 to 900 eagles remained through January and foraged in the spring-fed river channels which remained ice free. Annual population peaks were relatively consistent but the total eagle use days in fall and winter varied nearly two-fold between years (Table 3-1).

The size of the eagle population in the Council Grounds in fall and winter was most closely correlated with salmon availability. A multiple linear regression model with fish abundance (FISH), ambient temperature at dawn (TEMP) and proportion of river surface that was ice covered (ICE) as independent variables was analyzed on the 13 dates when all variables were quantified. The results were FISH ($F = 0.89$, $p > 0.37$), TEMP ($F = 0.37$, $p = 0.56$) and ICE ($F = 0.27$, $p > 0.62$). FISH was then used as the sole independent variable regression model with a second degree polynomial function and a significant correlation was found between number of eagles and FISH ($n = 14$, $r^2 = 0.70$, $p < 0.001$) (Figure 3-4). The number of eagles in the Council Grounds increased with fish abundance until about 1,400 carcasses were available. These results suggest that when food abundance is greater than a threshold level, it no longer limits eagle population size in the Council Grounds. The downward turn in the relationship at higher levels of fish abundant may be a function of date. The highest fish count occurred in mid-January, 1983. Most eagles had already migrated south by that time.

Table 3-1. Number of eagles use days from September through January as determined by ground censuses, and peak counts in the study area during the winters of 1979-80 to 1982-83.

Year	Eagle Use Days ¹	Peak counts ²
1979-80	126,407	3439
1980-81	161,064	3214
1981-82	175,085	3126
1982-83	220,634	3664

¹Eagle use days were calculated as follows:

$$EUD = \sum_{i=1}^{n-1} d_i \left(\frac{c_i + c_{i+1}}{2} \right)$$

where d = number of days between count i and i + 1; i = count number; n = number of counts; and c = number of eagles seen on a given count (from McClelland et al. 1982).

²Data are totals from river sections covered exclusively by aerial censuses plus totals from ground counts. Ground counts were done 0-3 days before or after aerial counts.

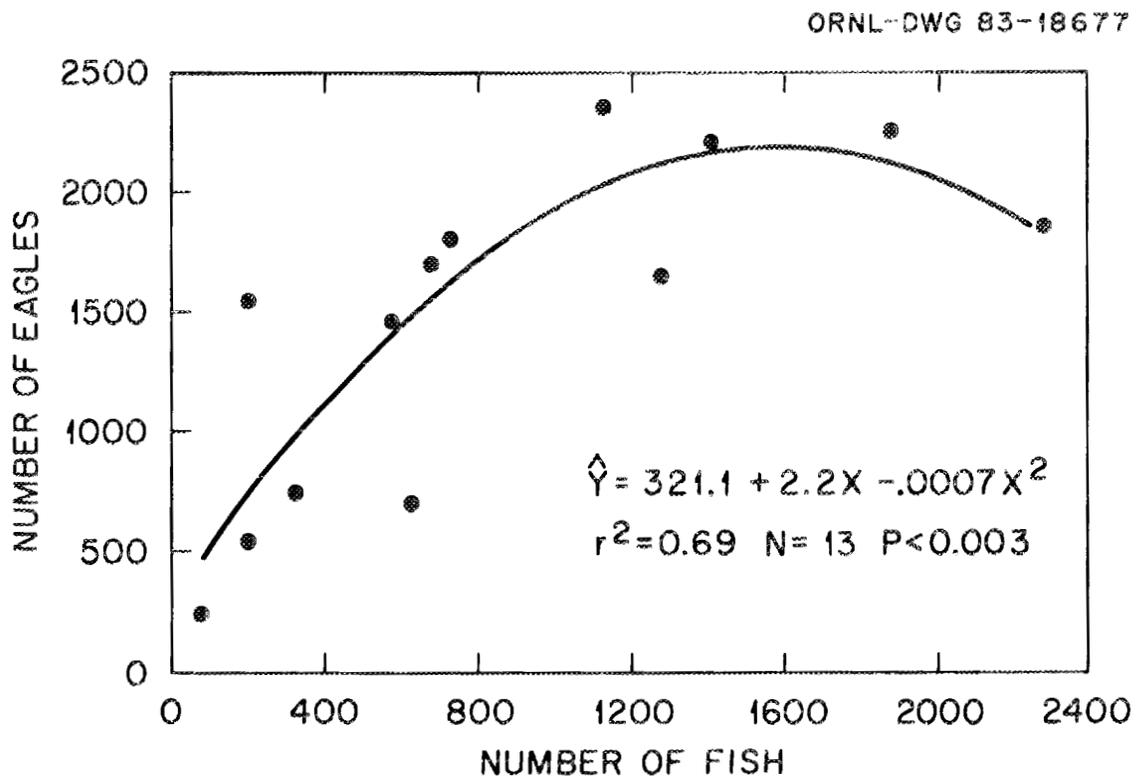


Figure 3-4. Relationship between food availability and eagle numbers in the Council Grounds.

Distribution of eagles within the river sections covered by ground censuses also appeared to be strongly influenced by food. This relationship was only qualitatively determined, however. During spring the birds aggregated both at the Council Grounds, where salmon carcasses frozen in river ice in winter thawed and became available, and at eulachon spawning grounds on the lower Chilkat River (Figure 3-5). In summer, the Tsirku River Delta was the site of most eagle activity (Figure 3-6). Sockeye salmon en route to Chilkat Lake were more easily captured in the shallow channels of the delta than elsewhere. In fall, eagles concentrated along the Klehini River to feed on the early run of chum salmon (Figure 3-7) and thereafter, the birds shifted to the Council Grounds to feed upon late-spawning chums (Figure 3-8).

Subadults comprised 15 to 40% of the population. The subadult proportion was lowest in late winter and late spring, most variable in summer, and highest in early fall (Figure 3-9). During the autumn population build-up, subadults arrived earlier on average than adults. Most subadults were in the valley by October and their numbers did not increase thereafter ($n = 25$, $r^2 = 0.001$, $p < 0.87$). In contrast, the adult population increased through November ($n = 25$, $r^2 = 0.17$, $p < 0.04$). Presumably, the late arriving adults had remained at breeding areas until mid-fall.

Food Sources

Chilkat eagles were opportunistic foragers. Although they preferred to scavenge, live prey were taken when carrion was not available. During fall and winter the birds fed primarily on dead or

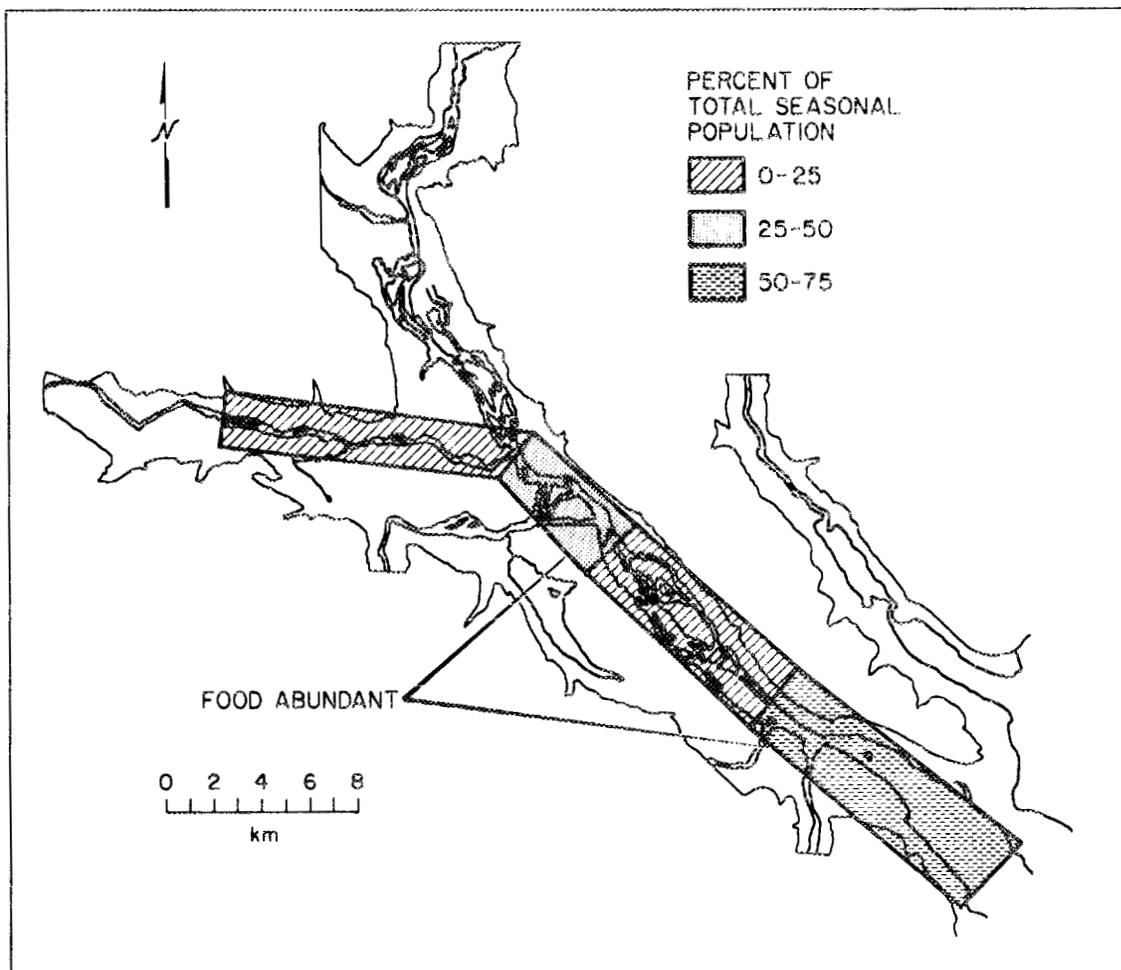


Figure 3-5. Distribution of bald eagles within portions of the study area during spring (5/1-6/21) 1980 and 1983.

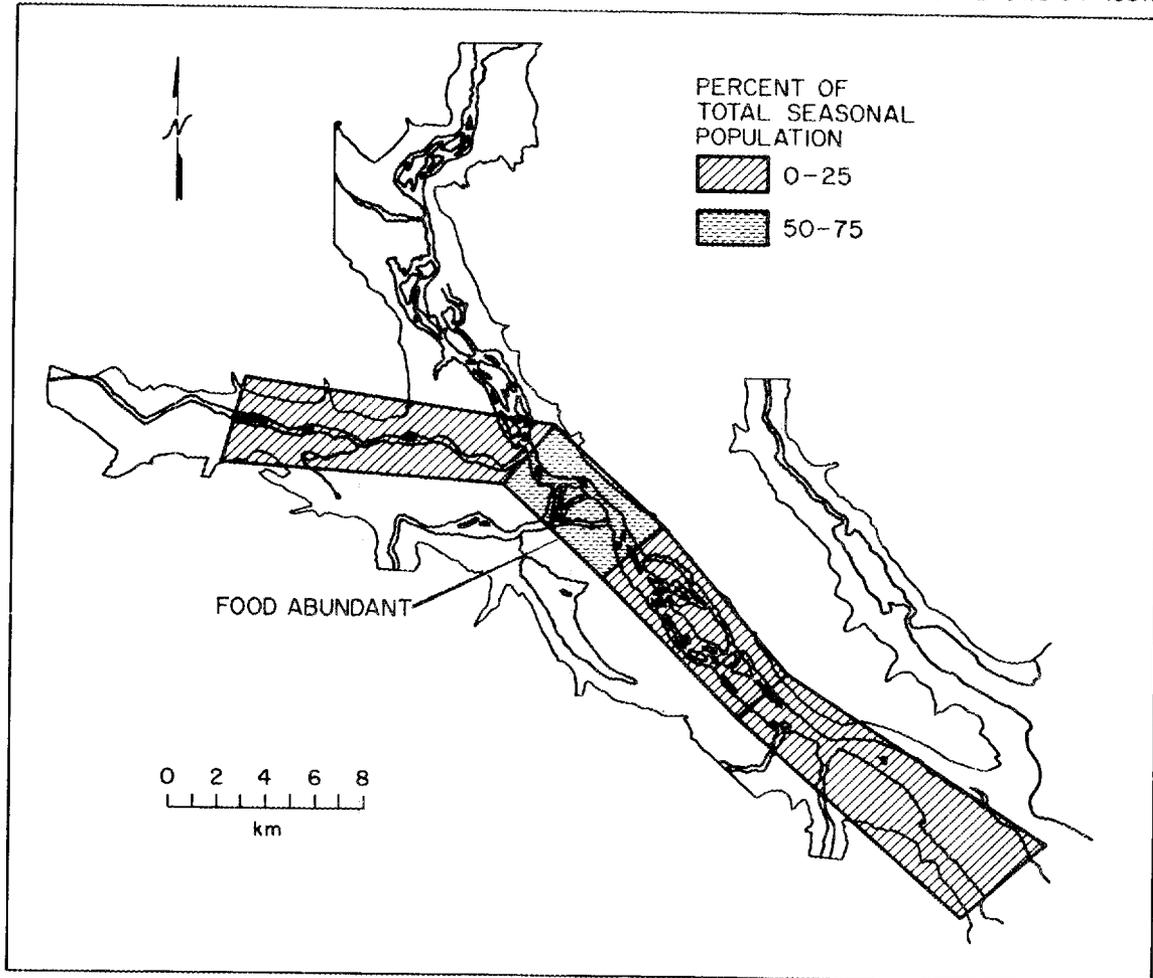


Figure 3-6. Distribution of bald eagles within portions of the study area during summer (6/22-8/31) 1980-1983.

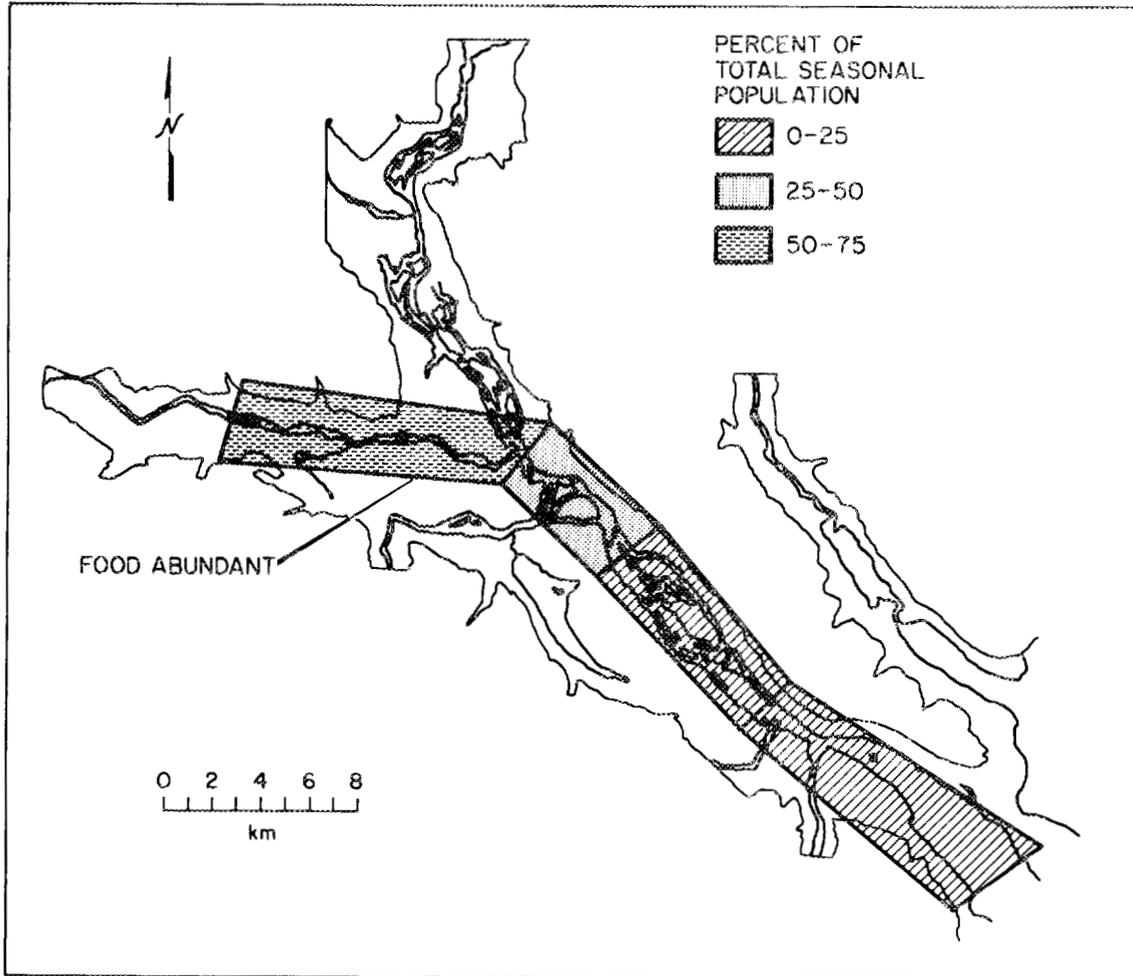


Figure 3-7. Distribution of bald eagles within portions of the study area during autumn (9/1-10/20) 1980-83.

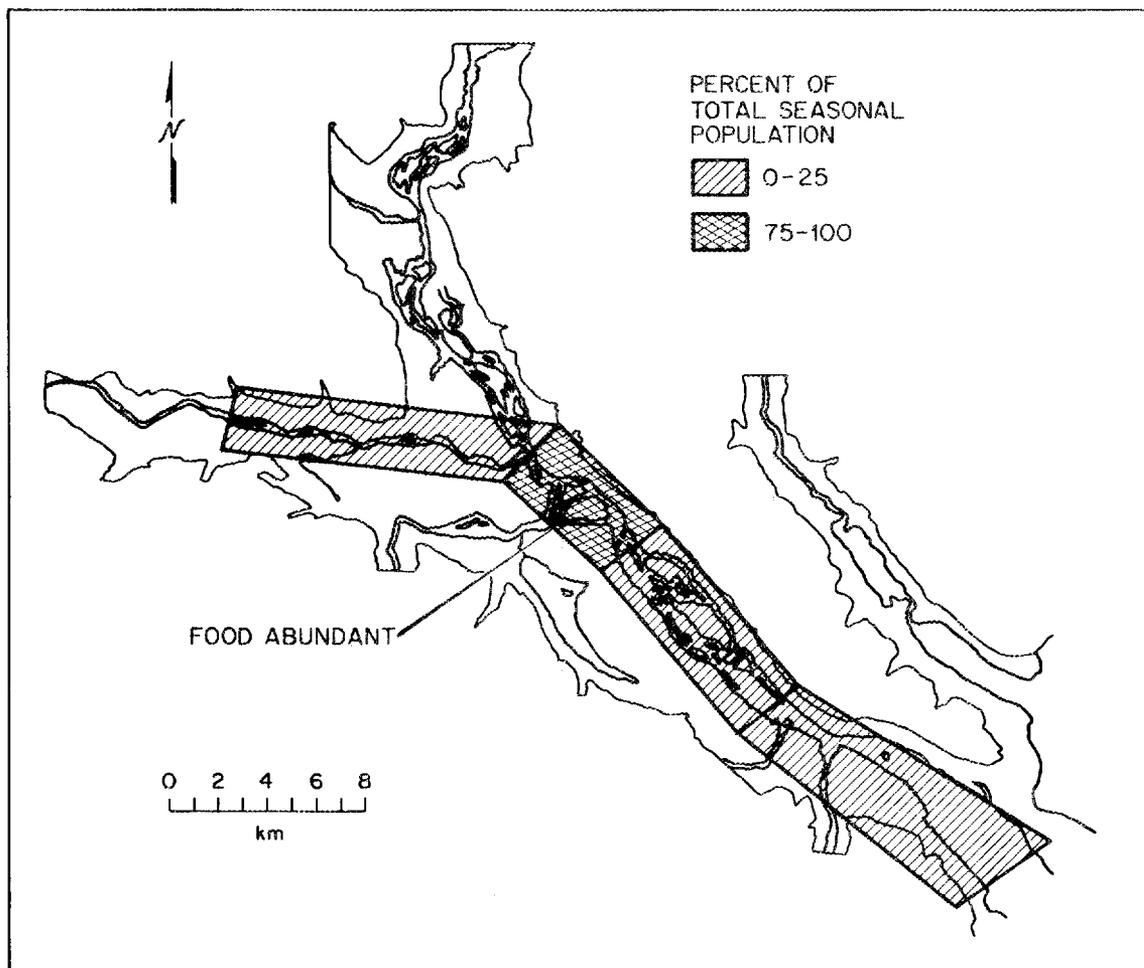


Figure 3-8. Distribution of bald eagles within portions of the study area during winter (10/21-2/28) 1980-83.

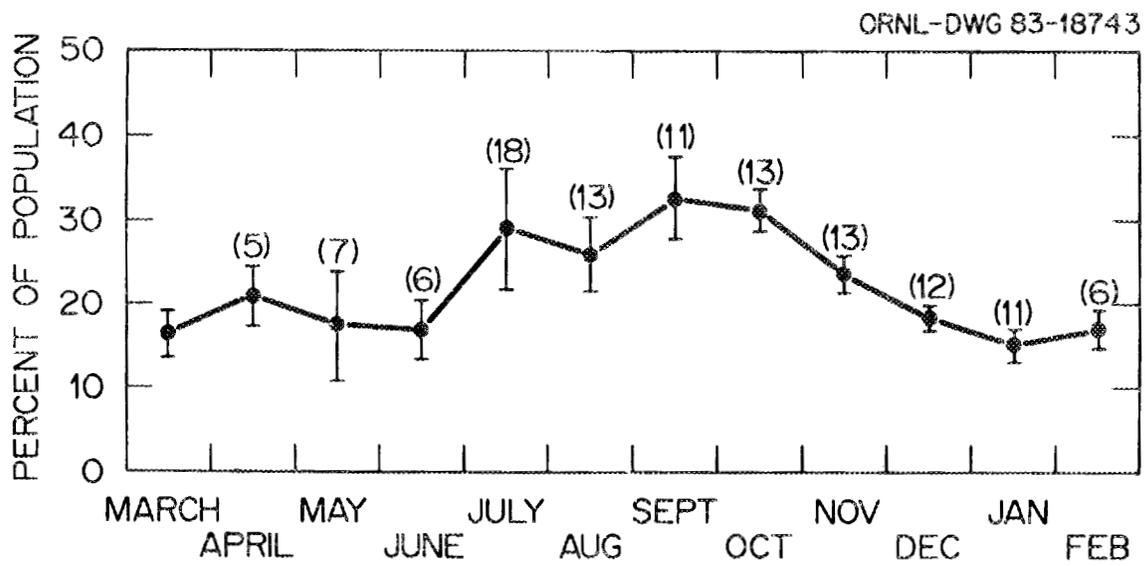


Figure 3-9. Proportion of the population comprised by subadults. Data shown are monthly means and standard deviations from 5/80-8/83.

nearly dead salmon that had completed spawning. Inspection of 37 chum salmon taken by eagles revealed that all of the fish had completed spawning prior to capture. Thirty-two of the fish had been taken after dying naturally while the remaining five had been captured in a live but weakened condition. In summer, when salmon were present but not yet spawning, both healthy fish and fish killed by bears or wolves were preyed upon by eagles.

The diets of nesting eagles appeared to be much more variable than those of nonbreeders. Breeders commonly took waterfowl, resident fish and snowshoe hares (Lepus americanus). Mammalian carrion were also occasionally consumed.

