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AGONISTIC ASYMMETRIES AND THE FORAGING ECOLOGY OF BALD EAGLES[1]

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Abstract. We investigated the effects of both asymmetries and differing food levels on contest outcomes of wintering Bald Eagles (*Haliaeetus leucocephalus*) feeding on chum salmon (*Oncorhynchus keta*) carcasses. Large eagles, regardless of age, were more successful in pirating than smaller eagles. Small pirating eagles were usually unsuccessful unless they were adults attempting to supplant other small eagles. Feeding eagles were more successful in defeating pirating eagles according to (1) whether their heads were up prior to a pirating attempt, (2) how long their heads had been up, and (3) whether they displayed. During periods of food scarcity pirating eagles were less successful, a fact attributed in a proximate sense to the increased incidence of retaliation by feeding birds. When food was scarce and eagles had a choice between scavenging and pirating, they chose to scavenge more often.

Body size appears to be an important factor in determining social dominance and influencing differences in foraging modes of wintering Bald Eagles.

Key words: asymmetries; Bald Eagle; dominance; food abundance; foraging; Haliaeetus leucocephalus; *pirating.*

INTRODUCTION

The theft of food resources procured by another organism is one of the most familiar forms of exploitation between individuals. Food theft has been recorded across a wide range of taxonomic groups including mammals, birds, reptiles, fish, insects, and arachnids (references in Brockmann and Barnard 1979 and Barnard 1984). Barnard (1984:1) listed constraints on the utility of theft, including: the availability of producers, the number of individuals stealing from them, the cost of stealing in terms of producer avoidance, defense and retaliation, the value of the limited resource, and the chance of alternative strategies for resource exploitation. Empirical studies are needed that examine the effects of these constraints on both the strategies animals use to compete for scarce items and on contest outcomes (Parker 1974, Davies 1982, Ewald 1985).

We present an analysis of two foraging modes (i.e., pirating and scavenging) used by Bald Eagles (*Haliaeetus leucocephalus*). Our objectives were: (1) to examine the consequences of asymmetries on contest outcomes and (2) to determine the effects of food scarcity on foraging strategies.

Bald Eagles should be a good species in which to investigate our objectives; they obtain food by hunting, scavenging, and intra- and interspecific stealing (i.e., pirating and kleptoparasitism, respectively) (Spencer 1976, Brockmann and Barnard 1979, references in Lincer et al. 1979), and individuals are adept at obtaining food by two or more of these methods (Young 1983, Hansen 1986). Food shortages may have exerted strong selective pressures on the foraging ecology of the Bald Eagle, particularly during the winter season (Sherrod et al. 1976, Hansen 1984, Stalmaster and Gessaman 1984). Eagles make long-distance movements in search of food, reduce their energy requirements by seeking sheltered microclimates during periods of cold stress, engage in social activities (i.e., roosting, soaring) where information on food location can be learned, and show elaborate social feeding behavior (Griffin 1981, Knight and Knight 1983, Young 1983, Stalmaster and Gessaman 1984, Fischer 1985, Keister et al. 1985, Hansen 1986, Knight and Knight 1986).

METHODS

Data were collected from 27 December 1983 to 13 January 1984 along a 10-km segment (river miles 46.5–40.5) of the North Fork of the Nooksack River, Whatcom County, Washington (48°54′ N, 122°08′ W). Up to 300 Bald Eagles may aggregate here at a time during winter to feed on carcasses of primarily chum salmon (*Oncorhynchus keta*) that have spawned and died, creating temporarily abundant patches of food (Knight et al. 1980, Knight and Knight 1983, Stalmaster and Ges-