Daily Activity

Fall and Winter

Eagles generally flew from roosts to the feeding grounds at dawn. Some perched in streamside trees or on gravel bars while others foraged (feeding behavior is described in Chapter IV). Upon reaching apparent satiation, the birds usually took a perch and rested. Each bird probably fed to satiation once or twice each day. Feeding times were staggered and birds were present at food patches during all daylight hours. The densities of eagles in streamside trees and on gravel bars were extreme at times; over 1500 occasionally gathered in a one km section of streamside trees, and densities on gravel bars sometimes exceeded 325 per km².

When thermals formed, eagles often left the feeding grounds to soar. Masses of soaring eagles commonly ascended to such heights

that they could not be seen with 10 power binoculars. One of the most impressive sights we on the research team witnessed was when a high pressure air mass abruptly moved over the Council Grounds in mid-morning. Within minutes, over 1000 eagles left the river bars, flew with labored wing beats to the bases of the newly formed thermals and slowly soared in upward spirals out of sight. Much social interaction including chasing flights and aerial talon-locking generally occurs during these mass aerial displays.

In late afternoon, many birds flew from feeding grounds to night roosts. Some eagles roosted singly, but most roosted communally. Roosting aggregations of 200-300 birds were common.

Spring and Summer

The activity patterns of subadults and non-breeding adults gathered at food patches in spring and summer was not recognizably different from the patterns of eagles in fall and winter.

Breeding eagles usually repelled conspecific intruders that entered the air space above their nests and many also defended feeding territories surrounding the nests. This behavior, however, appeared to be flexible; it was practiced under some food regimes but abandoned under others. Breeders did not confine themselves to their feeding territories. They commonly joined non-breeders that were foraging outside of occupied territories.

The three radio-tagged nestlings left their breeding areas one to two weeks after fledgling and joined flocks of non-breeders. Adults in the Chilkat Valley also abandoned their breeding areas in fall and winter.

Habitat Use

Fall and Winter

Eagles were unevenly dispersed among the habitat types within the Council Grounds. Eagle density in habitats adjacent to foraging sites was about 10 times higher than in those disjoint from food (Figure 3-1 and Table 3-2). Among the habitats near feeding grounds, eagle densities were greatest in streamside cottonwood stands. Eagles hunted, rested, and avoided predation while in the cottonwoods. Gravel bars near food were sites of active feeding or loafing by eagles. The relative use of these two habitat types varied with ambient temperature; as temperature dropped, eagle density in gravel bars decreased ($n = 26$, $r^2 = 0.47$, $p < 0.0001$). Among habitats disjoint from food, eagle densities were greatest in cottonwoods, intermediate in conifers and on gravel bars, and least in mixed coniferous and deciduous stands (Table 3-2). Conifer stands, although quite far from the feeding grounds, received substantial use during winter storms and when human disturbance was occurring at feeding grounds.

At night eagles occupied cottonwoods or conifer stands. Roosting on gravel bars or in mixed stands was rarely observed although on moonlit nights some eagles were occasionally seen feeding on gravel bars. In early fall, many birds roosted in streamside cottonwood stands. By mid-fall, however, most eagles had shifted to roosting in conifer trees on a ridge southwest of the river. Two sites in particular within the conifer forest were used regularly throughout the four winters of study. Typically, 100 to 200 (though occasionally 500)

Table 3-2. Diurnal use of habitat by bald eagles in the Council Grounds during fall and winter 1979-80 and 1980-81.

Classification of habitat	Relative density of eagles ¹ (x ± S.D.)
<u>Within or adjacent to feedings grounds</u>	
All types	0.11 ± 0.01
Gravel bar river	0.06 ± 0.02
Cottonwood river	0.10 ± 0.03
Cottonwood east of river	0.04 ± 0.03
Cottonwood west of river	0.18 ± 0.04
<u>Disjoint from feeding grounds</u>	
All types	0.01 ± 0.01
Gravel bar delta	0.02 ± 0.02
Cottonwood delta	0.04 ± 0.05
Mixed	0.01 ± 0.01
Conifer	0.02 ± 0.02

¹Relative density of eagles = $\frac{\text{percent of survey total in habitat type}}{\text{area of habitat type (ha)}}$.

eagles per night were counted either entering or leaving each communal roost. On some nights, up to 22% of the Council Grounds population was found in a single roost. The communal roosts were located in stands of Sitka spruce and western hemlock which were topographically shielded from wind.

Nesting Habitat

Nests were generally located in old growth stands of cottonwood or spruce trees near water (Table 3-3). Nest trees were typically tall, mature, and healthy. Human activity was minimal near most nests.

Productivity

Approximately 89 breeding areas were distributed over the study area at an average density of 0.38 per km (Figure 3-10). Sixty-two of the territories were thought to include 1 nest, 25 had 2 nests, and 2 had 3 nests.

Breeding pairs generally returned to nests in late February or March. In 1983, 53% of the eggs were laid before 4/30, 44% between 5/1 and 5/15, and 3% thereafter. Matching occurred in late May and early June. By mid-September, most eaglets had fledged.

Productivity in the study area was surprisingly variable among years (Table 3-4). The percent of territories active each spring varied from 32 to 60% and the number of fledglings ranged from 5 to 38. Large differences were also found between river sections. Reproduction was consistently high in estuary habitats, intermediate but variable at the Council Grounds and Chilkat Lake, and relatively low along the Klehini and Chilkat Rivers (Figure 3-11).

Table 3-3. Habitat characteristics of 59 breeding areas. Data are frequencies or means and standard deviations.

NEST SITE					
Habitat type		Timber type		Land form	
Hardwood	0.69	Old growth	0.97	Riverine	0.76
Conifer	0.08	Second growth	0.00	Lake-side	0.15
Mixed	0.22	Logged area	0.03	Intertidal	0.08
Human disturbance					
None (no activity within 400 m)				0.51	
Low (occasional activity within 200-400 m)				0.14	
Moderate (occasional activity within 50-200 m)				0.22	
High (frequent activity within 50 m)				0.14	
NEST TREE					
Species		Age		Relative height	
Black cottonwood	0.88	Immature	0.00	Sub-canopy	0.00
Sitka spruce	0.12	Mature	0.71	Canopy	0.78
Western hemlock	0.00	Decadent	0.29	Super-canopy	0.22
<u>Height</u> 30 ± 7.7 m		<u>Diameter</u> 99 ± 25 cm		<u>Nest height</u> 23 ± 6 m	
<u>Distance to water</u> 75 ± 85 m		<u>Base elevation above high water</u> 11 ± 23 m			

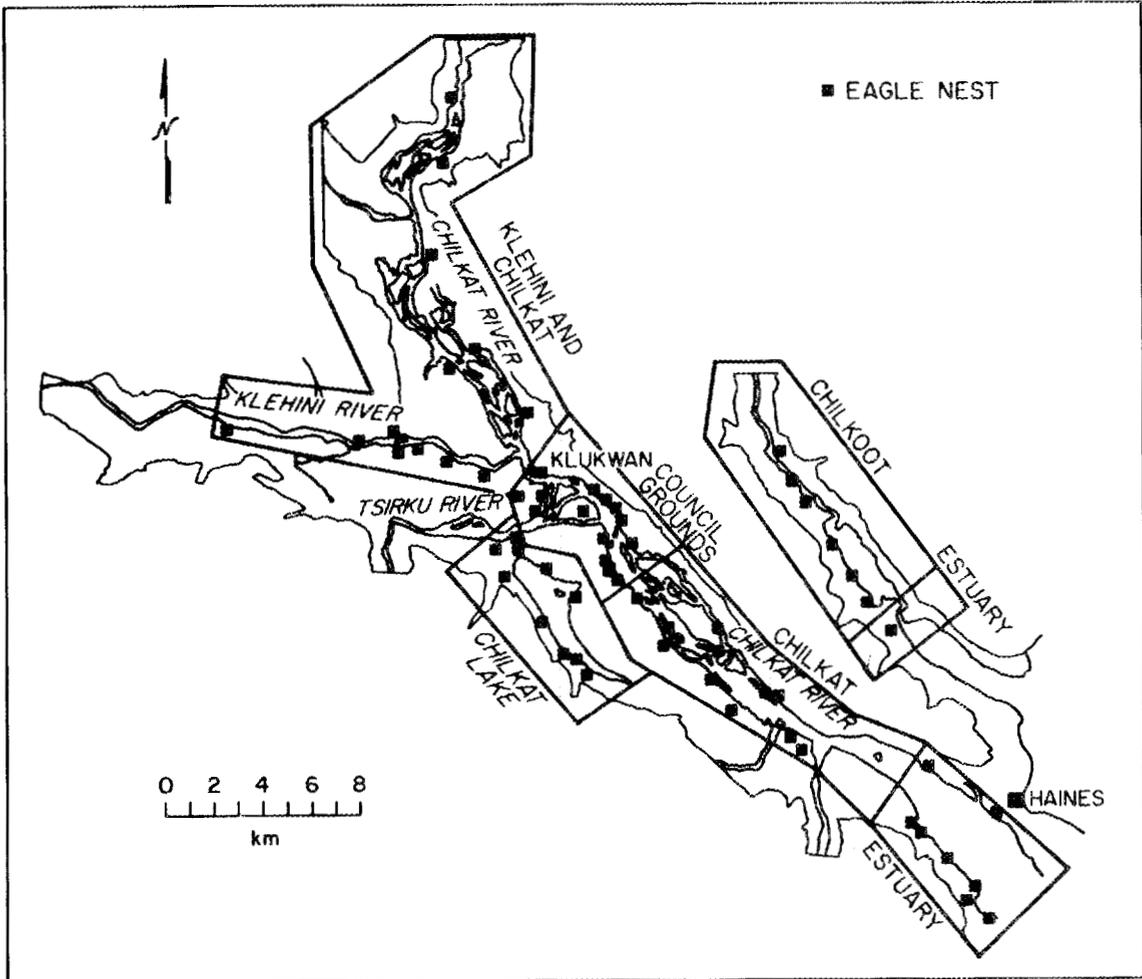


Figure 3-10. Bald eagle breeding territories and nesting habitat subunits.

Table 3-4. Annual productivity of bald eagles in the study area.

Year	<u>Breeding areas</u>	<u>Active</u> ¹		<u>Successful</u> ²		<u>Young</u>	
	No.	No.	%	No.	% ³	Per succ. nest	Total
1979	64	31	48	-	-	-	-
1980	82	26	32	4	15	1.25	5
1981	72	31	43	10	32	1.30	13
1982	73	41	56	25	61	1.52	38
1983	77	46	60	9	20	1.22	11
Mean	76	35	46	12	32	1.32	17

¹Active - One or two adults on nest during aerial survey in May.

²Successful - Nest with young in mid-August.

³% Successful - No. successful nest/no. active nests.

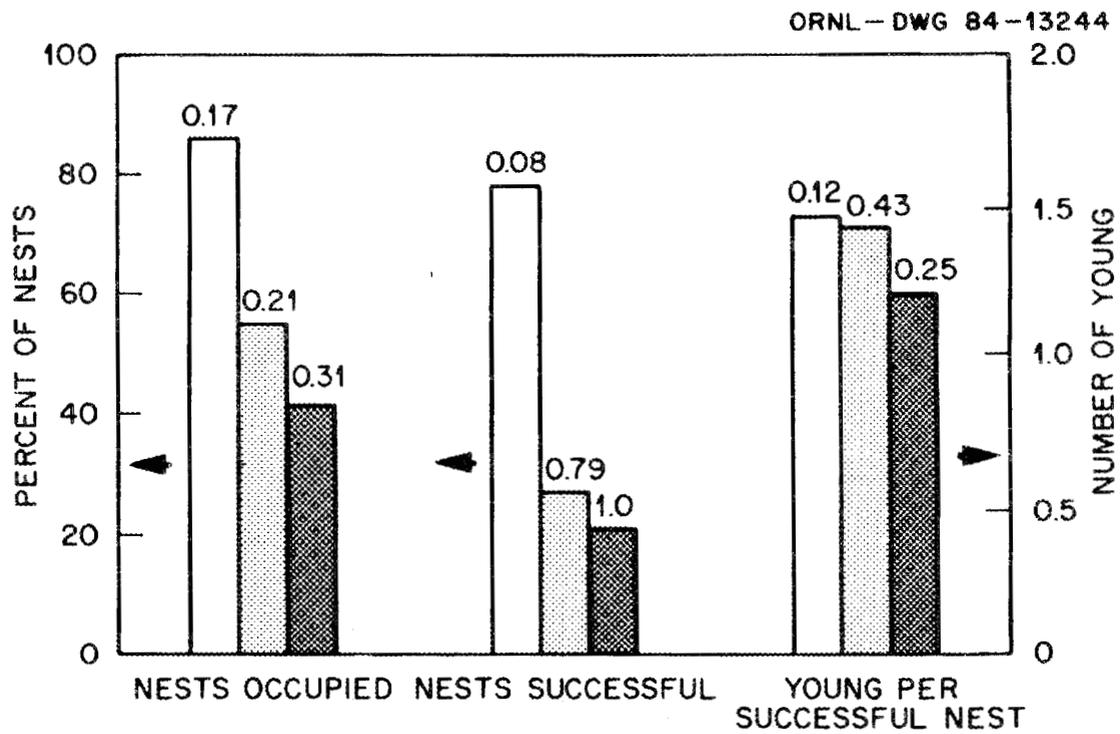


Figure 3-11. Variation in three reproductive parameters among sections of the study area over four breeding seasons (1980-83). Coefficients of variation are shown on top of each bar.

Movements

Local

Eagles radio-tagged in the study area generally remained there at least until food became limiting. The minimum length of stay for eagles after being radio-equipped was 50 days on average. Movements between sections of the study area were relatively infrequent; birds were recorded in a new river section only once every 17 days on average.

Migratory

The 15 subadults with radios scattered southward along the northeast coast as far as Washington after leaving the study area in fall or winter (Figure 3-12). The southernmost record was for a bird that departed the Chilkat River on November 29 and was recovered 57 days later on the southwest coast of Washington (1500 km distant). In 1982, an estimated 73% of the subadults moved south of Alaska by the end of April while the others stayed in southeast Alaska throughout summer.

Movement patterns of adults were different from those of the younger birds. The adults generally remained in northern southeast Alaska, less than 320 km south of the Chilkat Valley (Figure 3-13). Two adults were recorded at the Stikine River in May where several hundred eagles fed on spawning eulachon. The movement patterns of adults in spring and summer do not suggest that these birds engaged in breeding.

Two of the 15 subadults and 4 of 16 adults marked in the Chilkat Valley were relocated in the valley the following autumn. The actual return rates were probably higher because transmitters may have failed, lost power, or detached from birds.

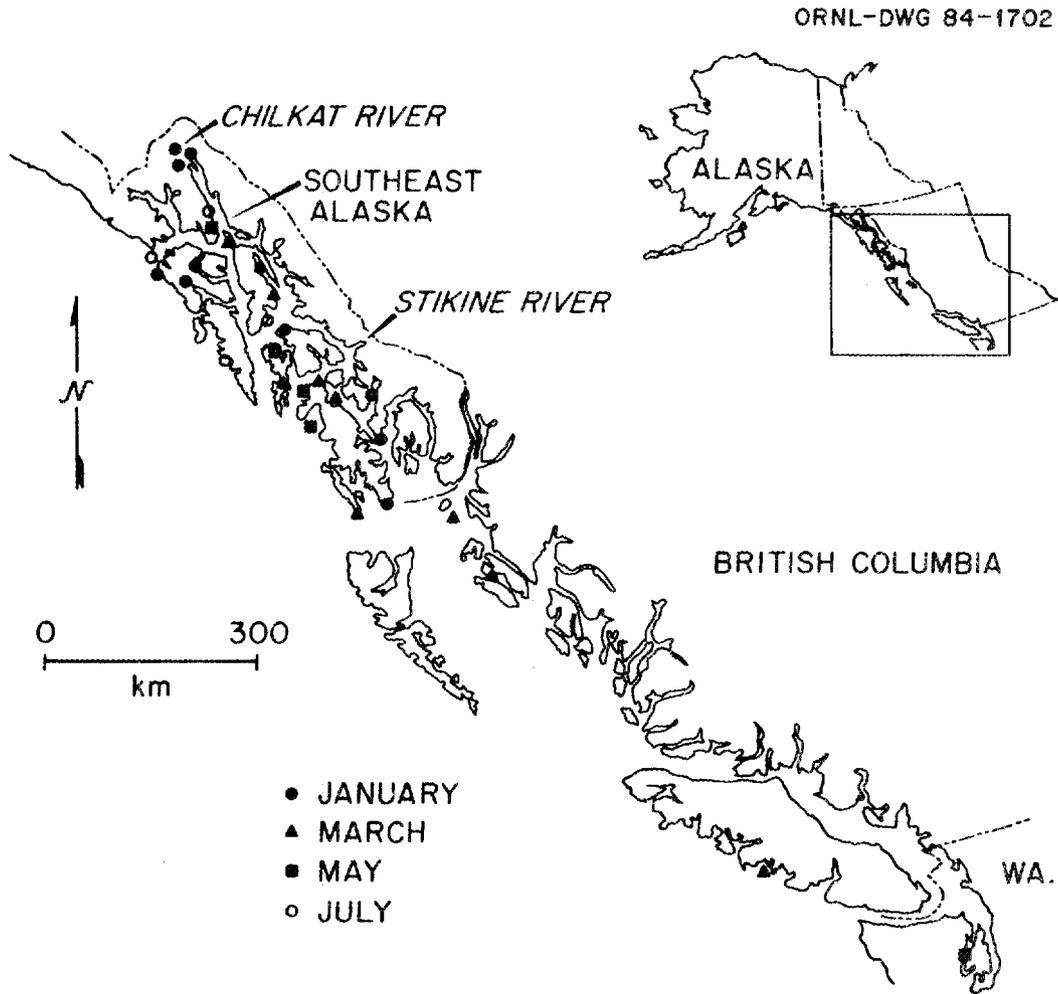


Figure 3-12. Relocation points of subadults that were radio tagged on the Chilkat River in late fall and early winter in 1979-82. Some points represent more than one relocation for a single individual (from Hodges et al. ms).

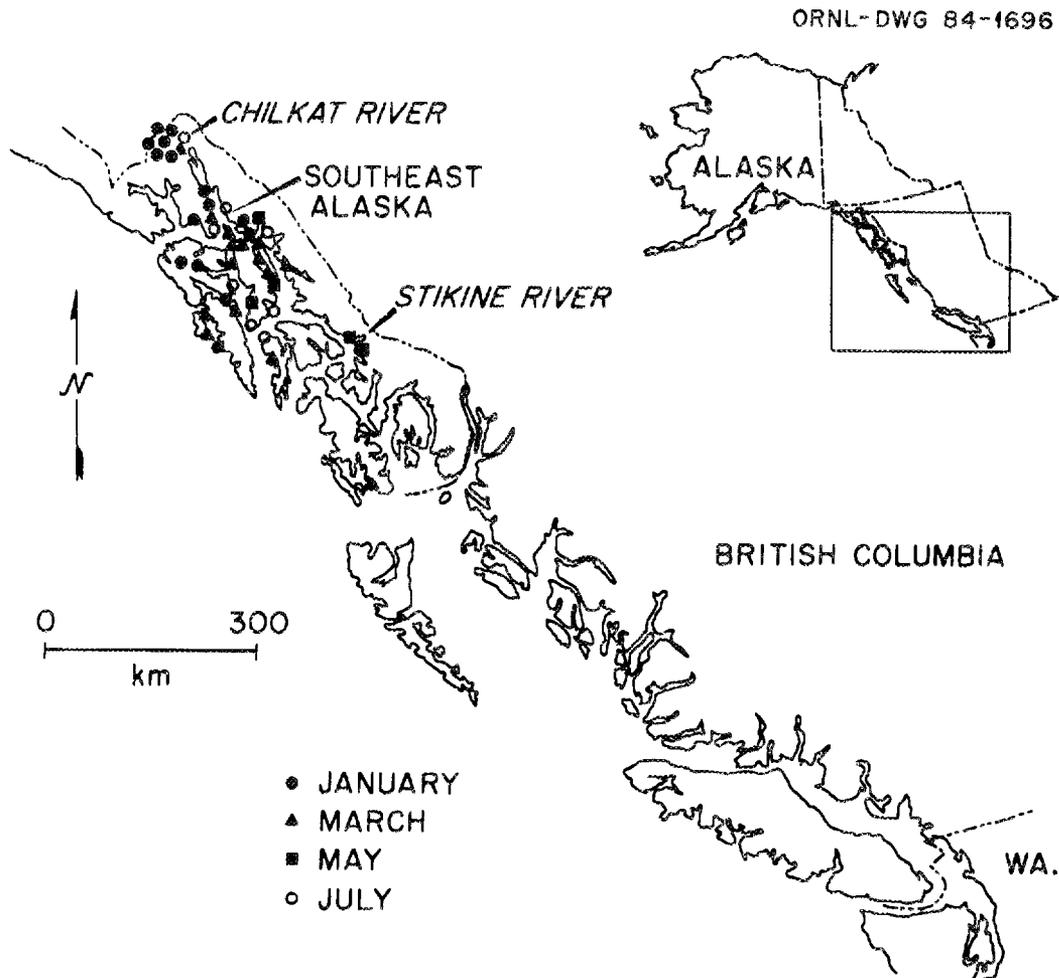


Figure 3-13. Relocation points of adults that were radio tagged on the Chilkat River in late fall and early winter in 1979-82. Some points represent more than one relocation for a single individual (from Hodges et al. ms).

DISCUSSION

Influence of Food on Bald Eagle Ecology

The thread that interconnects virtually all aspects of bald eagle ecology is the bird's relentless pursuit of food. The distribution of eagles within the study area shifted primarily in response to changing food availability. Similarly, the total number of eagles in the study area in fall and winter was correlated up to a threshold with abundance of salmon carcasses. The existence of a threshold suggests either (a) food levels in the Chilkat Valley at times exceeded the amount needed to attract all potential immigrants from elsewhere in the immediate region or (b) density dependent mechanisms prevented the population at the food patch from exceeding a certain maximal level regardless of food abundance. Elsewhere along the northwest coast the relationship between food abundance and the size of fall and winter eagle aggregations was strong enough for an energetics model to accurately predict population size as a function of food levels and weather conditions (Stalmaster 1983).

Migratory movements also show the eagle's affinity for food patches. Radio-tagged birds leaving the Chilkat in winter headed south. Subadults flew as far as British Columbia and Washington where salmon were still spawning and weather conditions were less harsh. When food levels improved in southeast Alaska in spring and summer, some of the subadults returned north.

Radio-tagged adults flew about 200 km south from the Chilkat and remained in central and southern southeast Alaska during spring and

summer. Some of them joined feeding aggregations while others dispersed along the shoreline. These adults presumably stayed in southeast Alaska to acquire breeding territories; however, none were apparently successful. Subadults in contrast, not constrained by breeding, were able to move great distances in search of food.

Young (1983) also found that eagles made broadscale migratory movements in search of food. Birds radio-tagged in northwest Montana in fall moved south and wintered in Idaho, Wyoming, Oregon, Utah, and Nevada. In spring they returned to Montana and then continued north. Some adults eventually flew to nest sites in northern Alberta and the Northwest Territories. The birds ate a variety of prey types while migrating. They foraged both singly and in groups.

For non-breeding adults and subadults, movements between ephemeral food patches continues year around. In southeast Alaska, non-breeders are often dispersed along the shoreline between active breeding areas (pers obs) and there is a possibility that nesting adults and non-breeders strongly compete for food.

Energy Conservation and Habitat

The way eagles use habitat is further evidence of the ecological importance of food stress. Trees are used as hunting perches so they aid in food procurement. They also serve to minimize energy expended in thermoregulation. Stalmaster (1981) found in Washington that ambient temperature, wind speed, long-wave radiation, and rainfall conditions are all most stressful to eagles on gravel bars, intermediate to eagles perched in deciduous habitat, and least stressful to eagles

in conifers. Further, he calculated that eagles saved 6% of their daily energy budget by roosting in conifers rather than in deciduous trees. In the Chilkat Valley, eagles maximized time spent in protected habitats when weather was harsh. At feeding grounds they used gravel bars less and cottonwoods more as temperature dropped. They also moved to conifers during storms and at night.

Communal Roosting

Eagles may gather at roosts not only because they provide favorable microclimates, but also to improve chances of finding food (Hansen et al. 1980, Stalmaster 1981, Knight and Knight 1983). According to the Information Center Hypothesis (Ward and Zahavi 1973) birds may breed in colonies or roost communally to acquire knowledge of the location of food. Hungry birds are thought to identify roost mates that had fed earlier that day, and the next morning follow the successful foragers to food patches. In support of this hypothesis, Knight and Knight (1983) showed that eagles often followed others when departing from or arriving at communal roosts. Moreover, following was most frequent when food was scarce.

Regulation of Survival

The fact that eagles move in relation to changing food supplies, spend much time foraging or trying to learn of new food patches by perhaps soaring and roosting communally, have elaborate feeding behavior (Chapter IV), and use habitat to conserve energy, all suggest that survival has been limited over evolutionary time by food stress.

On Amchitka Island, Alaska, Sherrod et al. (1977) estimated a 90% mortality rate for eagles prior to reaching maturity and suggested starvation was the primary cause. Each year in the Chilkat Valley, approximately 2-5 emaciated eagles are found. Some have no visible injuries and recover after captive feeding. Others suffer wing injuries due presumably to gunshot wounds, fights with conspecifics, or collisions with branches.

Predation may also be a selective force in eagle evolution. Although eagles are exceedingly effective in self defense, it is possible that they are occasionally caught off guard and killed by wolves, lynx (Lynx canadensis), or bears. The birds are very wary around these animals and usually avoid perching on the ground at night when visibility is poor. The possibility that prehistoric man commonly killed bald eagles for feathers and body parts cannot be ruled out.

In bald eagles survival is probably limited primarily by energy stress and perhaps by natural predation or persecution by man. Also of interest are the factors regulating reproduction. I provide evidence in Chapter V that food also limits breeding. Chapter VII explores the adaptations and strategies bald eagles use for coping with food shortage.

The Chilkat Valley: Normal or Anomalous?

These studies show the Chilkat Valley to be one of the most fascinating and important units of sea eagle habitat yet described. Not only does it support breeding and non-breeding eagles year around, it also provides a very large food supply in fall in winter when

little food is available elsewhere. This food supply attracts over 3,000 eagles -- undoubtedly one of the greatest concentrations of raptors in the world.

The behavior of Chilkat eagles, however, is not anomalous. During most of the year, eagle density is no higher there than many other places in the region. Furthermore, the habits of birds at the large fall and winter gathering are not perceivably different from those of eagles further south along the coast (as described by Servheen 1975, Hansen et al. 1980, Stalmaster 1981, and Knight and Knight 1983). Finally, the movement studies show that the Chilkat eagles are not an isolated population, rather they are a fluid subset of the regional population.

CHAPTER IV

FORAGING BEHAVIOR: HUNTERS, PIRATES, AND
EVOLUTIONARILY STABLE STRATEGIES

Naturalists have long commented on the bald eagle's proclivity for robbing food from conspecifics and from weaker birds like gulls and crows. Ben Franklin thought the practice so cowardly that he campaigned against the eagle's placement on the seal of the new United States.

More recently, scientific inquiries into eagle foraging behavior have failed to ascertain why pirating is common even when food is abundant. In western Washington, 84% of second eagles coming to food patches kleptoparasitized conspecifics (Stalmaster 1981) while 58% of all birds arriving at occupied patches chose to steal (Knight and Knight 1983). Kleptoparasitism is found in several bird species (Brockman and Barnard 1979). Interestingly, a cost/benefit analysis in great egrets (Casmerodius albus) revealed that stealing offered less reward than other foraging tactics (Kushlan 1978). Both Kushlan (1978) and Stalmaster (1981) concluded pirating is adaptive when food is scarce but suboptimal at other times.

Another intriguing feature of eagle foraging behavior is the high frequency of turnover of ownership at food items. Even the most aggressive pirates after winning food are themselves often soon displaced. Knight and Knight (1983) found 83% of stealing attempts were successful. This situation is unusual among animals; resource defenders typically enjoy a substantial advantage over challengers.

A third interesting characteristic of contests between eagles is the high rate of display (pers. obs.). Stereotypic postures and calls are done by both feeders and challengers. Their function, however, is unknown.

The three features mentioned above are of more than heuristic interest; their *raison d'etre* may further understanding of the adaptive significance of eagle foraging behavior and to deeper insights into contest behavior in general. To that end, evolutionary game theory was employed as a theoretical construct for analyzing eagle behavior.

The Theory of Games (Von Neumann and Morgenstern 1953) was developed to model economic activity in human society. Maynard Smith and Price (1973) adapted the paradigm to evolutionary problems where the currency is not money but Darwinian fitness. Evolutionary game theory, like optimization theory (see Krebs and McCleery 1984), considers the costs and benefits of resource procurement strategies open to organisms and identifies "best" strategies. Game theory is unique, however, in that it addresses situations where strategy payoffs are dependent upon the frequency of each strategy across the population. It predicts that one or more unbeatable strategies (evolutionarily stable strategies or ESS's) may become fixed in a population. ESS theory has been applied to a variety of frequency dependent problems involving animal contests, sex ratios, parental investment in offspring and plant growth (Maynard Smith 1982a). Further validation of the theory is needed, however. Herein, I use ESS theory to better understand bald eagles, and also use eagles as subjects for field tests of game theory.

THE FEEDING BOWL

A conceptual model of the food acquisition problems faced by bald eagles is presented in Figure 4-1. In the FEEDING BOWL game, birds use foraging strategies derived from two tactics - searching for unclaimed prey and stealing from conspecifics. Individuals may employ pure strategies where they hunt (take an unclaimed food item) or steal exclusively. Or they may perform mixed strategies where they hunt at times and steal at others. The objective of each player is to find the strategy that maximizes its fitness - the ESS. Conditions may change during the game, however, so strategies may have to be modified. The frequency of each strategy, attributes of players, and food abundance are dynamic through time.

A mathematical analysis of the FEEDING BOWL could determine the ESS for each player if all pertinent parameters were quantified. Unfortunately, such information is seldom obtainable. Thus my approach is to test qualitative rather than quantitative predictions of game theory. Each prediction will be tested against the null model that constraints prevent evolution from approaching optimization.

This chapter explores some of the ways that the three variables in the FEEDING BOWL influence foraging strategies and explains the three features mentioned earlier. The chapter is arranged such that methods are followed by a description of feeding behaviors and pathways. Thereafter predictions on each of the three variables of the FEEDING BOWL are derived, tested, and discussed. I provide evidence that:

- (1) the Chilkat eagle population has reached an evolutionarily stable

THE FEEDING BOWL

- THE SETTING
 - EAGLES AGGREGATE AT FOOD PATCHES. CONSTRAINTS ON FEEDING ARE FOOD LEVELS, INTRASPECIFIC COMPETITION, AND RISK OF INJURY
- THE STRATEGIES
 - HUNT PREY ITEMS WITH A FREQUENCY OF P
 - PIRATE FROM CONSPECIFICS WITH A FREQUENCY OF 1-P
- THE OBJECTIVE
 - EACH PLAYER WINS BY CHOOSING A “BEST STRATEGY” — THE COMBINATION OF HUNTING AND STEALING THAT MAXIMIZES FITNESS
- THE VARIABLES
 - FREQUENCY OF HUNTING AND STEALING POPULATION WIDE
 - ATTRIBUTES OF THE PLAYERS: SIZE, AGE, POSITION, HUNGER LEVEL
 - FOOD AVAILABILITY

Figure 4-1. Conceptual model of factors influencing the foraging ESS.

state in foraging strategies; (2) differences in size, position, and hunger level of competitors affect contest strategies and outcome; (3) eagles assess the abilities or status of opponents and act accordingly; (4) displays serve to advertise traits conferring dominance and intentions; and finally, (5) that food abundance influences contest intensity.

METHODS

All observations were done at the Council Grounds (Figure 2-2) in fall 1980-81 and winter 1983. Subjects were monitored from a blind or automobile at distances of 20-150 m using a 20-45 power spotting scope and 10 x 40 binoculars. Data were entered onto cassette tapes in the field and later transcribed. The four types of observations were completed as described below.

Variation about mean values are expressed as standard deviations in this and all subsequent chapters.

Contests at Focal Salmon Carcasses

Interactions occurring over a total of 49 chum salmon carcasses were recorded in November and December 1980-81. Feeding grounds were visually scanned until an eagle with a whole or nearly whole salmon was located. Contests between carcass owners and challengers were then monitored until the fish was either fully consumed or vacated. Carcasses weighed on average 4.3 kg and were fed upon by 2-18 ($x = 7.8$) birds. For each of 467 observed displacement attempts I recorded: the age, relative size, and behavior of each competitor; contest outcome;

and instances of contact where the talons of one bird struck the body (feet excluded) of another. The pre-attack behavior of pirates, however, was not tallied. Behaviors are defined in Table 4-1. Eagles were placed in one of three age classes based on plumage and beak color: juvenile (0.5-1.5 years old), subadults (2.5 years to maturation), and adults (after Sherrod et al. 1977 and Stalmaster 1981). When possible, relative sizes of opponents were ascertained by visual inspection. These data were used to assess: the frequencies and pathways of behaviors; the effects of size, age, and position (in the air or on the ground) on contest outcome; and the risk of injury while feeding or pirating. To examine the influence of food abundance on contest intensity and outcome, observations were partitioned into periods of high and low food availability. Food was considered abundant when fish carcasses appeared plentiful and eagle numbers were stable or increasing (period one: 11/4/80-11/27/80 and 11/17/81-12/9/81; period three: 12/6/80-12/8/80 and 12/17/81-12/23/81). Food was considered limiting when carcasses appeared sparse and eagle numbers were declining (period two: 12/1/80-12/5/80 and 12/10/81-12/16/81). Later studies verified that eagle population size was closely related to food abundance (Chapter III).

Focal Eagle Observations

The influence of hunger level on foraging strategy and behavior was quantified by watching individual eagles from when they arrived at the feeding grounds until satiation was reached. Soon after dawn, an eagle approaching a food patch from the direction of the night

roosts was selected ad libitum as a focal subject. Its behaviors and interactions with conspecifics were monitored. The lengths of feeding bouts were measured with a stopwatch. Food intake was approximated by counting and recording number of bites of fish consumed per two minute interval. Subjects were considered satiated when they stopped feeding and their crops appeared full and they vacated the food patch. Mean number of bites to satiation was 114 ± 29 .

It was possible to keep individual birds under surveillance for full feeding periods only when food was relatively abundant and eagle numbers fairly low. Suitable conditions prevailed in winter 1983 only between 1/28 and 2/11 during which time a sample of 14 subjects was obtained. Data were analyzed by determining the proportion of the total number of bites taken prior to the performance of each behavioral act. Actual percent satiation was used in analysis of the count data. Rate data were partitioned by whether subjects were hungry (had taken 0-50% of total bites) or more satiated (had eaten 51-100% of total).

Foraging Tactics at Experimental Food Patches

An experiment similar to those of Stalmaster (1981) and Knight and Knight (1983) was completed to determine the frequency of hunting and stealing by birds arriving at feeding groups for their first meals of the day. Before dawn on 12 mornings between 11/30/81 and 12/23/81 two to five ($x = 3.0 \pm 0.8$) salmon carcasses, all similar in size and quality, were linearly arranged on a gravel bar at intervals of about 4 m. When a food patch contained both carcasses claimed by eagles and unoccupied carcasses, the foraging tactic of each new arrival was

recorded. These observations were subdivided into periods when food was abundance and periods when food was scarce as described above.

Display and Attack

A food patch containing about six fish was created each day of observation between 2/14/83 and 2/25/83 to assess if displays correlate with subsequent supplanting attempts. Observations were made when both occupied and vacant carcasses were present. The display behavior of new arrivals were tallied from the time they landed until they either settled at unoccupied carcasses, attempted stealing, or flew away.

DESCRIPTION OF BEHAVIORS AND PATHWAYS

A repertoire of foraging behaviors and behavioral pathways are presented in Table 4-1 and Figure 4-2. Birds intent on feeding either hunt or pirate directly or first perform HEAD OUT/UP or WING TIP displays. Displacement attempts are initiated from either the air or the ground. Birds gaining access to a fish feed while scanning for attackers and occasionally performing CROUCH-VOCALIZE or HEAD OUT/UP. If attacked by a pirate, feeders either yield or act to defend their food. Physical contact may occur if feeders fail to respond to attackers, if feeders retaliate, or if opponents CHARGE. Such contact may be violent with the talons of one bird being embedded in the body of another. Birds still unsatiated after losing possession of a fish or eating all remaining flesh return to foraging. When replete, the birds generally take a perch and become inactive. The effects of the

Table 4-1. Partial ethogram of bald eagle foraging behaviors. Frequencies are averages for all individuals.

Behavior	Description	Actor	Proportion of contests
<u>Foraging tactics</u>			
HUNT	Pursue prey that is unclaimed by a conspecific	-	42%
AERIAL (pirate)	Fly towards feeder and descend upon it with feet and talons outstretched	Challenger	34%
LEAP (pirate)	Jump from the ground to a height of a few meters and drop towards feeder with talons extended	Challenger	16%
WALK (pirate)	Trot towards feeder with wings drooped and head extended	Challenger	8%
<u>Defensive behaviors</u>			
RETREAT	Move rapidly from prey as challenger approaches	Feeder	58%
RETALIATE	Swing feet upwards to meet approaching challenger	Feeder	32%
<u>Aggressive behaviors</u>			
CHARGE	While on the ground, lunge towards opponent and strike out with talons	Feeder and/or challenger	13%
<u>Displays</u>			Proportion of displays
CROUCH-VOCALIZE	Squat close to ground, droop wings slightly, retract neck and vocalize	Feeder	41%
HEAD OUT/UP	Droop wings slightly, alternately extend head horizontally and vertically while raising and lowering tail and vocalizing	Feeder or challenger	53%
WING TIP	Raise wings and undulate metacarples while performing Head Out/Up	Challenger	6%

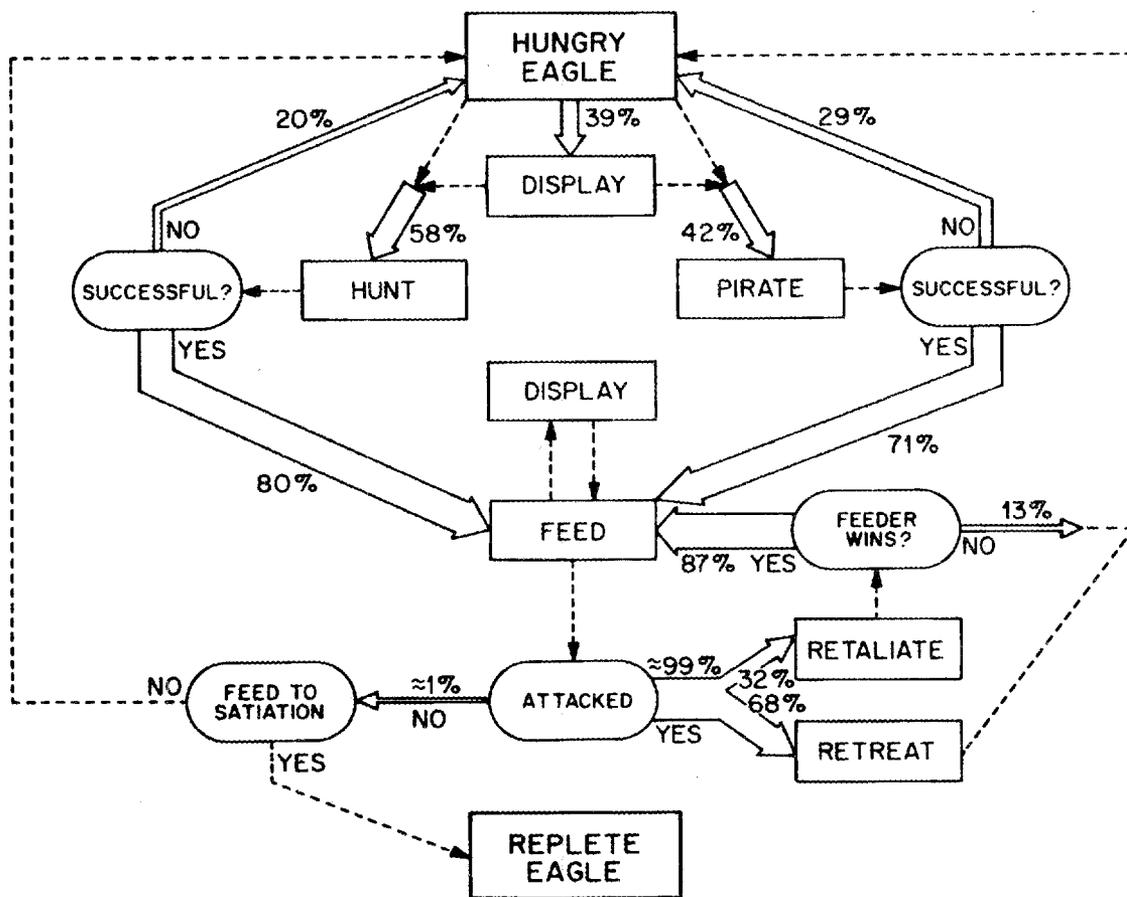


Figure 4-2. Behavioral states and pathways of foraging eagles. Arrow width is proportional to transition frequency where frequency is known. Dashed lines denote pathways, not transition probabilities.

frequency of hunting and stealing across the population, individual phenotypes, and food abundance on transition rates between behavioral states are discussed in later sections.

VARIABLE 1: FORAGING STRATEGIES AND THE ESS

Predictions

The best strategy for a player of the FEEDING BOWL is dependent upon the frequency of hunting and stealing population wide. The situation is depicted by the producer-scrounger model of Barnard and Sibly (1981) (Figure 4-3). In this model producers invest in securing a resource which scroungers parasitize. Payoffs to scroungers are frequency dependent; their fitness is higher than producers when scroungers are rare, but lower than producers when scroungers are common. Where the payoff curves intersect both types do equally well. A population containing producers and scroungers should converge on this ESS point. Therefore the first prediction of the FEEDING BOWL is: the frequencies of hunting and stealing population wide have stabilized at the ESS point where payoffs of each are equal.

Results

Frequency of Foraging Strategy

Eagles arriving at experimental food patches in early morning when they were presumably hungry, kleptoparasitized food holders with a frequency of 68% (n = 122). Focal subjects, whose full feeding periods were monitored, pirated with a frequency of only 58% (n = 60) (Figure 4-4). This difference may have been due to the effect of

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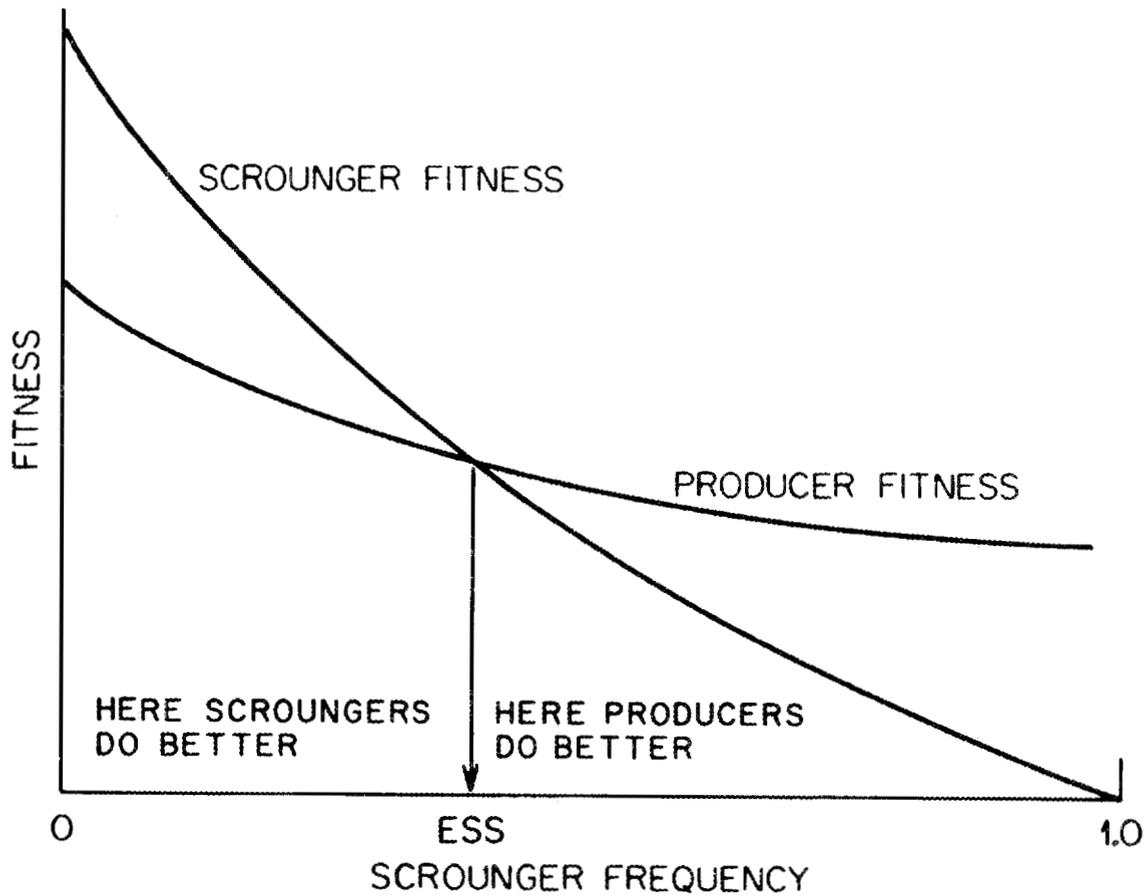


Figure 4-3. The producer-scrounger model. Scroungers exploit the investments made by producers, so the fitness of a scrounger decreases as scroungers become more common in the population. Scroungers fare better to the left side of the graph and producers do better to the right. The frequency of scroungers should stabilize at the ESS point where the fitness of the scroungers and producers are equal (after Barnard and Sibly 1981 and Parker 1984).

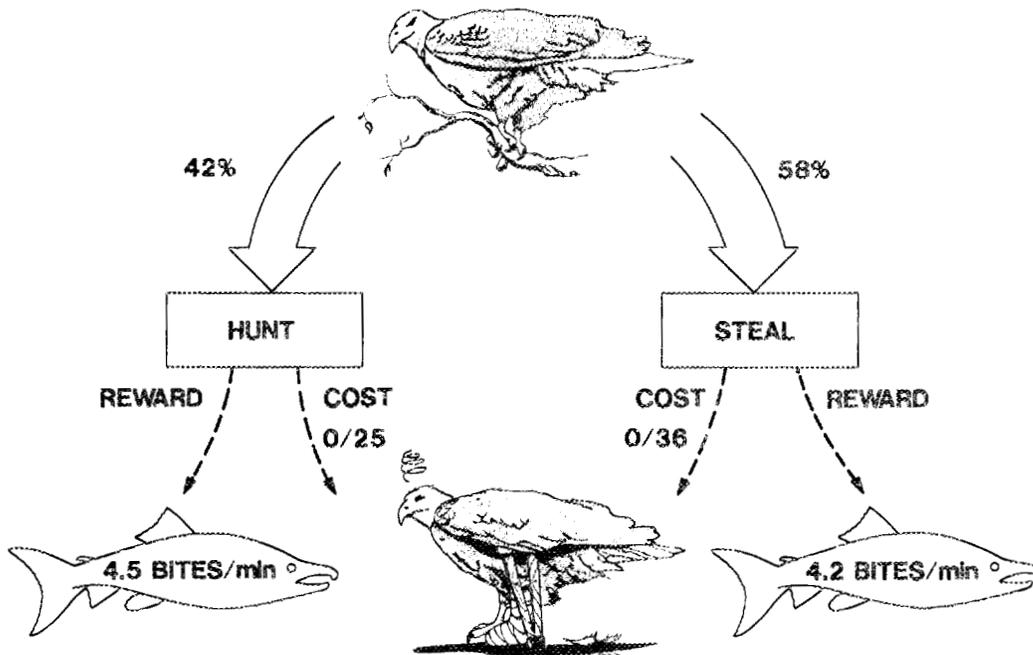


Figure 4-4. The frequencies of hunting and stealing and respective payoffs in feeding rate (bites/unit search and consumption time) and costs in incidence of injury for 14 eagles monitored over full feeding periods.

hunger level on foraging strategies. The birds when less than half satiated pirated slightly more (65%) (but not significantly more) than when more than half satiated (50%) (Chi Square, $n = 60$, $\chi^2 = 1.5$, $p > 0.1$) (Table 4-2).

Rewards

Both hunters and pirates had a high probability of gaining access to food. Of 467 displacement attempts at focal salmon carcasses, 71% were successful (Table 4-3). Efforts to procure suitable food by hunting were successful 25 of 31 times (81%): 6 attempts secured frozen and thus inedible carcasses.

A much more direct measure of the payoffs of each foraging tactic was actual feeding rate. The 14 focal eagles derived similar amounts of flesh per unit search and consumption time through hunting and stealing. Pirates gained 4.2 bites/min and hunters 4.5 bites/min (Figure 4-4); differences were not significant (Matched Pair Signed Ranks Test, $n = 14$, $t = 40$, $p \gg 0.05$). So the rewards of each tactic were nearly equal. How did the costs of each tactic compare?

Risks

No injury was suffered by the 14 focal eagles during 35 pirating and 25 hunting attempts (Figure 4-4), although both hunters and pirates, undoubtedly risk injury. During observations at focal salmon, a pirate was struck by the talons of a feeder in 1 of 467 displacement efforts. The bird appeared unhurt. Hunters may be injured while trying to subdue or retrieve prey. I witnessed in summer two occasions where birds in pursuit of fish were swept downstream and submerged by fast

Table 4-2. Food acquisition tactics of eagles at different levels of satiation (more than 50% and less than 50%).

Hunger level	Foraging strategy	
	Pirate	Hunt
High	21	11
Low	14	14

Table 4-3. Outcomes of contests over food. Results are partitioned based on food availability.

Food abundance	Displacement attempts	Displacement attempt successful		Owner retaliates		Retaliation successful	
	No.	No.	%	No.	%	No.	%
High	312	236	76	87	28	74	85
Low	155	94	61	64	41	60	94
Total	467	330	71	151	32	134	89

water; both survived. Hunters are also at risk because some food items are possibly associated with danger (e.g., predators like wolves or man) and first feeders are the most likely victims of such "booby traps." Evidence in support of this notion comes from observations at experimental food patches. Eagles approaching the conspicuous food patches in early morning generally landed in nearby trees, waited until one bird finally went to a fish, then moved to displace it. Time from discovery of food until the first bird began to feed (24.8 ± 17.2 min) was longer than from that time until the first displacement attempt (4.4 ± 4.9 min) (Two Sample t-test, $n = 24$ and 23 , $t = 3.1$, $p < 0.0025$). This suggests there are disadvantages to being the first bird to a prey item.

Discussion

Returning to the first feature of eagle foraging behavior raised in the Introduction - why do bald eagles steal from conspecifics even when food is abundant? Is the behavior suboptimal except during times when food is scarce as suggested by Stalmaster (1981)? Or are the foraging tactics at an ESS where the payoffs of each are equal as predicted by Barnard and Sibly (1981)?

My data strongly support the latter explanation. First, pirating frequency may not be as high as the 80% indicated by Stalmaster (1981). He monitored only hungry eagles, which may steal more than do replete birds. Chilkat eagles examined over full feeding periods robbed 58% of the time (Figure 4-4). Second and more importantly, the payoffs of each strategy were very similar. The 14 focal eagles ingested nearly

equal amounts of food per unit of searching and consumption time through hunting and stealing while incidence of injury was 0 for both (Figure 4-4). Based on these observations, then, the foraging strategies across the population were at an evolutionarily stable state.

A large enough sample would surely reveal that each strategy has unique risks. Pirates may be wounded by opponents and hunters may have higher rates of drowning or predation. Even so, the conclusion that the population is at an ESS would hold so long as feeding rate minus cost of injury was the same for hunting and stealing.

VARIABLE 2: DIFFERING ROLES

Attributes of Players, Contest Outcome, and Winning Strategies

The FEEDING BOWL game is complicated by the fact that each player has unique characteristics. Maynard Smith and Parker (1976) assert that competitors may differ in three ways: in fighting ability or position (called resource holding power or RHP); in expected gain in victory (resource value); and in ways uncorrelated with the first two (e.g., roles like owner and intruder). Further, they predict that when such differences are known by both contestants, one will emerge as winner without escalated fighting, if the contested resource is not particularly valuable.

Discernable traits that probably influence RHP in bald eagles are size, age, and position. In Alaska, females average 24% heavier than males and the largest females are 81% heavier than the smallest males (Imler 1941), so large size differences between two birds usually indicate they are of different sexes. Growth is determinate in this

species and subadults are only slightly lighter than adults. Age is thought to correlate with plumage until maturity is reached at four to six years (Southern 1964, Servheen 1975). Whether a bird is positioned above or below an opponent would seem to affect its chances of winning because talons serve as the primary weapons. An aerial attacker has its feet in a position to threaten a feeder on the ground. Resource value varies with hunger level. A bird with a crop that is nearly full can derive less benefit from a salmon than can one with an empty crop. Relative hunger level may be discernable from crop size or the length of time a bird has been eating.

I predict, then, that size, age, position, and hunger level will be used as cues to settle contests without escalated fighting.

How might these asymmetries influence the "best" combination of hunting and stealing for a player in the FEEDING BOWL? Parker (1984) identifies a "phenotype limited" ESS where a set of strategies is specified for each phenotype. It is a strategy that cannot be invaded by another strategy played by that phenotype. When applied to the producer-scronger model, the ESS will be a conditional pure strategy -- e.g. play producer if relatively large, otherwise play scronger (Figure 4-5) (Parker 1984). Accordingly, players of the FEEDING BOWL should choose a strategy contingent upon their phenotypes or roles (e.g., hunt if small, steal if large).

Results

Contest Outcome, and Incidence of Fighting. Size differences were great enough to rank opponents during 40 contests. The larger of each

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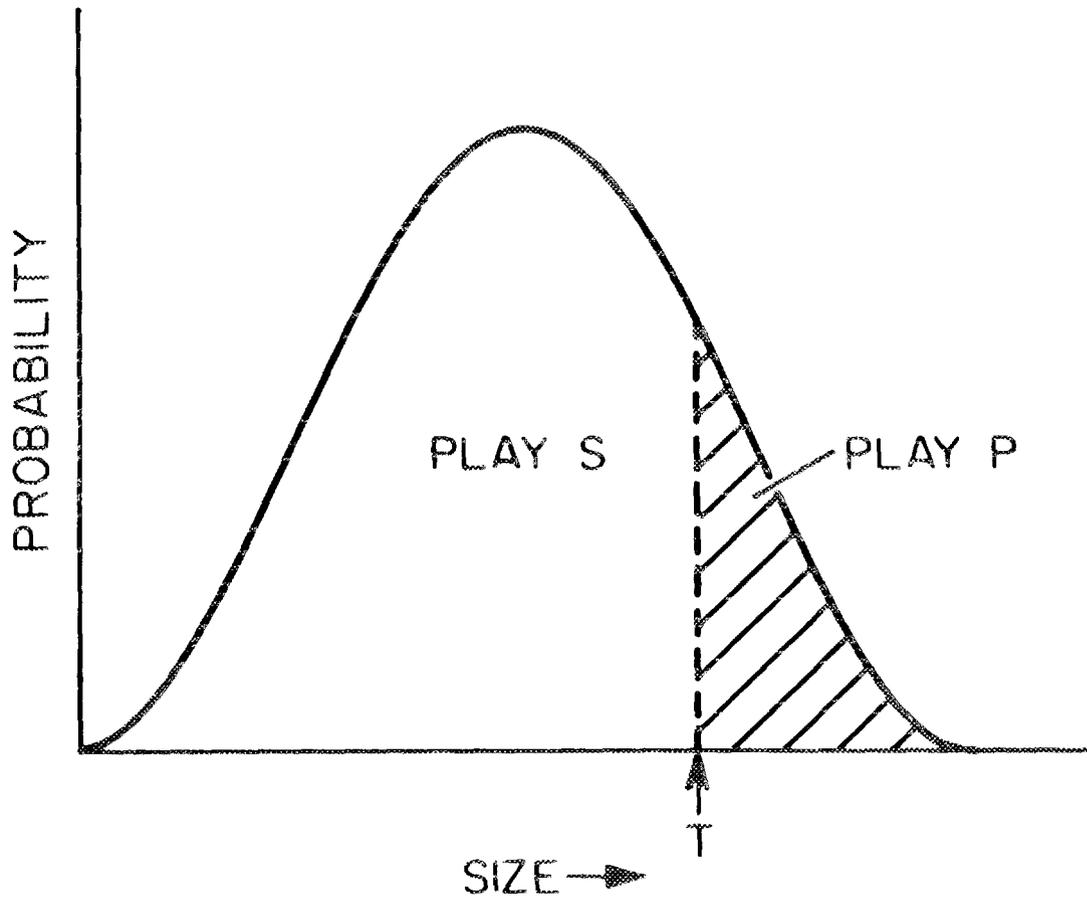


Figure 4-5. The distribution of size in a hypothetical population in which there is competitive advantage to large size in strategy P. The ESS is to play P if $S > T$, play S if $S < T$ (from Parker 1984).

pair won 85% of the time (Table 4-4) (Chi-Square, $n = 40$, $\chi^2 = 19.6$, $P < 0.001$). Controlling for a possible position effect, the larger won every time it attacked the smaller, but lost 50% of the contests when it was the feeder.

Age had less influence on who won. Birds of an older age class won 92 contests and lost 94 against birds of a younger age class (Table 4-5). Older birds were no more successful in supplanting younger ones (70% of attempts) than were younger in displacing older (74% of attempts) (Chi-Square, $n = 186$, $\chi^2 = 0.44$, $p > 0.5$). Juveniles attacking adults, however, won decidedly more frequently than adults pirating from juveniles (Chi-Square, $n = 53$, $\chi^2 = 7.34$, $p < 0.01$).

The data were inconclusive on a position effect. Evidence in support of a position effect is (a) aerial and leap supplanting efforts were successful 67% of the time ($n = 411$), and (b) feeders were in more danger than pirates; during the 411 displacement attempts feeders received talon blows to the body 7 times while only 1 pirate was struck.

Table 4-4. Effect of relative size on supplanting success.

	Bigger attacks smaller	Smaller attacks bigger	Total
Bigger wins	28	6	34
Smaller wins	0	6	6
Total	28	12	40

Table 4-5. Outcomes of supplanting attempts partitioned by age. Age groups above the horizontal lines attacked the age groups listed below the horizontal lines.

Attacker	Juvenile			Subadult			Adult			Older	Younger
	Juv	Sub	Adult	Juv	Sub	Adult	Juv	Sub	Adult	Younger	Older
Wins	2	6	22	8	23	36	18	44	171	70	64
Loses	2	4	1	2	10	17	10	18	72	30	22

The positional advantage to aerial attackers, however, is confounded by the possibility of assessment; attackers may select inferior opponents. WALK displacements were more successful (80%, $n = 51$) than AERIAL or LEAP displacements (67%). This may contradict the evidence suggesting a position effect, or it may have resulted from the possibility that aerial attackers have a positional advantage over feeders, but ground attackers have greater advantage in being able to stand by a feeder and more accurately judge its relative abilities.

Expected gain also influenced contest outcome. The degree of satiation of contest winners ($39 \pm 34\%$) was less than that of contest losers ($68 \pm 35\%$) (Mann Whitney U Test, $n = 36$ and 38 , $Z = 3.47$, $p < 0.0005$).

Escalated fighting between foraging eagles was rare. CHARGE was performed during 13% of the 467 displacement attempts at focal salmon carcasses; only once did CHARGE result in talon to body contact. As mentioned earlier, feeders were struck 7 times and attackers only 1 time as pirates descended on feeders. Contact occurred in 1 of 74 contests during the focal eagle observations. Thus, talon to body contact occurred in only 10 of 541 contests (1.8%).

Phenotype limited strategies. The relationship between foraging strategy and phenotype was properly quantified only for hunger level. As reported earlier, hungry birds pirated slightly more (65%) (but not significantly more) than did more satiated birds (50%) (Figure 4-6). Individuals did, however, gain more bites through pirating when less than half satiated (514 bites or 4.5 bites/min) than when more than half satiated (351 bites or 3.8 bites/min) (Matched Pairs Signed Ranks Test, $n = 12$, $t = 13$, $p = 0.04$).

Less direct data suggest that age and size may also influence foraging strategy. At experimental food patches juveniles and subadults were first feeders more often than expected by the proportion they comprised of all feeders (Chi-Square, $n = 21$, $\chi^2 = 7.4$, $p < 0.01$) which implies that they may hunt more than adults. Also, one focal eagle that was very small hunted exclusively.

Discussion

Contest settlement. The data show that the outcome of contests between foraging eagles was influenced by size, hunger level, possibly position, but not age. Large eagles won over small (Table 4-4) which suggests that most females are dominant over most males. Also, hungry eagles won over more satiated. Eagles positioned in the air did have greater likelihood of victory and less chance of injury than opponents on the ground. But ground based displacement attempts were more successful than aerial attempts. The confounding possibility of assessment causes this work to be inconclusive on the existence of a position effect.

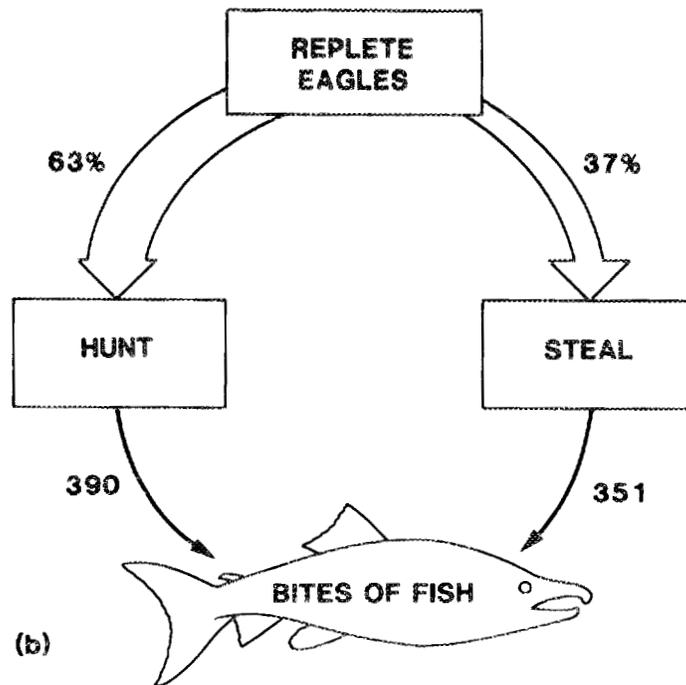
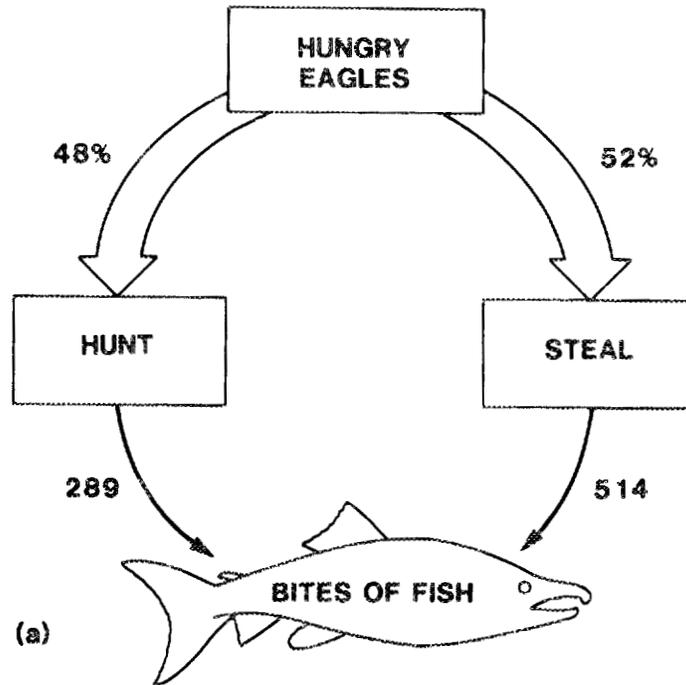


Figure 4-6. Foraging strategies and payoffs for eagles when less than 50% satiated (a) and when more than 50% satiated (b).

Age had surprisingly little influence on contest outcome. The only difference between age classes were in juveniles and adults. Juveniles displaced adults more than adults supplanted juveniles (Table 4-5). In contrast, Stalmaster (1981) found in Washington State, that younger age groups were subordinate to older age groups. A possible explanation is that the effects of age are subtle compared to those of size and hunger level and my sample size was inadequate to detect their presence. Stalmaster (pers. comm.) found significant differences between age groups only after about 1000 observations, a figure double my sample size.

Escalated fighting on the Chilkat was uncommon. CHARGE was done in only 13% of the contests and talon to body contact occurred in only 1.8% of the contests. No cases of injury were observed.

Thus, this work shows that differences between opponents in size, hunger level, and possibly position and age, are used by eagles to settle contests - usually without escalated fighting.

Phenotypes and ESS's. My data suggest that individuals do select foraging strategies conditionally upon their phenotypes or roles. Birds derived more food from pirating when hungry than when more satiated (Figure 4-6). Furthermore, juveniles and subadults hunted more often than adults as indicated by the fact that the young birds were first feeders at food patches disproportionately often. Stalmaster (1981) found a similar pattern.

An ecologically important outcome of conditional strategies is that payoffs are not equal among phenotypes or roles. In this case, young or small birds may have been making the best of a bad situation.

Subadult eagles wintering in Washington appeared to obtain slightly less than basal metabolic energy requirements while adults obtain slightly more (Stalmaster 1981).

The best strategy for a player in the FEEDING BOWL, then, depends upon its RHP and expected gain in victory. Mathematically determining the ESS for an individual, however, is a very complex multivariate problem where frequency distributions and ESS points (Figure 4-5) for size, hunger level, age, and position may each comprise an axis. The means by which evolution solves such problems are not understood. In contests where opponents differ in size and ownership status, ownership is used as a settlement cue only if size differences are small (Riechert 1978). The decision rules of more complex contests have not yet been worked out.

Assessment: Sizing Up the Competition

The prediction that asymmetries serve as cues for settling contests is based on the assumption that both contestants have full knowledge of the asymmetries. How is such knowledge gained? Animals may assess the attributes of opponents relative to their own. Maynard Smith (1982a) shows that an assessor strategy can be an ESS if assessment is cheap relative to the cost of escalated fighting. It follows for the FEEDING BOWL that eagles should assess the relative fighting ability or expected payoffs of opponents and act accordingly. If so, small or nearly satiated feeders should be the targets of supplanting attempts a disproportionate share of the time.

Results

Pirates tried to displace feeders smaller than themselves more often (28 times) than feeders that were larger (12 times) (Table 4-4) (Chi-Square, $n = 40$, $\chi^2 = 6.4$, $p < 0.02$). This result is evidence of assessment if large and small eagles were equally represented in the population, which is a reasonable assumption. Similarly, the focal eagles were attacked more often when they were greater than half satiated (1.7 ± 0.99 attacks) than when they were less than half satiated (1.1 ± 0.92 attacks) (Table 4-6) (Wilcoxon Matched-Pairs Signed-Ranks Test, $n = 8$, $t = 3.5$, $p < 0.025$).

Discussion

Eagles apparently assessed the relative attributes of conspecifics and often chose to displace the individuals most likely to yield (small and replete birds). Pirates sometimes appeared to evaluate feeders quickly while flying overhead. Other times the birds landed and seemed to study feeders intently before attacking. The latter method may allow more accurate assessment but it is done with a loss of a possible positional advantage enjoyed by aerial attackers.

How are relative size and hunger level judged by eagles? Size is probably easily discerned by comparing a feeder to nearby conspecifics or to prey items if the feeder is alone. Hunger level may be revealed by crop size; empty, half-full, and full crops are discernable to a human observer. Another possibility is that time spent feeding is the cue since intake is a function of time.

It is now possible to address the second question raised in the Introduction - why even the most aggressive birds, after displacing a

Table 4-6. Number of supplant attempts directed towards feeders at high and low ranges of satiation. The total times subjects controlled food during the high and low ranges were 110 minutes and 107 minutes, respectively.

Subject number	Level of satiation	
	< 50%	> 50%
1	3	3
2	1	2
3	0	1
4	0	1
5	1	1
6	2	2
7	0	2
8	1	0
9	1	1
10	0	3
11	1	1
12	1	
13	2	3
14	2	3
\bar{X}	1.07	1.71
s	0.92	0.99

feeder, were generally themselves soon displaced. Simply stated, food holders had the odds against them. First, a position effect possibly favored attackers. Second, as feeders ate their expected payoff in victory decreased and thus likelihood of winning decreased. And third, pirates assessed the relative size and hunger level of opponents and chose to displace those most likely to yield. So, when a feeder lost a contest, it could gain the advantage of attacking and was likely to win the next contest. This unusual situation where resource defenders are at a disadvantage to challengers approached the infinite regress envisioned by Parker (1974) a decade ago.

Information Transfer: Attributes or Intentions?

Much debate has centered on information transfer during animal contests (see Caryl 1979, Hinde 1981, Moynihan 1982, Maynard Smith 1982b, Krebs and Dawkins 1984). The basic disagreement is whether ritualized displays evolved to communicate intentions. Maynard Smith (1982b, p. 2) defines intentions as "what the animal is going to do, or attempt to do, next." The view of some classical ethologists is that selection favors signals that effectively transmit information from actor to receiver (see Krebs and Dawkins 1984). Accordingly then, displays by an individual should correlate with its subsequent behavior and thus be accurate signals of intentions (Caryl 1979). Maynard Smith (1982b), in contrast, says displays may communicate information about an animal's RHP but not about its intentions. He clarifies the distinction by example. The roar of a red deer stag (Cervus elaphus) varies with the animal's size and is thus indicative of its fighting

ability (Clutton-Brock et al. 1979). Consider a stag which retreats without fighting after a roaring contest compared to a stag which escalates under the same circumstances. Roaring communicates size which is a component of RHP. The difference between retreat and escalation, however, is a matter of intention, and not RHP. The distinction is said to be important because displays of RHP are reliable and thus evolutionarily stable while signals of intentions are not. For example, a small stag is incapable of producing the deep roar of a large one. There is nothing, however, to prevent the stag from "lying" about whether it intends to attack. The argument centers exclusively on signal reliability. It says displays of intentions theoretically cannot exist because they are inherently unreliable and thus would lose their meaning and fall to disuse.

War of Attrition and Hawk-Dove Games

The first step toward resolving the issue is considering the predictions on information transfer of two prevalent game theory models - War of Attrition and Hawk-Dove models. In War of Attrition games contest costs increase as a continuous function of time spent fighting and are thus settled by the length of time opponents persist in the contest (Parker 1984). In Hawk-Dove games levels of fighting are discrete (e.g., Doves display and Hawks escalate) so contest costs may change abruptly. Signals of intentions clearly could not be stable in War of Attrition because there is no cost to cheating. The only rational strategy for a player is to falsely signal that it is willing to persist in the contest forever. So displays cannot reliably signal information about what an animal will do next in War of Attrition contests.

What about Hawk-Dove games? Where the assessor strategy is possible and cheap, game theory predicts and empirical tests confirm (see Krebs and Dawkins 1984) that animals high in RHP often display to advertise that the odds are in their favor. This follows because cues of RHP can be, like the roaring in red deer, inherently reliable. Interestingly though, displays in such games should be good predictors of what an animal will do next; the contestant highest in RHP should act to take the resource while its opponent retreats. In this case, assessment cues can signal information about both RHP and about intentions. It also logically follows that assessment cues can signal asymmetries of types other than RHP, namely resource value and uncorrelated asymmetries, if such signals can be reliable.

Below, I present evidence that displays in bald eagles signal differences in expected gain and also that they are good predictors of subsequent behavior. Further, I argue that some types of displays may have evolved primarily to signal intentions.

Results

The focal eagles performed the HEAD OUT/UP and WING TIP displays at higher rates when less than 50% satiated ($0.20 \pm 0.20/\text{min}$) than when more than 50% satiated ($0.05 \pm 0.09/\text{min}$) (Wilcoxon Matched-Pairs Signed-Ranks Test, $n = 10$, $t = 6$, $p < 0.014$).

During observations of eagles arriving at experimental food patches, 16 eagles landed and did not perform HEAD OUT/UP or WING TIP. Six of these birds (38%) then attempted displacements while the remainder either hunted or flew away (Figure 4-7). Of the 27 arrivals

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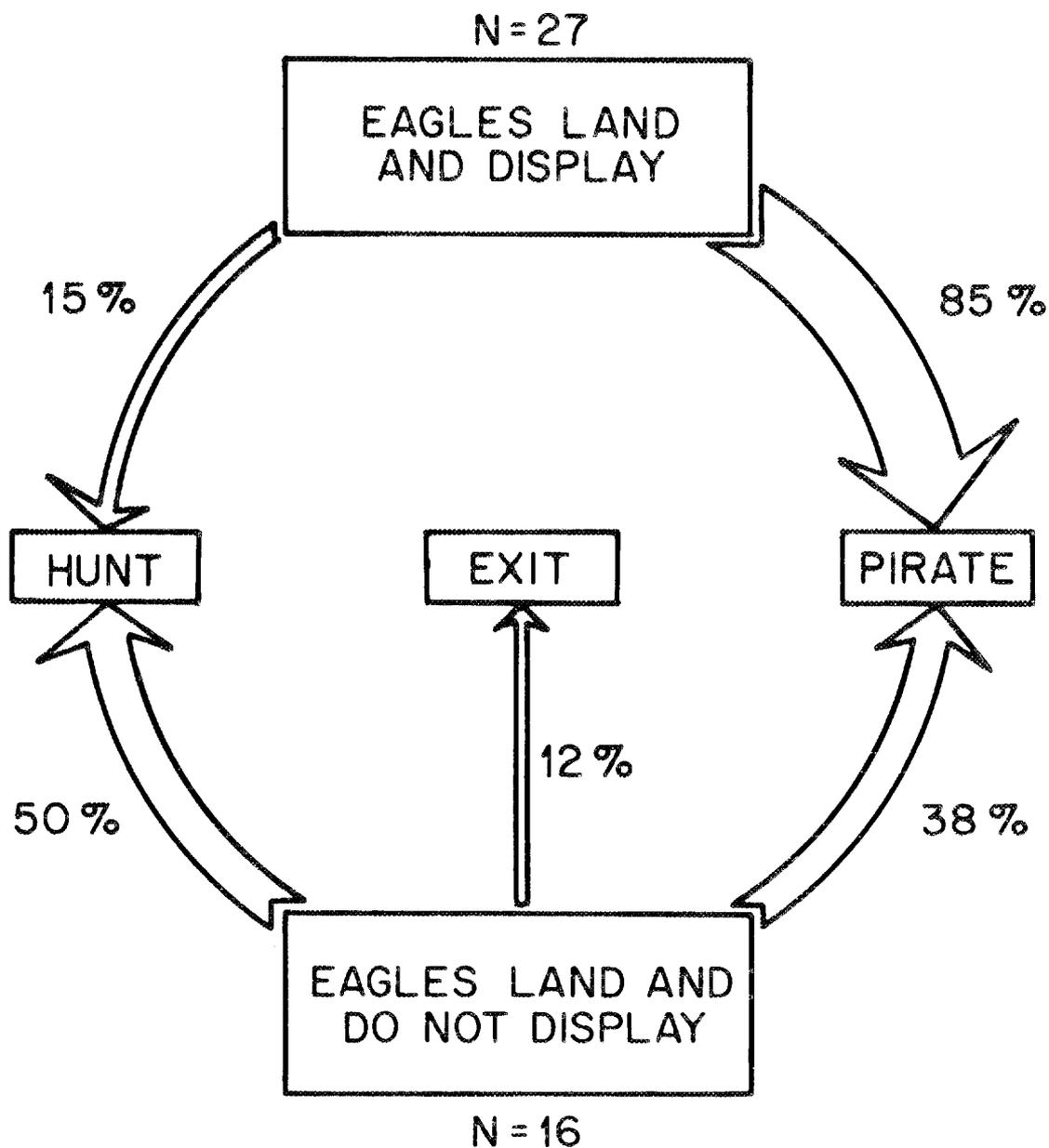


Figure 4-7. Relationship between display and subsequent behavior of eagles arriving at experimental food patches in early morning. Exit denotes flying from food patch.

that did display, 23 (85%) tried to supplant feeders. These data show a positive correlation between display and attack (Contingency Coefficient: C , $n = 43$, $C = 0.44$, $p < 0.01$).

Discussion

Reliable Cues of Expected Gain. The fact that display rate decreased as eagles ate indicates that HEAD OUT/UP and WING TIP displays are used by hungry eagles to advertise high expected gain. How could signals of hunger level be reliable? These displays draw attention to the throat region and a distended crop is sure sign of a cheater. Thus HEAD OUT/UP and WING TIP are reliable by their form. These displays probably have become ritualized signals of resource value over evolutionary time precisely because they are reliable yet cheap to produce.

Controlling Dishonest Signals of Intentions. So assessment cues of expected gain in bald eagles and RHP in red deer are stable because they cannot be effectively performed by cheaters. I now examine if signals that can be easily produced by all members of a population can reliably advertise player abilities or status. Hansen and Rohwer (in press) show that the epaulets of red-winged blackbirds (Agelaius phoeniceus) are adjustable badges of social status. All adult males can rapidly expose or fully cover their red patches by flexing muscles controlling scapular feathers. Males defending nesting territories expose their badges to advertise that they possess traits conferring dominance. Floating males cover their badges when intruding into territories to avoid escalated fights with owners. Owners are very successful in evicting territorial intruders though the asymmetries

favoring owners are unknown. Theoretically, the differences could be in RHP, resource value, or role (owner, intruder). How can coverable badges be reliable? Why don't intruders simply expose their patches and feign ownership? The consequences of cheating is rapid attack by legitimate owners. Red-wing mounts placed in occupied territories were struck by owners in only 3.5 ± 4.0 min after placement and some were literally torn apart shortly thereafter. This work shows that signals that are easily produced by all individuals can be reliable if the consequences of signaling inaccurately are costly.

In Hawk-Dove games, then, assessment cues may be signals of RHP (red deer and others) or expected gain (bald eagles). Signals may be reliable either because "low status" individuals are unable to perform them convincingly (red deer and bald eagles), or because the cost of cheating is escalated fighting (red-winged blackbirds).

Signal Evolution and Meaning. The eagle studies revealed that display conveyed not only assessment information but also information about what the actor would do next. Display indicated with an accuracy of 85% that attack would follow. Clearly the message sent from a hungry eagle is, in anthropomorphic terms, "I am hungry and likely to beat you, so I intend to attack unless you retreat." The scenario can be generalized for any case where individuals with traits conferring dominance reliably advertise this fact in order to win resources. The conclusion is that assessment cues can signal RHP or expected gain and also intentions.

Still unresolved is the question of which type of message is responsible for the evolution of ritualized displays. Maynard Smith

(1982b) argues that it is RHP information that renders displays stable over evolutionary time because only RHP information is reliable. I suggest, however, that after assessment has occurred in a contest, pure signals of attack or retreat can be reliable. A possible example comes from Reichert (1978) who examined contests at web sites of the spider Agelenopsis aperta. Contests usually begin with an assessment phase where each competitor performs displays that vibrate the web and thus transmit information on size to the opponent. Following assessment may be phases of signaling, threats, and escalated fighting. The threat displays are likely candidates for pure signals of intentions. They may signal that an individual, after having assessed the relative size of its opponent, is willing to escalate. Actors will benefit if such signals convince opponents to retreat without fighting. Indiscreet use of threat, however, is severely penalized by the escalated fighting it may precipitate. In this case then, the reliability of a pure signal of intent is maintained by a high cost to cheaters. So, following the same logic by which Maynard Smith concludes that ritualized displays evolved as cues of RHP, I argue that some displays evolved as pure signals of intentions.

Conclusion

As is often the case between dissenting views, both classical ethologists and game theorists may be partially correct in the question of whether ritualized displays communicate intentions. In War of Attrition contests, signals of what an animal will do next are unreliable and thus not evolutionarily stable. In Hawk-Dove games, however, displays may reliably advertise an animal's RHP, expected

payoff, or intentions. Here, reliability may be insured by either a potential cheater's inability to perform the display or by high cost cheaters may pay in escalated fighting. Some ritualized displays probably evolved primarily as cues for assessment but also convey information about intentions. Other displays may have evolved exclusively to signal intentions.

VARIABLE 3: FOOD AVAILABILITY

In the dynamic northwest coast environment, disturbance at various scales cause fish stocks and hunting conditions for eagles to change rapidly (see Chapter II). Food availability in the Council Grounds, for example, can change from overabundance to scarcity in only two or three days (Figure 3-2). How do fluctuating prey levels affect the FEEDING BOWL game? The value of a salmon to an eagle is a function of the cost of finding and acquiring other carcasses. When food is plentiful relative to eagle numbers the value of owning a fish is small because others can be easily procured. The value of a fish increases as the resource becomes scarce and the cost of obtaining another rises.

Earlier in the chapter, the influence of differences in expected gain between players on individual foraging strategy was examined. I now explore how changes in resource value population wide affect contest intensity and pirating frequency.

Parker (1984) derives the following equation from the Hawk-Dove model when cost of injury (C) is high relative to resource value (V):

$$p = \frac{V}{C} \quad (4.1)$$

where p is the probability of playing Hawk (fight at escalated level). An obvious conclusion from equation 4.1 is that animals will take greater risks in fighting as a resource becomes more valuable. It follows that eagles should escalate more as food becomes sparse.

Less obvious is how pirating frequency will change with food abundance. Stalmaster (1981) suggests that pirating rates should decline as food levels rise but that they do not because of constraints on evolution. All would agree that as food becomes scarce the payoffs to both hunters and pirates drop (Figure 4-8). Hunters find fewer carcasses and pirates find fewer victims. What is not clear is whether the y -intercepts of the hunting and stealing fitness curves decrease by equal amounts as food gets scarce. If the payoffs of the strategies change proportionally then the ESS point for frequency of pirates will remain constant regardless of food abundance. On the other hand, if the rewards of one tactic decline more than rewards of the other as food declines, the ESS point will shift and pirates will be either more or less common. One cannot predict a priori which of these scenarios describes the FEEDING BOWL because the payoffs and costs of each strategy under different food regimes are not well known.

Results

Escalation

During periods when food was sparse relative to eagle numbers, rates of display and RETALIATION of feeders against pirates and instances of contact increased. Rates of display (CROUCH VOCALIZE,

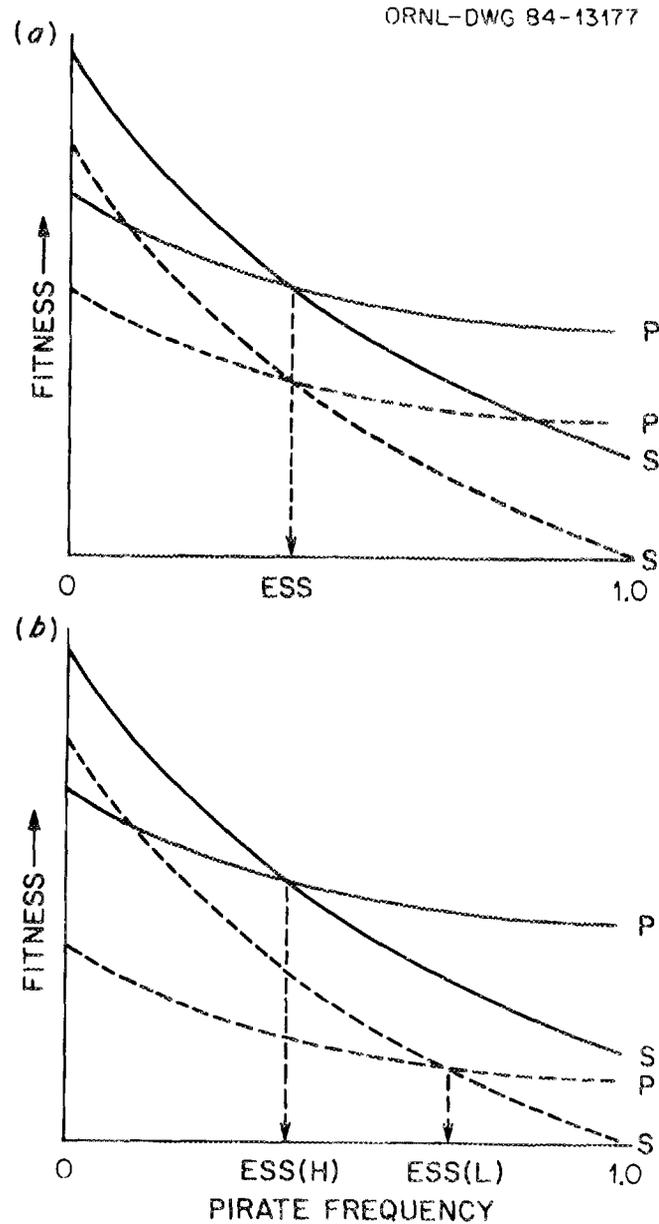


Figure 4-8. Two possible effects of resource levels on the foraging ESS in producer-scrounger games. (a) The fitness curves of producers (P) and scroungers (S) for when food is scarce (dashed lines) are both shifted downward equal distances along the Y axis from when food is abundant (solid lines) and the ESS point does not change. (b) The 1-intercepts of the fitness curves change disproportionately as food levels drop and the ESS point under low food levels (L) differs from the ESS point under high food levels (H).

HEAD OUT/UP, and WING TIP) increased from 0.07 ± 0.05 per min when food was plentiful to 0.18 ± 0.17 per min when food was scarce (Mann Whitney U Test, $n = 25$ and 9 , $Z = 2.19$, $p < 0.014$) (Table 4-7). Feeders retaliated against pirates in 41% of the displacement attempts when food levels were low and in 28% of the attempts when levels were high (Chi-Square, $n = 467$, $\chi^2 = 8.66$, $p < 0.01$) (Table 4-8). Seven instances of talon to body contact occurred during the 155 displacement attempts when food was plentiful and 2 instances occurred during 312 contests when food was scarce.

Foraging Strategy

Frequency of pirating at experimental food patches did not change significantly from when food was abundant (70%, $n = 96$) to when food was scarce (62%, $n = 26$) (Table 4-9) (Chi-Square, $n = 122$, $\chi^2 = 0.79$, $p > 0.30$). Supplanting success did vary with food abundance. Pirates won 61% ($n = 155$) of contests when feeding was good and won 76% ($n = 312$) of contests when feeding was poor (Chi-Square, $n = 467$, $\chi^2 = 11.2$, $p < 0.001$).

Discussion

As predicted by the Hawk-Dove model, escalation did increase as resource value rose. Display rate, RETALITATION against pirates, and contact all were inversely related to food abundance. These data support other research which shows levels of aggression are influenced by environment (see Ewald and Orians 1983). Further, they suggest that aggression is the mechanism of density dependent population

Table 4-7. Rate of CROUCH VOCALIZE, HEAD OUT/UP, and WING TIP displays by eagles competing over focal salmon carcasses. Dates of periods are: One - 11/17/81 to 12/9/81; two - 12/10/81 to 12/16/81; three - 12/17/81 to 12/23/81. Criteria for judging food level are presented in Methods.

Period	Food level	Display rate ¹	Sample size ²
One	High	0.07 ± 0.06	17
Two	Low	0.18 ± 0.17	9
Three	High	0.07 ± 0.05	8

¹Number of displays per min eagles were present at focal salmon.

²Number of focal salmon observed.

Table 4-8. Responses of feeders to challenges by pirates under varying food regimes. Dates of periods are: one - 11/4/80 to 11/27/80 and 11/17/81 to 12/9/81; two - 12/1/80 to 12/5/80 and 12/10/81 to 12/16/81; ; three - 12/6/80 to 12/8/80 and 12/17/81 to 12/23/81. Criteria for judging food level are presented in Methods.

Period	Food level	Displacement attempts No.	Retaliations		Retaliations successful	
			No.	%	No.	%
One	High	205	56	27	45	80
Two	Low	155	64	41	60	94
Three	High	107	31	29	29	87

Table 4-9. Frequency of foraging tactics under differing food regimes. Period and food level is described in Table 4-8.

Period	Food level	Hunt	Steal	Pct. steal
One	High	21	47	69
Two	Low	10	16	62
Three	High	8	20	71

regulation. Resource shortages bring increased escalation which forces low status individuals to leave a population (see Chapter VII).

Interestingly, as food levels declined, the frequency of stealing rose slightly but not significantly and the success rate of pirates dropped. Presumably, feeders won more contests when food levels were low because they were more willing to escalate than were pirates. Why this is so is not clear.

The data, thus, are inconclusive on the effect of food levels on the pirating frequency ESS point (Figure 4-8). More observations over a wider range of food levels are needed to determine if the ESS point changes in the FEEDING BOWL as food supplies vary. Figure 4-8 is interesting, nonetheless, because it shows that a constant ESS point is theoretically possible in producer-scrounger type contests despite changing food abundance. This outcome runs counter to the intuitively appealing assertions of Kushlan (1979) and Stalmaster (1981) that pirating has high payoff when food is scarce but is maladaptive when food is plentiful.

CONCLUSIONS

Evolutionary game theory has proved to be an effective approach for analyzing bald eagle foraging behavior. By testing predictions derived from game theory several facets of contest behavior of eagles have been revealed. Contrary to the claims of Ben Franklin and some modern ecologists, pirating by eagles is neither vindictive nor suboptimal. Eagles may hunt and pirate at rates which maximize fitness. Data from 14 focal eagles suggests that frequency dependent selection has adjusted the rates of hunting and stealing population wide to the ESS point where the rewards of each are equal. The best strategy for each eagle is dependent upon its phenotype. Small, young, or more satiated birds probably do better by hunting while large, hungry adults benefit from stealing and hunting. Interestingly, pirates assess the phenotypic traits of feeders and often try to steal from those that are most likely to retreat. Hungry eagles capitalize on the assessment capabilities of others; they dissuade attackers by advertising that they are hungry and willing to fight. A result of assessment is that contests are usually settled without escalated fighting. Because of assessment behavior and the fact that a bird's dominance decreases as it eats more, food defenders are at a disadvantage to challengers. Consequently there is a continual turnover of owners at a prey item.

These findings on foraging behavior have important implications for our knowledge of adaptations for survival and reproduction in this species, a topic that is discussed in Chapter VII.

The work also served to validate predictions of game theory. A producer-scrounger type population (Barnard and Sibly 1981) appeared

to be at an evolutionarily stable state. Also, differences between players and assessment behavior typically resulted in contest settlement without escalation.

Lastly, new perspectives were offered on the function of displays and the effects of resource dynamics on contest strategies. Evidence was provided that assessment cues may carry information not only on RHP but also on expected gain and intentions. Furthermore, a case is made that some ritualized displays evolved as assessment cues while others evolved as pure signals of intentions. These displays are held reliable because cheating is either impossible or costly. Finally, it was shown theoretically that ESS's may or may not change in response to resource dynamics depending on whether the rewards for different strategies vary proportionally.

CHAPTER V

REGULATION OF BREEDING

INTRODUCTION

Most studies of bald eagle reproduction were done in environments that had been severely altered by man (Chapter I). Even the earliest of these works showed a downward trend in productivity. The breeding population in a portion of Florida dropped from 72 pairs in 1946 to 43 pairs in 1957 and then to 35 pairs in 1964 (Sprunt 1969). New Jersey had 35 pairs in 1937 and only 2 in 1965. A trend of relatively fewer subadult eagles migrating over Hawk Mountain, Pennsylvania in fall suggests that reduced fecundity was widespread in eastern North America. The subadult proportion fell from a mean of 37% during 1931-45 to 23% during 1954-60 (Sprunt 1969). Breeding losses continued through the 1960's (Sprunt et al. 1973). By the mid-1970's, however, productivity stabilized in some regions (Nesbitt et al. 1975) and began to increase in others (Grier 1982).

The factors responsible for these dramatic fluctuations in productivity are not well known. Human disturbance, loss of habitat, and shooting were suggested by some investigators (Sprunt 1969). More recent studies strongly implicate chemical contaminants. An inverse relationship was found between DDE (a metabolite of DDT) in eagle eggs and the number of young produced per breeding area (Grier 1982, Wiemeyer et al. 1984). The recent increase in eagle reproduction in some areas is attributed to a ban on the use of DDT in 1972 (Grier 1982).

Reproductive Patterns in Pristine Environments

If anthropogenic disturbance limits productivity in man altered ecosystems, what factors regulate breeding in natural environments? While eagle populations in the relatively pristine habitats of southeast Alaska are large and stable, breeding rates are surprisingly variable. Hansen and Hodges (in press) found the proportion of adults engaged in breeding was 84, 38, 43, and 14% in 1970, 1971, 1972, and 1979, respectively. Thus, more than half of the adults failed to breed in 3 of 4 years of study. Surpluses of non-breeders are common in other avian species (Brown 1969a), but the only record, to my knowledge, of non-breeder frequency exceeding that mentioned above is for tawny owls (Strix alyco). Southern (1970) found 100% of his study population failed to breed one year.

Moreover, a substantial downward trend in eagle productivity in southeast Alaska is apparent in recent years. In Seymour Canal on Admiralty Island, the percentage of active nests dropped from a mean of 33.4 (± 5.8)% during 1972-78 to a mean of 18.8 (± 3.6)% in 1979-83 (Hodges 1982, Hodges, unpublished data) (Figure 5-1). The average number of young per active nest also fell from 1.6 (± 0.2) to 1.4 (± 0.1) during those years. Similar reductions in nest activity occurred throughout southeast Alaska (Hodges and Robards 1982).

These surprising patterns in productivity in what is thought to be pristine habitat call into question the factors that influence breeding in this population. Has natural disturbance produced long term population cycles that include periodic breeding depressions? Or,

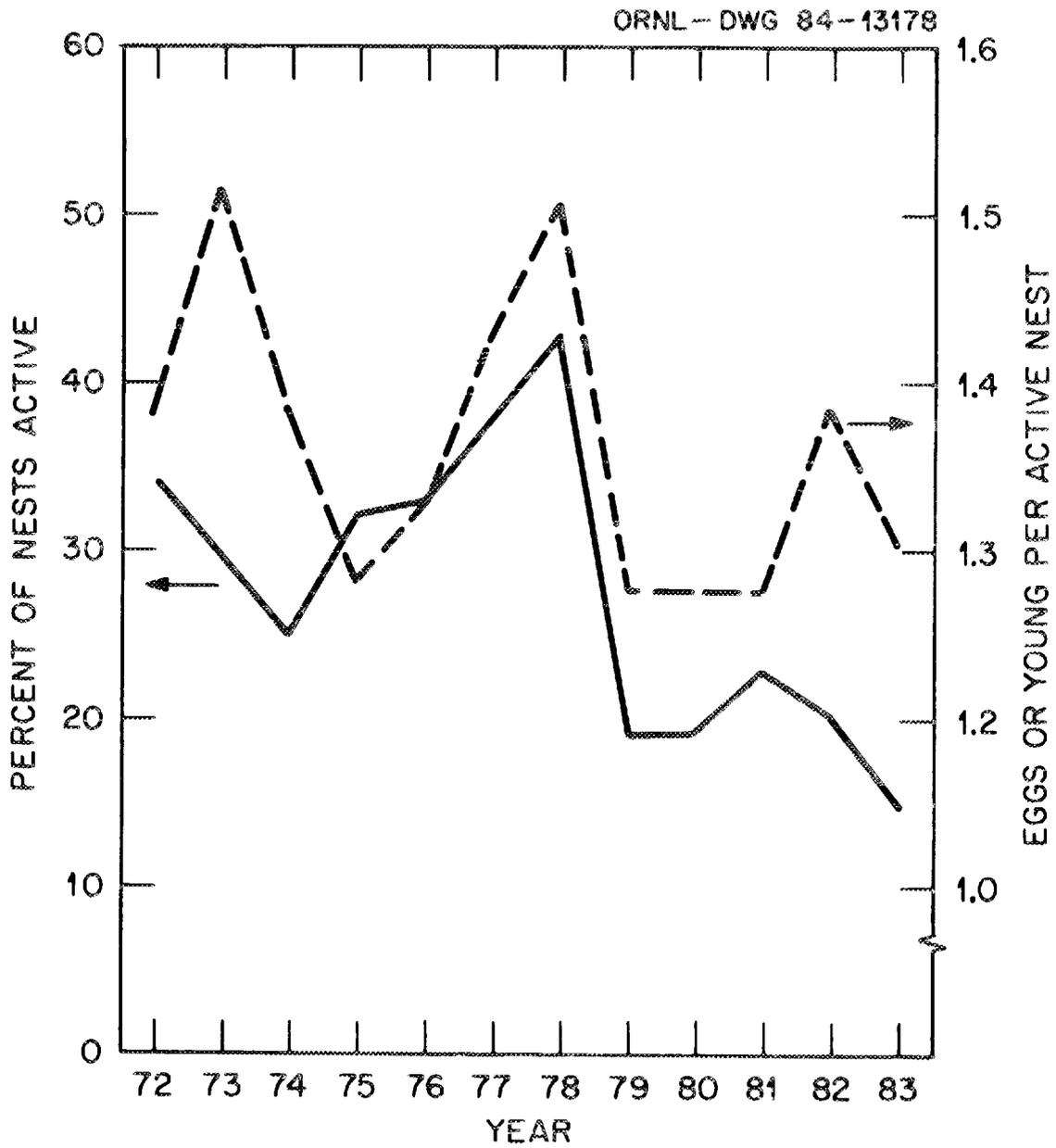


Figure 5-1. Proportion of nests active (solid line) and offspring per active nest (dashed line) in June in Seymour Canal, southeast Alaska (from Hodges 1982 and Hodges, unpublished data).

has anthropogenic disturbance artificially reduced breeding? In the latter case, surpluses of non-breeders may be harbingers of serious population declines.

Hypotheses and Predictions

This chapter reports on tests of three alternative explanations for the regulation of breeding by bald eagles in southeast Alaska. These hypotheses involve chemical toxins, habitat and food (Table 5-1).

DDE is known to inhibit calcium transport in birds such that females produce thin shelled eggs which are easily broken (Welty 1975). Other toxins including PCB's, dieldrin and mercury also accumulate in eagles and may inhibit reproduction but their specific effects are not known (Wiemeyer et al. 1984). Under the chemical toxins hypotheses, contaminated females lay inviable or thin-shelled eggs and nest failure results. Thus follows the prediction that bald eagles in southeast Alaska harbor high levels of toxins and produce thin-shelled eggs.

Loss of suitable nesting habitat is also cited as a cause of reduced breeding (Sprunt 1969, Nesbitt et al. 1975, Evans 1982). Attempts to correlate habitat attributes with productivity, however, have either failed to find relationships (McEwan and Hirth 1979) or have been inconclusive (Grubb 1976). If habitat limits breeding, it follows that active and inactive nests will differ in habitat characteristics as will successful and unsuccessful nests.

A third explanation for breeding reductions, seldom invoked for bald eagles, is food limitation. In other raptors, circumstantial evidence indicates that food abundance influences breeding rate, clutch

Table 5-1. Tests and predictions of three alternative hypotheses on the factors regulating breeding in bald eagles. Predictions in the body of the table are expected outcomes of tests assuming each hypothesis is correct.

Tests	Predicted Outcomes of Tests Under Each Hypothesis		
	Hypothesis 1: Chemical toxins	Hypothesis 2: Habitat quality	Hypothesis 3: Food limitations
Perform chemical analyses of eagle tissue and eggs	High levels of toxins and thin egg shells	Normal levels of residues and normal eggs	Normal levels of residues and normal eggs
Examine differences in habitat attributes between active and inactive nests and between successful and unsuccessful nests	No significant differences	Significant differences	No significant differences
Supplement food at breeding areas	No effect	No effect	Increase breeding density, advance laying date, raise clutch size, improve egg and chick survival

size and fledging rate (Southern 1970, Smith et al. 1981, Janes 1984). Timing of laying is also related to food supplies in several bird species (see Ewald and Rohwer 1982). Here I predict (1) surpluses of food in spring will increase breeding density, advance laying date, and increase clutch size; and (2) supplemental feeding of nesting pairs will improve the survival of eggs and chicks.

My field tests provided support for the food limitations and habitat quality hypotheses. These results are used to explain reproductive trends in southeast Alaska and in eastern North America. In Chapter VII, the implications of this work for density dependent population control and evolution of life history strategies are explored.

METHODS

The chemical toxins hypothesis was evaluated with results provided by the U.S. Fish and Wildlife Service Patuxent Wildlife Research Center. The center had analyzed 30 bald eagle carcasses and 10 eggs collected in southeast Alaska during 1970-80 (Wiemeyer et al. 1972, Wiemeyer et al. 1984).

Differences in habitat characteristics between active and inactive and between successful and unsuccessful breeding areas were examined with discriminant analysis. Included in the data set were forty-one breeding areas in the Chilkat Valley (excluding the estuary) for which habitat variables (Table 3-3, p. 50) and nest status were known. Habitat attributes at each territory were measured once and were considered to remain unchanged throughout the study. Nest activity for each year (1980-83) was paired with the habitat measures of a breeding

area. From each territory up to four observations were derived (one per year). Estuary nests were omitted from analysis because there was good reason to think that they were very productive not because of the unique habitat attributes of the coastal forest in which they were positioned but because they were adjacent to excellent feeding grounds. Thus, inclusion of these breeding areas in the habitat analysis would have biased the results.

A fortuitous "natural experiment" allowed for testing the effects of spring food supplies on incidence of breeding, laying date and clutch size. During spring 1980 and 1981, food was abundant nowhere in the freshwater habitats. In 1982 and 1983, the carcasses of salmon that had spawned in the Council Grounds in winter were preserved in river ice until spring-melting made them accessible to eagles. The food patch in March, 1982 was large enough to attract 200-300 birds for a 2-3 week period but was not quantified further. In 1983, fish counts revealed that about 900 carcasses were available daily for 5 weeks in late March and April.

The effects of the spring food patches on breeding density were examined in two ways: (1) the proportion of active nests throughout the Chilkat Valley in 1980 and 1981 when food was sparse was compared to that in 1982 and 1983 when food was locally abundant, and (2) the difference in nest activity between the Council Grounds and the Chilkat and Klehini River sections in 1980 and 1981 were compared to that in 1982 and 1983.

In 1983, laying dates in the Council Grounds were compared with those from other river sections. During April and early May,

39 occupied breeding areas were surveyed from air and ground every 2-5 days. The data of laying at each nest was assumed to be just prior to the first survey date that an adult was seen in incubating posture in the nest.

Eggs and chicks in 35 nests were counted by helicopter on June 7, 1983, approximately 4-6 weeks after eggs were laid. At that time, 56% of the offspring were hatched. Mean differences in clutch size within 3 km of the food patch and more than 3 km from the food were analyzed. Some eggs or young perished prior to the helicopter survey; 16% of the offspring in 9 nests are known to have been lost between May 7, 1983 and June 7, 1983. Comparison of clutch sizes, despite the late survey date, seems valid because the offspring in each river section were probably equally susceptible to mortality.

By late April of 1983, salmon carcasses in the Council Grounds were removed by high water and no food clumps were present in the valley. An artificial feeding experiment was initiated in mid-May. Food was provided at nine active breeding areas which were randomly selected from those that were accessible. At experimental breeding areas, approximately 500 g of spawned-out salmon was provided per family member per day. This amount is equivalent to the average daily caloric requirement of adult bald eagles in winter (Stalmaster 1981). The fish were collected from the Council Grounds in January and kept frozen until needed. Food was placed three times weekly on gravel bars within each experimental breeding area such that it was visible from the nest.

The artificial feeding sites were observed from an inconspicuous vantage point to determine if the food was being utilized by territory

owners. Two pairs refused to take the supplemental food and were omitted from the experimental set in late May. The experiment was continued until July 9, 1983. The chicks remaining in each nest were counted by airplane between July 6, 1983 and July 9, 1983. Three separate flights were made over some nests to ensure accuracy. Survival rates of offspring and nest success between the helicopter flights of June 7, 1983 and airplane surveys of July 9, 1983 for the 7 experimental and 29 control nests were compared.

RESULTS

Chemical Toxins

The Patuxent Wildlife Research Center reported that 10 bald eagle eggs from southeast Alaska contained no abnormal levels of chemical residues and average egg shell thickness was not different from the pre-1946 norm (Wiemeyer et al. 1972, Wiemeyer et al. 1984). Examination of 30 bald eagle carcasses revealed no unusually high levels of chemical contaminants except for mercury. The mercury levels in livers averaged 5 ppm wet weight; a figure well below that thought to affect either survival or reproduction (S. Wiemeyer, pers. commun.). Thus, it is unlikely that chemical contaminants have depressed nest success in southeast Alaska.

Habitat Quality

Discriminant analysis showed no differences in the habitat characteristics of active ($n = 72$) and inactive nests ($n = 70$) when all habitat variables were included in the model ($n = 142$, $F = 1.37$,

$p > 0.18$). When variables were analyzed individually, three discriminated between active and inactive nests (dominance class of nest tree, elevation of nest tree above water and exposure to human activity).

Successful and unsuccessful nests were not separable by habitat attributes under either multivariate ($n = 142$, $F = 1.19$, $p > 0.30$) or univariate models. Therefore, selection of breeding areas by nesting pairs appears to have been related to specific habitat features. But the survival of eggs or chicks in nests was not habitat related.

Food Limitations

Breeding was also associated with food abundance. During spring 1982-83 when food was clumped in the Council Grounds, the proportion of active nests in the Chilkat Valley was greater than in 1980-81 when no food patches existed (Chi Square, $n = 291$, $\chi^2 = 12.8$, $p < 0.001$) (Table 5-2). Moreover, change in nest activity from years of sparse food to years of high food was greatest in breeding areas that were closest to food patches. In 1982-83, activity of breeding areas within 6 km of the salmon carcasses was higher than in breeding areas more distant from the food (Z-Test for Differences Between Proportions, $n = 109$, $Z = 2.3$, $p < 0.02$, Zar 1974) (Table 5-3). However, no such pattern existed in 1980-81 when food was not clumped ($n = 100$, $Z = 1.1$, $p > 0.13$) (Table 5-4).

To determine whether feeding conditions or habitat quality was more closely related to incidence of breeding, a model including the three significant habitat attributes and proximity of nests to food

Table 5-2. Proportion of active nests in the Chilkat Valley in years when food was relatively abundant or relatively sparse.

Treatments	Nest status	
	Number active	Number inactive
Food patches not present (1980-81)	55	90
Food patches present (1982-83)	87	59

Table 5-3. Nest activity within two portions of the study area in 1982-83 when food patches were present in the Council Grounds.

River sections	Nest status	
	Number active	Number inactive
Council Grounds	35	16
Chilkat/Klehini	26	32

Table 5-4. Nest activity within two portions of the study area in 1980-81 when food was relatively sparse.

River sections	Nest status	
	Number active	Number inactive
Council Grounds	17	28
Chilkat/Klehini	14	41

supplies was analyzed with data from 1982-83. The proximity to food variable was best able to discriminate between active and inactive nests (proximity to food -- $p < 0.02$; nest tree dominance -- $p < 0.15$).

Laying date was also influenced by proximity to spring food supplies. Pairs nesting within 3 km of food patches laid eggs earlier than those nesting further from food clumps (Chi-Square, $n = 39$, $\chi^2 = 10$, $p < 0.01$) (Table 5-5). Mean clutch size, however, was not significantly larger within 3 km of food supplies (1.94 ± 0.56) than elsewhere in the Chilkat Valley (1.71 ± 0.47) (Two Sample T-Test, $n_1 = 17$, $n_2 = 14$, $t = 0.32$, $p > 0.35$).

Finally, the supplemental feeding experiment showed that feeding conditions after eggs are laid also affects reproduction. Nest success during June was higher at breeding areas where food was provided than at controls (Exact Probability Test, $n = 35$, $p < 0.04$) (Table 5-6). In experimental nests 4 of 12 offspring survived while 2 of 48 survived in control nests.

Table 5-5. Effect of food availability on laying date.

Proximity of nests to food patches	Eggs laid	
	Before 4/26	After 4/26
< 3 km	11	8
> 3 km	2	18

Table 5-6. Effect of supplemental feeding of breeding adults on nest success between June 7, 1983 and July 7, 1983.

Treatments	Nest status	
	Number successful	Number unsuccessful
Food provided	3	4
Control	2	27

DISCUSSION

Evaluation of Hypotheses

In the Chilkat Valley, breeding rates and nest success varied independently and it is necessary to consider factors regulating each.

Incidence of Breeding

Egg-laying within a breeding area was related to both food abundance and habitat quality. Evidence favoring the food hypothesis comes first from the fact that more nests were active in the valley in years when food was plentiful. Broadscale factors like regional weather were probably not responsible for this pattern because available data on changes in nest activity elsewhere in southeast Alaska during those years (Figure 5-1) correlate poorly with trends in the Chilkat Valley. Breeding distribution within the valley provides stronger indication of a causal relationship between food supplies and egg laying. Only in years when food was abundant in the Council Grounds was the proportion of active nests near the Council Grounds significantly greater than that elsewhere in the valley.

There are two feasible explanations for why food supplies influenced breeding: (1) females may require extra food in spring to manufacture eggs (e.g., red-billed queleas, Jones and Ward 1976); (2) the distribution of breeding eagles throughout the Lynn Canal may shift with food availability. The latter possibility cannot be rejected with present data since females, already in breeding condition, may move to the Council Grounds when salmon is prolific because food supplies in spring are indicative of feeding conditions later in the nesting period. However, the ephemeral nature of food patches in southeast Alaska make it doubtful that food abundance at one point in time is predictive of feeding conditions months later.

The habitat quality hypothesis was also supported. Active and inactive breeding areas differed in dominance class of nest trees, elevation of nest tree above water and in nearness to human activity. The positive relationship between breeding and human activity is certainly coincidental. This variable was a good discriminator because many productive nests in the Council Grounds were near a road. Proximity to food, rather than nearness to a road, undoubtedly explains these nests being active.

What is the relative importance of food and habitat in accounting for incidence of breeding? In the analysis including the three habitat attributes and distance of nests to food, the food variable best discriminated between active and inactive breeding areas. Furthermore, habitat was probably associated with nest activity precisely because eagles use habitat while foraging. Nest tree dominance class and elevation above water are often indicative of the quality of an eagle's

view of the feeding grounds from its nest. In support of this, Janes (1984) suggested that regularly dispersed perches in the breeding territories of red-tailed hawks enhanced the birds' foraging efficiency.

Laying Date and Clutch Size

As predicted by the food hypothesis, plentiful food in spring advanced laying date. Perrins (1970) observed that nestling mortality increased late in the breeding season and hypothesized that evolution favored females that laid eggs as early as food supplies allowed. Supplemental feeding experiments on several species confirmed a positive relationship between food abundance and timing of breeding (see Drent and Daan 1980 and Ewald and Rohwer 1982). As with incidence of breeding, it is not clear if females lay earlier when food is plentiful because they need additional food to make eggs or because they anticipate feeding will be good later on. In any case, early laying would seem advantageous in bald eagles. Juveniles fledging earliest have more time to acquire the skills needed to survive their first winters.

Clutch size is also influenced by feeding conditions in some species (Drent and Daan 1980). The absence of this effect in Chilkat eagles may be explained if (1) clutch size does not change with food abundance in these birds, or (2) because of the small clutches of eagles, large samples are needed to detect the positive relationship between food abundance and number of eggs laid.

Nest Success

Results of tests on the regulation of egg and chick survival were straight forward; the chemical toxins and habitat quality hypotheses

were rejected while the food hypothesis was supported. No abnormal levels of toxins were found in eagle carcasses or eggs. Successful and unsuccessful breeding areas did not differ in habitat attributes. However, nest success was dramatically improved by supplemental feeding. The loss of some offspring from provisioned nests may have been due to competition for food from non-breeders. The experimental nests that failed were in river sections supporting the highest densities of non-breeders.

The conclusions of this work are: (1) food abundance in spring strongly influences where or if Chilkat eagles lay eggs and when they lay eggs; (2) habitat quality is important when breeding eagles select a breeding area, partially because habitat aids in foraging; and (3) food supplies during incubation and rearing regulate offspring survival. The data leading to conclusion (3) comprise the first experimental evidence for any species of diurnal raptor that food supplies influence egg and chick survival.

Implications

Chilkat Valley and Southeast Alaska

The reproductive patterns in the study area and throughout the region are now more easily interpreted. The variability between sections of the Chilkat Valley in nest activity and nest success probably reflected differential food availability. Productivity was consistently high in estuaries because food abundance and foraging conditions were relatively stable there. In contrast, these factors were variable in riverine habitats. Availability of salmon carcasses

in spring fluctuated due to events of the previous winter. Also, hunting conditions fluctuated with river turbidity; siltation is controlled by ambient temperature and rates of glacial melting. Thus, the number of chicks fledged from riverine nests was high in years when feeding remained good and low in other years.

Similarly, the downward turn in nest activity and young per active nest since 1978 in Seymour Canal is likely due to reduced food availability to breeders. Natural fish cycles, weather fluctuations, commercial fish harvest, or increased intraspecific competition could lead to broadscale food stress in breeding eagles.

Similar events probably control breeding throughout southeast Alaska. Loss of habitat, however, may become an increasingly important secondary factor. Although Hodges and Robards (1982) found only one habitat attribute of breeding areas (nest height) correlated with nest activity throughout the region, Hodges (1984) found that breeding habitat was being destroyed by clearcut logging of coastal forests. As mature forest is removed from shorelines, total habitat available for breeding declines.

Why are there so many non-breeders in southeast Alaska in some years? The most parsimonious explanation in light of the results presented herein is that breeding rate is controlled by food abundance. I believe only a portion of the potential breeding sites in the region offer food supplies sufficient for females to attain breeding condition. When those sites are saturated, the remaining adults are forced to forego breeding that year. Because food supplies fluctuate, the number of suitable breeding sites and thus breeding rates change between years.

Knowledge of the factors regulating food abundance is important for eagle management. Recent anthropogenic disturbance such as over-fishing may be artificially depressing breeding rates. If so, bald eagle numbers will plummet as natality fails to balance mortality. More likely, natural patterns of resource distribution allow more eagles to survive than can reproduce. Surpluses of non-breeders may thus be a natural feature of the northwest coast population. The recent decline in breeding rate may be only a portion of a long-term population cycle, one possibly mediated by density dependent processes. Each of these possibilities will be explored more fully in Chapter VII.

Eastern North America

The finding that food and habitat control bald eagle reproduction in southeast Alaska provides insights into historic trends of populations in eastern North America. Decimation of anadromous fish and coastal forests by Euro-Americans undoubtedly constricted the number of suitable breeding sites. Depressed breeding rates and the population declines described by 17th century naturalists probably followed. The decline in breeding was further exacerbated by DDT after the chemical was introduced in 1942.

The importance of food supplies to breeding may have become even more pronounced after eagles became contaminated. DDE is stored in body fat and may occur at levels that would be fatal if released to the nervous system (Welty 1975). Well-fed eagles may carry heavy loads of DDE and reproduce normally. Energy stressed eagles, however, metabolize the DDE laden fat and jeopardize reproduction or even survival. Clearly, enhancing food supplies would be a valuable technique for hastening the recovery of contaminated populations.

CHAPTER VI

ADAPTATIONS FOR SURVIVAL AND REPRODUCTION
AND POPULATION LEVEL CONSEQUENCES

Earlier chapters established that the Pacific northwest coast offered bald eagles extremely unstable food supplies. The cycles of anadromous fish and fluctuating weather conditions result in food availability being spatially and temporally variable. Periods of overwhelming abundance are offset by times of severe scarcity. Such a boom-bust food economy was probably prevalent over much of North America in pre-settlement times and consequently was a major force in shaping the evolution of bald eagles. Evidence that both survival and reproduction are regulated by food was provided earlier. How have eagles responded evolutionarily to the selective pressures imposed by periodic food shortages? This chapter first examines the adaptations and strategies of eagles for coping with food stress. Thereafter, the consequences of these adaptations at the population level are discussed.

STRATEGIES FOR SURVIVAL

The means by which eagles maximize survival can be conceptualized by considering how energy input is maximized, how energy output is minimized, and how injury is minimized (Figure 6-1).

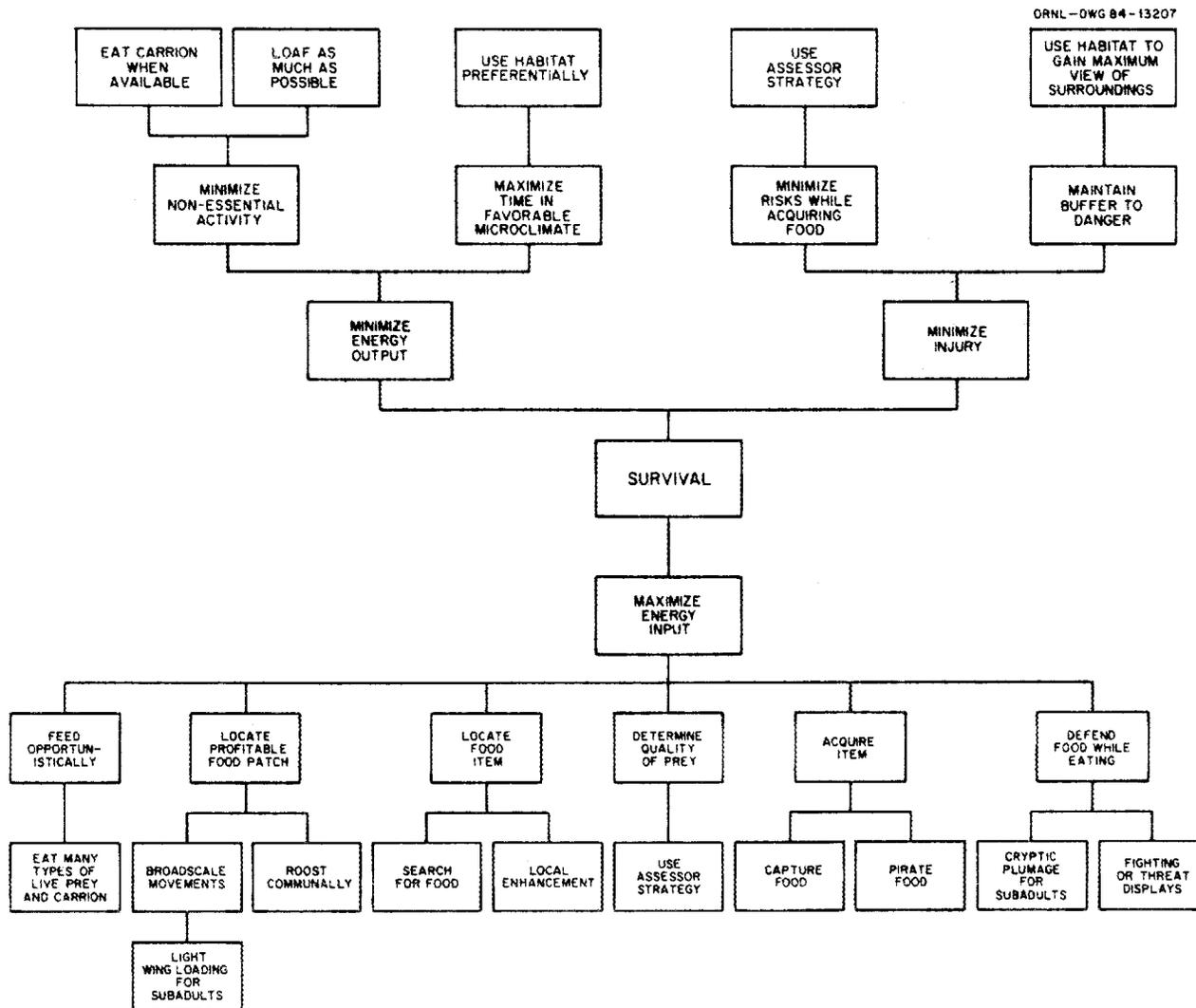


Figure 6-1. Conceptual model of adaptations and strategies with which bald eagles maximize survival.

Energy Input

Feeding Niche

Bald eagles are surprisingly opportunistic feeders (Chapter III). Although they are primarily piscivores, they will eat virtually any vertebrate (and many crustaceans) that they can safely subdue or that they find dead. This broad palate allows the birds to take advantage of a variety of types of food patches. When resources in one patch expire eagles are able to switch to another.

Locating Food Patches

Bald eagles locate ephemeral food supplies through broadscale movements. The telemetry studies reported herein (Chapter III) and those of Young (1983) revealed that an individual, when not breeding, may visit concentrated food supplies that are spread over areas exceeding 100,000 km² in size.

The mechanisms by which distant food patches are located are not known. McClelland et al. (1982) speculated that eagles may discover feeding sites by chance, then memorize their locations and return in subsequent years. He also suggested that some birds, particularly young ones, may learn of food patches by following other migrating eagles.

Over shorter distances, sight is undoubtedly used to find food supplies. Seeing either prey items or groups of eagles is often evidence of a feeding site. McClelland et al. (1982) estimated an eagle could detect a soaring conspecific up to 23 or more kilometers away and groups of soaring eagles at greater distances.

Knowledge of location of food that is within about a half day's flight could be acquired through communal roosting. As discussed in Chapter III, eagles successful in finding food may be followed from a roost the next morning by hungry conspecifics.

Recall that subadults from southeast Alaska wandered great distances in search of food during late winter and spring while adults attempted to obtain breeding territories. Natural selection appears to have favored differential morphologies for these ecologically different life history phases. Subadults have a greater wing area to body weight ratio than adults (Table 6-1). Light wing-loading facilitates soaring flight (Welty 1975) while heavy loading presumably aids in the agile flight needed in territorial defense (Feinsinger and Chaplin 1975).

Locating Prey Items

Once within a food patch, eagles locate individual prey items by searching for them and by searching for conspecifics that appear to be feeding. A bald eagle standing on the ground is more conspicuous than most prey items and thus a hungry eagle can increase its chances of finding food by cueing on both. Knight and Knight (1983) placed two clumps of on average five salmon carcasses each about 90 m apart on open gravel bars in an area supporting wintering eagles. They found that 95% of arriving eagles facing a choice between a food clump attended by other eagles and one unattended went to the former. They took this as evidence of local enhancement (food finding by cueing on other birds) but acknowledged the likely possibility that the new arrivals may have seen both food clumps and selected the attended clump

Table 6-1. Estimates of wing loading in adult and subadult bald eagles of each sex. Net weights (crop and stomach contents excluded) and wing lengths are from Imler (1941) who shot and measured eagles in southeast Alaska. Length of first secondaries were measured on museum specimens by Bortolotti (1984). Secondary feather lengths for subadults are averages of Bortolotti's young immature and old immature age classes. Wing area is calculated as if each wing is rectangular with a width equivalent to the length of the first secondary feather. These calculations are crude but useful for comparisons between age classes. Imler (1941) provides only averages so statistical analysis of these data is not possible.

Age	Sex	Net weight (g) (n)	Wing length (CM) (n)	First Secondary (cm) (n)	Wing area (cm ²)	Wing area (cm ²)
						Net weight (g)
Adult	M	4230 (35)	58.6 (35)	32.6 (18)	1910	0.45
Adult	F	5250 (37)	62.5 (37)	36.9 (14)	2306	0.44
Subadult	M	4050 (18)	60.6 (18)	36.4 (21)	2206	0.54
Subadult	F	5100 (18)	65.2 (18)	39.3 (13)	2563	0.50

for reasons unrelated to its high visibility. Stranger evidence of local enhancement comes from the Chilkat Valley. I placed a mount of an adult bald eagle in feeding posture along a river channel where there was no food and found that of 11 eagles separately approaching overhead with directional flight, 7 altered their flight paths to take a closer look at the mount and 4 did not respond. The interested eagles were presumably inspecting for food near the mount.

Assessment of Prey Profitability

After eagles locate food they often select those prey items that are most profitable. Stalmaster (1981) found that eagles preferentially go to salmon carcasses with skin ripped and flesh exposed -- these can be consumed more quickly. He also found that the birds reduce the likelihood of obtaining frozen (and thus inedible) carcasses by preferentially taking those that are in water.

Prey Acquisition

Procuring food by both hunting and stealing is another strategy for survival. The fact that the Chilkat population is in an evolutionarily stable state in foraging strategies (Chapter IV) shows that individuals use the combination of hunting and stealing that maximizes their fitnesses. The ESS is phenotype dependent; small and young birds probably hunt more and pirate less than large adults. Also, individuals switch from stealing to hunting as they grow more satiated.

Pirating is common under both high and low levels of food abundance because it offers rewards and costs comparable to hunting. Eagles obtain nearly equal feeding rates through each strategy and risk

of injury is low for both. Pirates achieve this low risk of injury by assessing the size and hunger level of opponents and selecting for attack those that are most likely to yield. They also use threat displays to dissuade feeders from defending their prey.

Defending Food

When an eagle secures food it is at a disadvantage to challengers because (a) the more a bird eats the less chance it has of winning a contest, (b) aerial attackers probably have a positional advantage, and (c) challengers typically select opponents they can defeat (Chapter IV). Hungry food holders probably have, however, at least one strategy in addition to fighting for dissuading attacks. They may use displays to advertise that they are hungry and thus willing to fight; this would reduce likelihood of attack.

Another way to avoid being kleptoparasitized is to not attract challengers. I propose that the drab and cryptic plumage of subadults acts to conceal them from conspecifics. A feeding subadult would be seen by, and thus attract, eagles from a much smaller area than would a feeding adult.

A cryptic plumage may also allow subadults better access into the territories of breeding adults - either because they are less likely to be seen by the owners or because their plumage signals to the breeders that the trespassers cannot breed and thus will not try to win territory ownership.

Neither of these hypotheses has yet been tested. The latter, however, has been used to explain subadult plumage in other species (Davies and Houston 1981, Ewald and Rohwer 1980, Steenhof 1983).

If there are advantages to being cryptic, why do adult eagles wear a very conspicuous plumage? Presumably a bright plumage helps in winning or defending a breeding territory (see Selander 1965).

Energy Conservation

Energy stress is reduced not only by maximizing consumption, but also by minimizing energy expenditures. Bald eagles use two behavioral strategies to conserve energy. They avoid nonessential activity and they seek favorable microclimates (Stalmaster 1981).

In western Washington, wintering bald eagles spent 97.7% of each day perching or roosting, and only 1% flying (Stalmaster 1981). For comparison, a non-breeding eagle in summer spent about 6% of each day flying (Gerrard et al. 1980). Stalmaster (1981, p. 94) concluded "Idleness [in bald eagles] appears to be an important strategy for winter survival." In fact, bald eagles probably prefer to take fresh carrion over live prey or decomposed carrion (Chapter III) because it offers a high return in calories for a relatively small investment in energy output or risk of injury.

The birds minimize the cost of thermoregulation by preferentially using habitat that offers a relatively favorable microclimate (Chapter III). They also depress their core temperature ($\approx 1.8^{\circ}\text{C}$) while roosting which conserves a projected 4.7% of total metabolic heat production (Stalmaster 1981).

Avoiding Injury

Risk of injury is minimized by selecting prey items judiciously and by maintaining a buffer to potential predators. The eagle's habits of taking carrion rather than live prey and using an assessor strategy while pirating were discussed earlier. Eagles lower risk of predation by perching and roosting in trees and by remaining constantly vigilant when on the ground.

STRATEGIES FOR REPRODUCTION

Acquiring a Mate

The process of mate selection is little understood in raptors. Bald eagles may establish or reestablish pair bonds while soaring or roosting at wintering grounds (McClelland et al. 1982) or while migrating to nest sites in early spring (Young 1983). Breeding pairs apparently do not travel together during most of the non-breeding season; pairing is rare at feeding aggregations except in late winter.

The number of years that mates remain together is also unknown. Anecdotal observations suggest that some pair bonds may last for several years. However, lost mates appear to be quickly replaced (S. Postupalsky, pers. comm.).

Food for Egg Production, Incubation, and Rearing

Egg production in birds is energetically expensive (Newton 1979). It is not known, however, when females acquire the reserves needed

for breeding (Figure 6-2). Newton (1979) raises two possibilities for raptors: (1) females may require nutrients for egg laying which occur at low abundance in food and thus can only be acquired over a period of several months; and (2) females may accumulate the necessary reserves in the weeks prior to egg laying. If bald eagles reach breeding condition in the weeks prior to laying date then different foraging strategies from those described above may be employed. The need to defend ownership of the nest precludes broadscale foraging movements. From the time the breeding area is established in spring until fledging time in late summer, food must be found within reach of the nest. Defending a feeding territory in addition to the nest itself is often the selected strategy. This strategy is presumably employed when the benefits of exclusive use of the food within the territory exceed the costs of evicting intruders. If food becomes very abundant in a feeding territory, however, breeders may cease defensive tactics because food is plentiful for all. Casual observations indicate that this is what happens in the Chilkat Estuary each spring when the eulachon run arrives. During the period when the fish are plentiful, nesting eagles stop defending their feeding territories and forage communally with non-breeders. These observations suggest that the feeding strategies of nesting eagles are not fixed, but rather vary with changing conditions.

An additional tactic for meeting energy needs is storing food in the nest. Whole or partial prey items often remain in nests for days. This apparent stockpiling may be a hedge against times when hunting is temporarily poor.

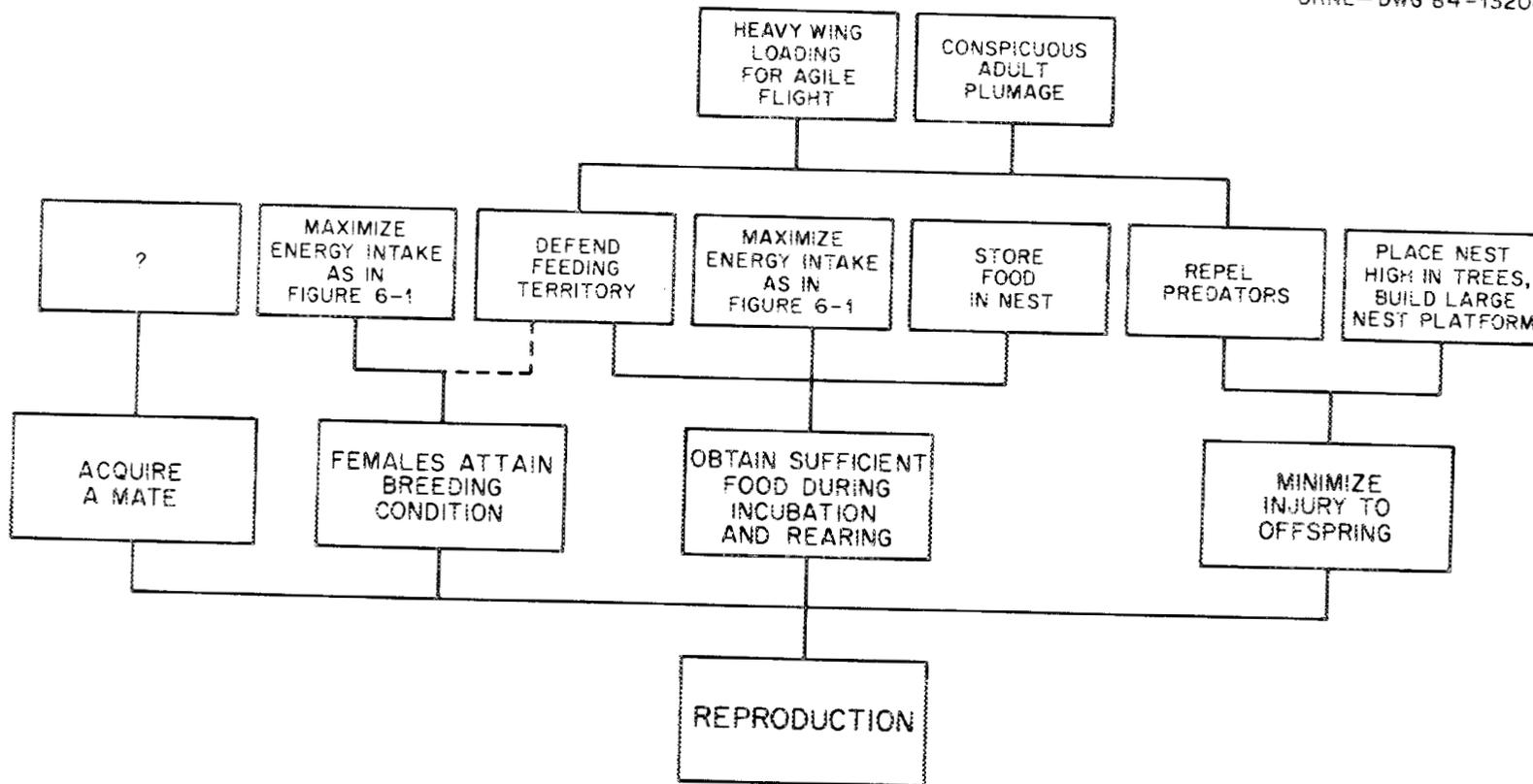


Figure 6.2. Conceptual model of adaptations and strategies for maximizing reproduction. Dashed line indicates a possible link.

Adaptations for defense of nest and feeding territory include relatively heavy wing-loading and conspicuous plumage. Bright plumage may advertise that a territory is occupied and heavy loading allows the agile flight needed to evict intruders.

Protection of Young

Injury to offspring is minimized by rearing young in large nests that are high above the ground and by parents warding off predators like ravens, magpies, or arboreal mammals. Nests placed high in trees are protected from all predators except those that can climb well or fly. The large nest platform reduces the chances that eaglets will accidentally fall from the nest. Finally, avian predators are driven off by nesting eagles in the same manner as are conspecifics.

POPULATION LEVEL CONSEQUENCES

The ephemeral food supplies of the northwest coast and the adaptations and strategies of bald eagles for minimizing food stress translate up scale and influence the properties of the regional population. Knowledge of these adaptations and strategies allows for the interpretation of the population characteristics described in Chapter III and offers insights into questions of conservation and management.

Dispersion

Bald eagles travel long distances in search of food. This mobility coupled with a broad feeding niche results in the species

being distributed over most of the North American continent. Furthermore, these traits allow the birds to cope with major landscape changes. Human development has, for example, destroyed many anadromous fish runs and reduced the abundance of large land and sea mammals that provided carrion for eagles. However, new food sources have also been created. Lake fish are killed by turbines at dams and hunting at waterfowl refuges produces large numbers of crippled ducks. Eagles are somewhat pre-adapted to utilizing novel food supplies and thus have been able to survive such landscape changes.

The dispersion of non-breeding eagles reflects the patterning of their food supplies; the birds are dense where food is abundant and scarce elsewhere. Because food is patchy along the northwest coast the non-breeding eagle population exhibits a clumped dispersion. An important consequence of eagles being drawn together at food patches is that social interaction is facilitated.

Sociality

To an individual eagle in a feeding aggregation, neighboring conspecifics are features of the environment which may aid or hinder the bird in its efforts to acquire resources. Either cooperative or competitive interactions may occur. A possible example of cooperative behavior is information exchange at communal roosts (Chapter III). If food occurs in large, unpredictable, and short-lived clumps then a bird knowing the location of a food patch will not pay a cost if it is followed to the food by roost mates. Exploitation competition will not

arise before the food expires for exogenous reasons (i.e., flooding). Further, the bird which finds food one day would benefit from roosting communally because it can then follow others to food when necessary at a later date. The hypothesis is plausible for eagles but not yet critically tested (see Knight and Knight 1983). The important consequence of such cooperative behavior would be more complete exploitation of the food resource by the population.

Interactions at communal roosts and while soaring may also facilitate pair bonding. Thus, the aggregation of birds from distant breeding areas may serve to enlarge the gene pool.

The most obvious type of social interaction at feeding concentrations are competitive. The pirating strategy (Chapter IV) is direct interference competition. Phenotypic differences allow some individuals to be successful at both stealing and defending food while others are good at neither. Small birds (and possibly young ones) have fewer foraging options. They are inept at stealing and if they do get food they are more likely than others to be attacked by pirates. The result is that when food is scarce these small or young birds do not get enough to eat. They must either move to another food patch or starve. The important conclusion is that social behavior in bald eagles is an important factor in the regulation of survival and thus of population size. Furthermore, the work on contest behavior in Chapter IV shows the actual mechanisms leading to this endogenous population control.

Regulation of Breeding

The strategy of broadscale movement in search of food is not an option for breeding adults during the nesting season. Breeders must forage within reach of their nests for the entire six month nesting period. If food is not available for as little as a week or two, the nesting effort may have to be aborted. A common strategy of breeders is to defend feeding territories. This results in breeding areas being regularly dispersed within suitable habitat.

The nesting studies of Chilkat eagles presented in Chapter V showed that nest site quality is determined primarily by food availability. Breeding density and offspring survival were highest where feeding was best. It is likely, then, that the total amount of suitable breeding habitat in southeast Alaska each year is determined primarily by food availability. Because the amount of food accessible to eagles varies between years, so does the abundance of suitable breeding habitat.

The number of breeders which acquire nest sites within the suitable habitat, I propose, is regulated by territorial behavior. The best competitors claim disproportionate shares of the habitat and the other eagles are forced to nest in marginal habitat or completely forego breeding that year (Figure 6-3). The large number of non-breeding adults found in southeast Alaska in some years (Hansen and Hodges, in press) is thus a consequence of a shortage of habitat offering sufficient food and of territorial behavior. Put more simply, more eagles can survive in the region than can reproduce. A surplus of non-breeders is probably a natural feature of the regional population.

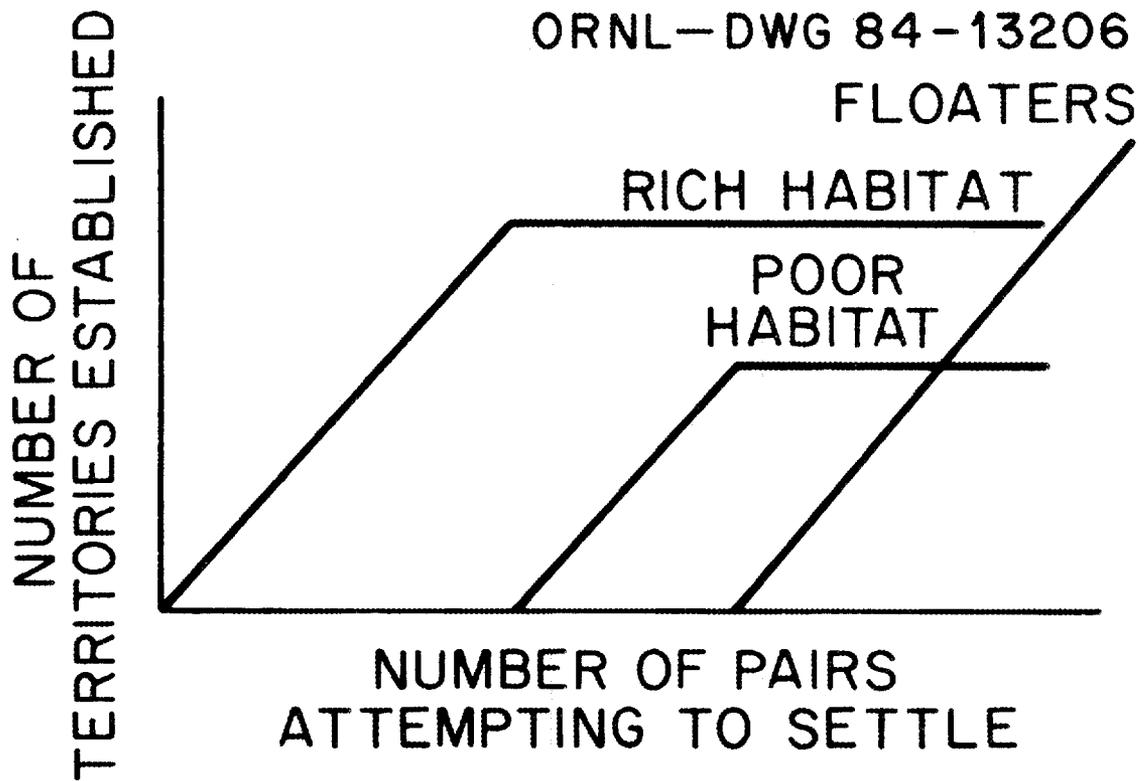


Figure 6-3. Hypothetical effects of territorial behavior on breeding densities in two habitats. In the model, birds occupy the rich habitat first until it is full, then other arrivals are forced to fill up the poor habitat. Finally, when all the available habitat is occupied, remaining birds are floaters and fail to get territories (after Brown 1969a).

The size of the surplus in any given year is dependent upon the survival rates of eagles (which are a function of the abundance of food clumps and intraspecific contest behavior as described earlier) and the abundance of breeding sites offering predictable food supplies.

Consequences of Non-Breeding Surpluses

The permanent presence of floaters may have important consequences on bald eagle evolution and population dynamics.

Delayed Maturation

If surpluses of non-breeders are a regular feature of a population for a long period of time, evolutionary responses may occur (Brown 1969b). A prolonged subadult period may be an adaptation to strong competition for nest sites.

Although large species of birds most often show delayed sexual maturity, there is no evidence that physiological constraints are responsible for this trend. Ducks and gallinaceous birds which breed in their first year are much larger than swifts or terns which do not breed until the second year (Selander 1965). Rather, it is believed that delayed maturation is favored by selection when it results in greater lifetime reproductive output (Lack 1954, Selander 1965, Wooller and Coulson 1977). If young eagles are poor competitors for suitable breeding sites, they may maximize lifetime reproductive fitness by avoiding the risks of trying to breed too early.

Clearly, delayed maturation in eagles would enhance survival of subadults because the evolution of traits which maximize survival would

not be constrained by traits which maximize reproduction. Young birds, not capable of breeding, are free to have cryptic plumage, and lighter wing loading which probably improve the ability to find and defend food.

Breeder/Non-Breeder Competition

Another possible consequence of a surplus of floaters is a long-term population cycle resulting from competition for food between breeders and floaters (Figure 6-4). Once suitable breeding habitat is saturated a surplus of floaters develops. If floaters intrude into breeding territories to forage, some breeders may get insufficient food and abandon their nests. Consequently productivity would decline and recruitment into the floater population would drop. The reduced intrusion pressure from fewer floaters would allow for increased productivity and the cycle would repeat itself. If the amount of suitable nesting habitat remains constant, in time an equilibrium may be reached where the number of floaters stabilizes as abundance of breeders remains somewhere below the point of habitat saturation. However, it is more likely that the abundance of suitable breeding habitat and survival rates of floaters vary considerably between years so that the ratio of breeders to floaters is ever changing.

The important implication of this model is that breeding rates, breeding density, and productivity may fluctuate between years in natural systems. Thus, the reduced breeding density and productivity in Seymour Canal since 1978 (Chapter V) may be part of a natural population cycle. Another possibility is that human activities have reduced fish stocks in the area and thereby lowered the amount of

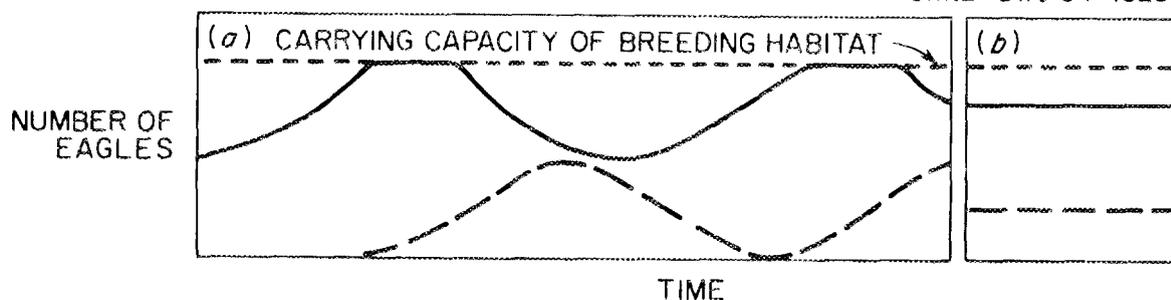


Figure 6-4. Theoretical long-term population cycles in bald eagles. (a) The number of breeders (solid line) increases until suitable habitat is saturated. Continued recruitment results in formation of a floating population (dashed line) which competes with breeders for food causing a reduction in breeding habitat. The reduced productivity leads to a drop in the number of floaters, food available to breeders increases, and the cycle begins anew. (b) In time an equilibrium may be reached where breeding and floating populations remain stable. It is unlikely, however, that the carrying capacity of the breeding habitat remains constant as shown in (a) and (b). The abundance of suitable breeding habitat probably fluctuates between years so the populations of breeders and floaters do not reach equilibrium.

suitable breeding habitat. The ramifications of the latter possibility are sufficiently serious to merit further study of the problem.

This chapter has explored some of the traits and strategies eagles have evolved or learned for maximizing survival and reproduction in the variable northwest coast environment. Also discussed were the ways in which these characteristics are manifested at the population level. The last chapter will examine in more detail the factors that regulate resource abundance along the northwest coast and the responses of eagles at various hierarchical levels to resource dynamics.

CHAPTER VII

ENVIRONMENTAL DETERMINANTS OF BEHAVIOR AND ECOLOGY:
A LANDSCAPE PERSPECTIVE

Since the pioneering work of Crook (1965) there have been myriad studies on the environmental correlates of social behavior. Collectively, these studies have played a major role in the development of behavioral ecology. Much, however, remains to be done. The ground swell of evidence that natural systems are not static but remarkably dynamic over many time scales (Delcourt et al. 1983) has stimulated interest in the general principles which govern how environmental dynamics influence organisms (Pickett and White 1984). This endeavor is greatly aided by the recent emergence of landscape ecology (Risser et al. 1984) which links disturbance and landscape change, and hierarchy theory (Allen and Starr 1982) which explores the interactions of levels of organization in nature. In this final chapter, I draw on these disciplines to synthesize my findings on environment-eagle interrelationships and to identify patterns which may be generalized to other systems.

As discussed in the INTRODUCTION, biotic populations are ultimately constrained by resource limitations and by vectors of disturbance which disrupt physiological processes in organisms (e.g., predation and disease). Disturbance, moreover, drives resource change through space and time. Thus it influences organisms directly through physiological disruption or indirectly by way of resource dynamics. Disturbance and resource dynamics operate at various hierarchical scales and elicit organismal responses at differing organizational levels.

As a way of integrating the effects of the northwest coast environment on bald eagles, I will describe: the distribution through time and space of the resources limiting eagle survival and reproduction; the disturbance regimes responsible for these dynamics; the responses of eagles to changing resources; and the organizational levels at which these responses occur.

PERTURBATION OR DISTURBANCE: A QUESTION OF SCALE

The ecological meanings of perturbation and disturbance can be confusing and thus they are differentiated here at the outset of the chapter. Ecologists normally view populations at steady-state as actually exhibiting dynamic equilibrium where frequent but mild perturbations cause the population to fluctuate about a mean. When perturbations are sufficiently irregular or extreme to push the population well away from the mean they are called disturbances (Karr and Freemark 1984). The threshold between perturbation and disturbance, however, is difficult to define because it is scale dependent. To illustrate the point, consider oscillations in the average energy status of eagles gathered at a food patch (Figure 7-1). The small fluctuations may be, for instance, responses to day/night cycles and the larger ones responses to local winter storms. The storms are clearly disturbances to individual eagles (some of whom may starve) but are mild and regular perturbations which are barely felt at the level of the regional population. For this reason then, disturbance can only be defined relative to a specified entity.

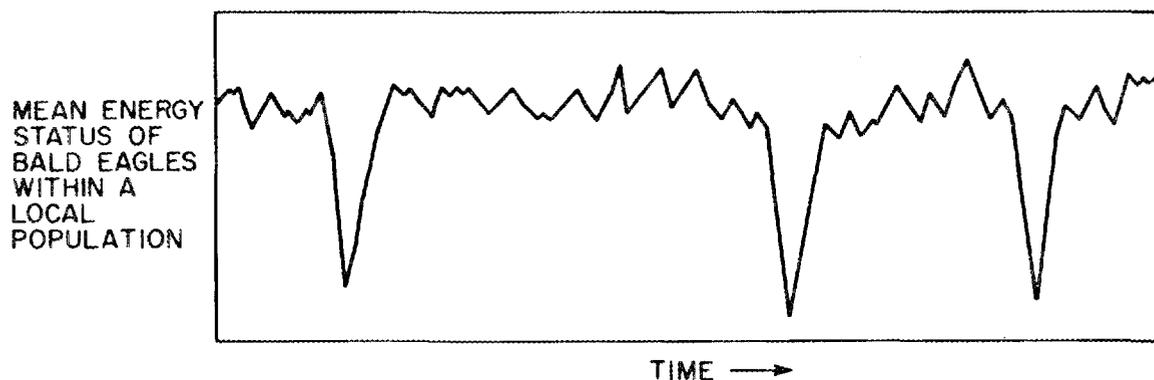


Figure 7.1. Hypothetical example to illustrate that the distinction between perturbation and disturbance is scale dependent. The larger oscillations are responses to disturbance at the level of individual eagles in a local population but are only perturbations at the level of the regional population.

RESOURCE DYNAMICS

Chapter VI presented a conceptual model showing that bald eagles enhance survival by avoiding food stress and injury (Figure 6-1, p. 122). The resources used to accomplish these objectives are food and habitat. Food intake directly improves energy status and habitat is used to reduce energy lost to thermoregulation. Further, habitat serves to maintain a buffer to danger and thus to minimize injury. Similarly, the main requirements for reproduction are achieving a positive energy balance and avoiding injury for all family members (Figure 6-2, p. 131). Thus, the primary resources that ultimately constrain fitness in bald eagles are food and habitat.

How are these resources distributed along the northwest coast? How does their distribution change over time and what are the forcing mechanisms?

The Patchwork Landscape

The vegetation across a natural landscape is seldom consistent, rather it is differentiated into a hierarchy of subunits (Watt 1947, Shugart 1984). For example, individual trees comprise stands which form communities which comprise forests. Each subunit is a patch that aggregates with other patches to form a higher level unit. A landscape, then, is a mosaic of patches which can be hierarchically classified. Because forces such as disturbance and succession constantly alter patches, the landscape is dynamic through time. It can be viewed as a patchwork quilt within which the colors, shapes, sizes, and positions of patches are ever changing.

This general notion of landscapes is useful for visualizing the distribution and dynamics of resources required by bald eagles. From the perspective of an eagle, the northwest coast is a dynamic mosaic of habitat units and food patches. Eagles can derive benefits from some patches but not from others. Consequently, the birds enhance fitness by maximizing time spent in favorable patches and minimizing time in unfavorable patches. This optimization problem is complicated by the fact that patches change due to disturbance.

Types of Habitat Patches

Habitat units functionally meaningful to eagles are defined by the seral stage of the vegetation and proximity to food supplies. The stages of primary succession in southeast Alaska are pioneer herb/shrub, alder/willow thicket, cottonwood forest, spruce/hemlock climax forest,

and, on poorly drained sites, muskeg (Chapter II). A gravel bar in the herb/shrub stage which is near a food source allows eagles to feed with full view of any approaching predators. Alder/ willow thicket and muskeg are of minimal value to eagles. Mature cottonwoods along streams offer hunting perches and nest sites and climax conifer forest provides sites for perching, nesting, and roosting. Habitat patches are distributed along the northwest coast at present such that old growth conifer forests dominate most marine shorelines and gravel bars edged by black cottonwoods cover flood plains.

Types of Food Patches

Food patches for eagles can be functionally defined by food availability but not by food abundance. The importance of the distinction can be illustrated by example. Salmon are abundant in the Chilkat River system in August, however, because of the turbid river water, eagles can only see and catch fish in the shallow channels of the Tsirku Delta. Thus food is only accessible to eagles on the delta, despite its abundance throughout the river. The northwest coast is comprised of units offering unique levels of food availability to eagles.

Food is distributed over the region in two ecologically important patterns: in large ephemeral clumps (e.g., salmon runs) and in small but regularly dispersed and predictable units (e.g., individual fish in an estuary). The coarse-grain pattern attracts groups of eagles while the fine grain pattern is the mainstay of nesting eagles.

Dynamics of Food and Habitat Patches

Perturbation affects the resources important to eagles at several scales (Chapter II) (Figure 7-2).

Day/night and tidal cycles effect the daily activity patterns of fish and the hunting conditions for eagles throughout the region. They inhibit food availability at some times of day and enhance it at other times.

A local storm may alter food availability in portions of the region for a week or more by causing flooding or burying food under snow. Storms may also deposit precipitation on tree branches and alter microclimate within stands.

Seasonal weather patterns influence both food and habitat over the region on a time scale of months. Changing water temperature and turbidity control the timing of anadromous fish runs. Summer warming and glacial melting raise turbidity in rivers and estuaries and restrict hunting by eagles. Seasonal weather also influences canopy density of deciduous trees and changes microclimates within stands.

A variety of abiotic and biotic factors control regional fish population cycles which have periodicities of two to six years.

Vegetative succession occurs over time scales of tens to hundreds of years. It is influenced by exogenous factors like glaciation, windthrow, and insect infestation. Endogenous factors such as nutrient cycling also influence succession. Successional processes are important determinants of the habitat types over the region.

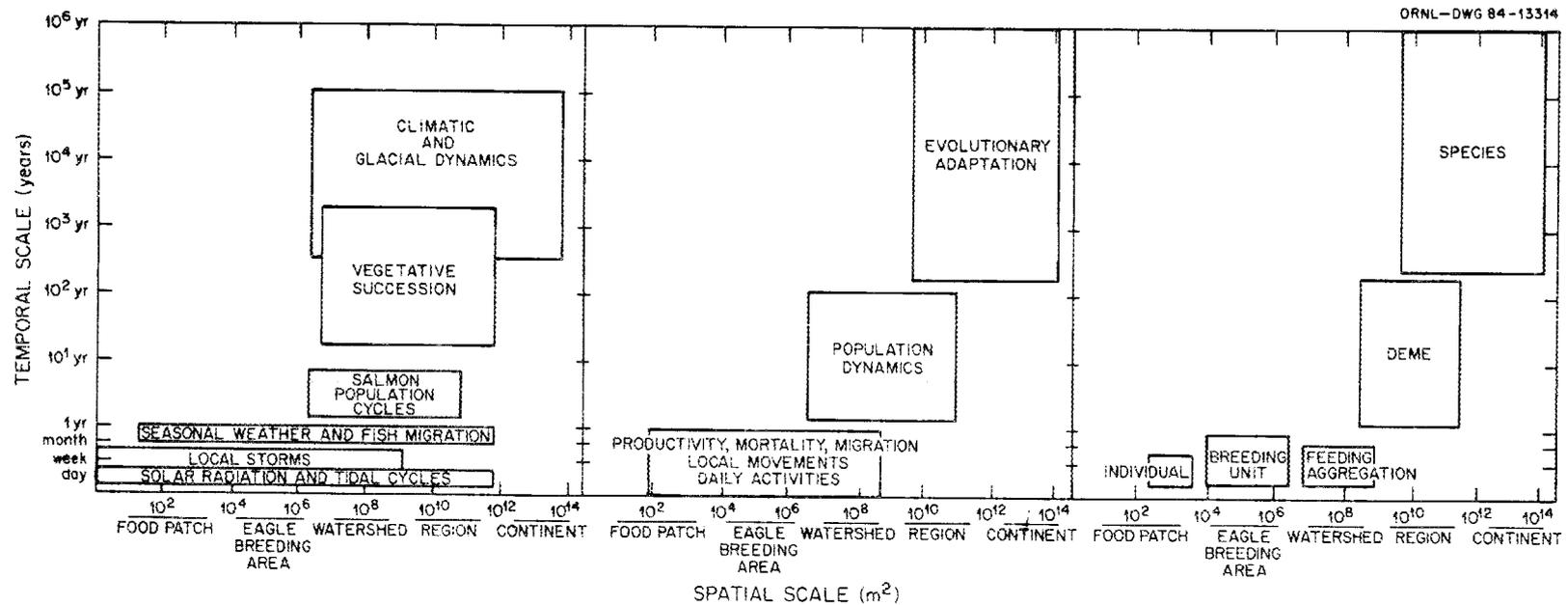


Figure 7.2. Spatial and temporal domains of perturbations and responses of bald eagles along the northwest coast and the organization levels at which they are felt (Adapted from Delcourt et al. 1983).

Finally, global climate fluctuation and glacial cycles with 100,000 year periodicities control the distribution, abundance, and evolution of fish and vegetation across continents.

RESPONSES OF EAGLES

Environmental change may elicit responses in organisms at several hierarchical levels (Figure 7-3). Bald eagles respond to the shifts in resources described above at the individual, population, and evolutionary levels (Figure 7-2).

Day/night and tidal cycles influence the daily activity patterns of eagles (e.g., foraging is done by day and roosting at night).

Eagles respond to changes in food and habitat resulting from local storms by moving between watersheds, by altering habitat use patterns (e.g., taking refuge in conifer forests), and changing levels of intraspecific aggression. Differential mortality may result from severe storms.

Seasonal weather and fish migration patterns influence the migratory movements, productivity, and survival of eagles across regions.

Resource changes on the scale of one to a hundred years (e.g., prey population cycles and vegetative succession) influence the dynamics of the regional eagle population.

Finally, long-term climatic and glacial cycles which operate over thousands of years may result in genetic changes in the population.

Such evolutionary changes are felt at the species level while population responses influence demes. The smallest scale responses, organismal, are felt at the level of individuals, breeding pairs, and feeding aggregations.

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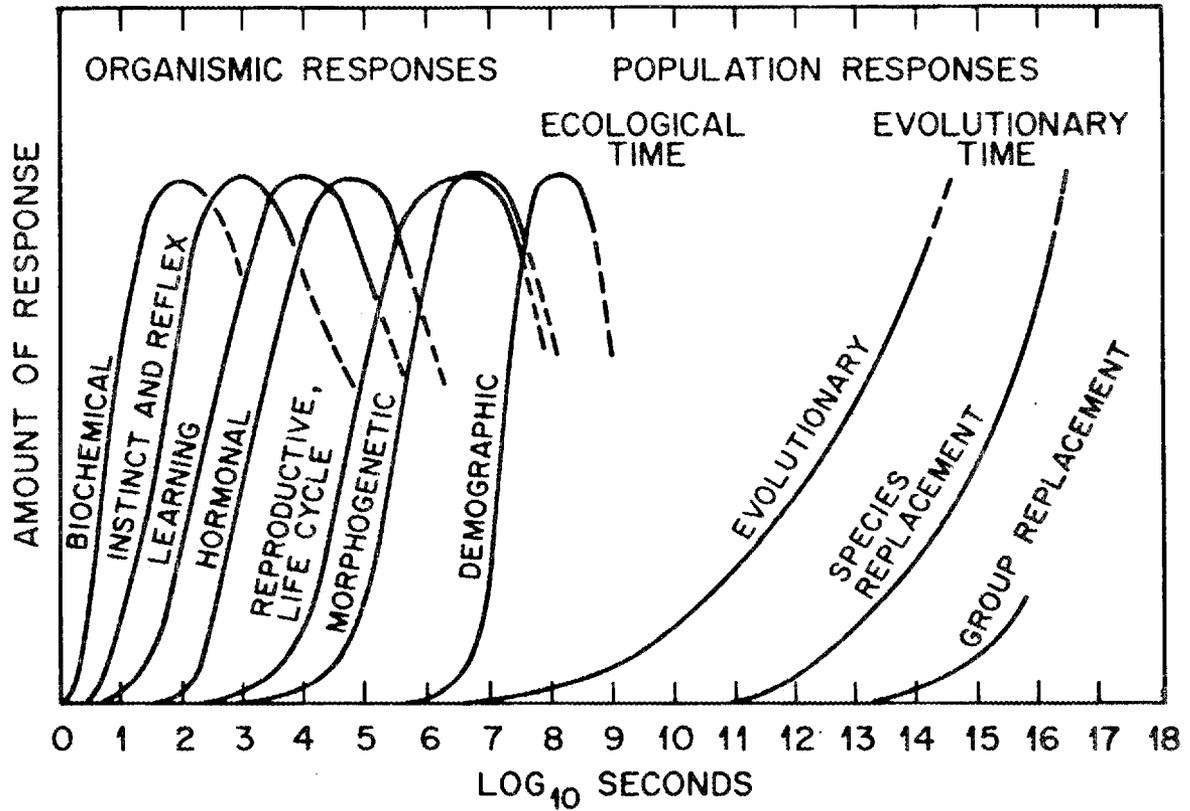


Figure 7.3. A hierarchy of biological responses. Organismic responses are evoked by changes in the environmental detectable within a life span, population responses to long-term trends (from Wilson 1975).

IMPLICATIONS FOR BEHAVIORAL ECOLOGY AND CONSERVATION

This example with bald eagles has shown that environment/animal interactions are neither unidimensional nor simple. Much to the contrary, it is evident that a hierarchical array of perturbations drives the dynamics of resources that limit biotic populations. Disturbance also influences populations directly by disrupting physiological processes. Animals respond to perturbation and resource dynamics at several scales including organismal, population, and evolutionary levels. These responses are felt at organizational levels ranging from individuals and breeding pairs up to species.

This landscape perspective on the nature of environment/animal interactions has important implications for behavioral ecology. First, it is evident that resolution of a problem demands that it be approached on the appropriate scale. For example, effective studies of bald eagle population dynamics require measurement of environmental change and population response on the order of tens of years over regional spatial scales (Figure 7-2). Events of lesser scale may simply not be felt at the population level.

A second implication is that in dynamic systems ecological change may out pace evolutionary response times such that the adaptations of organisms lag behind present conditions. The result is adaptive anachronisms which are suboptimal for modern conditions (see Janzen and Martin 1981). In this regard, evolutionary game theorists may be prudent to consider the outcomes of models where ESS's are thwarted by changing environments (Andersson 1980 provides an interesting example).

Finally, the landscape perspective allows insights on the adaptive significance of learning. Clearly, learning is an important means by which animals fine tune their behavior to changing conditions.

The landscape approach also offers insights for conservation biology. Natural disturbance and perturbation were said to be inherent features of ecological systems. Is anthropogenic disturbance not just more of the same? Man-induced events of comparable scale and magnitude to natural events will elicit similar biotic responses. If the biotic population is adapted to environmental change of that scale, dynamic equilibrium should be maintained. However, many anthropogenic events have no natural counterparts. For example, DDT was introduced in North America on a continental scale in less than 10 years. This was a disturbance of a magnitude and scale that was 'unusual' in the evolutionary history of the species and consequently it pushed regional populations into disequilibrium. Only since a ban on the substance are eagle populations recovering (Chapter V). The point is that a well-honed understanding of environment-organism relationships may greatly hasten advancement in conservation biology. Perhaps this approach will not only allow for interpretation of the effects of past incidences of man-caused environmental change, it may also be a predictive tool.

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