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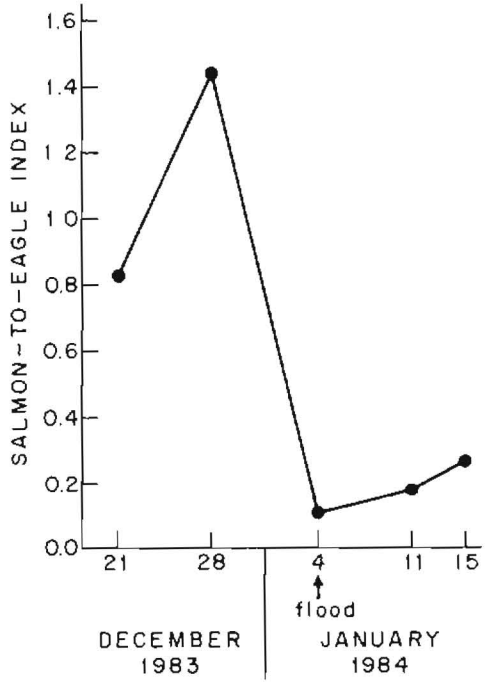

FIG 1. Relative salmon-to-eagle index (i.e., the abundance of salmon relative to the number of eagles) within the Nooksack River study area, 21 December 1983 to 15 January 1984 The flood occurred on 4 January.

saman 1984). Salmon carcasses are too heavy (mean mass = 3.652 kg: Stalmaster and Gessaman 1984) for an eagle (mean body mass = 4.5 kg: Stalmaster and Gessaman 1984) to carry so birds must feed where carcasses are deposited. Although a salmon carcass provides food for several eagles, rarely does more than one eagle feed on a carcass at a time.

Feeding behavior was videotaped at three locations using a 200-mm lens from blinds situated >50 m from the food. Eighteen hours of feeding behavior (the first 1–2 h after feeding began each morning) were taped during 17 d. At each location we removed all naturally occurring carcasses and arranged three uneaten carcasses (averaging 7.4 kg in total mass [range 3.1–11.5 kg]) each at two stations 50 m (range 40–70 m) apart. At each station, carcasses were: (1) placed 2–4 m apart, (2) cut open to expose flesh and viscera, and (3) placed half in and half out of water. Stations averaged 129 m (range 55–180 m) from human dwellings and 40 m (range 12–85 m) from vegetative cover (i.e., trees and shrubs). Stations were prepared and we were in the blinds at least 30 min before first light.

Eagles in our study area were not individually marked, therefore the possibility of repetitive sampling of individuals existed. This potential source of error could lead to uncertainties in whether our results were due to (1) effects of age and size or (2) chance differences in individual characteristics. We cannot eliminate the possibility of duplication, however we feel it was uncommon for the following reasons: (1) sampling took place over a 17-d period, (2) sampling occurred at three different feeding stations, (3) a large number of eagles was present during our study, and (4) radio-telemetry studies of Bald Eagles on our study area indicate they frequently performed inter- and intrariver movements (BioSystems Analysis 1981).

Interactions among feeding eagles were classified according to Stalmaster (1981:109–112) and recorded by frequency, position (i.e., from the ground or from the air), and success of pirating attempts. We listed eagles as either adults (heads and tails mostly white) or immatures (brown or mottled plumage). Eagles either scavenged or pirated salmon carcasses. Scavenging was securing an unoccupied carcass; pirating was either an aerial or ground approach to an eagle already at a carcass. Preference experiments were conducted by recording the foraging outcomes of newly arrived eagles (range: 5–15 birds) at feeding stations when choices existed of equal numbers of unoccupied and occupied carcasses. A feeding attempt was considered successful either when a bird began feeding on an unoccupied carcass or when a bird successfully supplanted an eagle at a carcass and began to feed. When possible, pirating eagles were classified as being either larger or smaller than their opponent. For our preference experiments, however, size estimates were made in relation to size of the other eagles already present at the feeding station. Here, we categorized the eagles present as: (1) small, (2) large, and (3) undecided.

The effects of changing food levels were determined by calculating a salmon carcass-to-eagle index (i.e., the abundance of salmon relative to the number of eagles) (see Knight and Knight 1983 for methods). Bald Eagles and salmon were censused every 4–7 d from 21 December to 15 January (see Knight and Knight 1983 for methods). The effects of changing food levels were determined by comparing observations of foraging eagles prior to a flood with observations following the flood. Before the flood, both eagle and salmon numbers were increasing; after the flood there were few salmon, resulting in a much lower salmon carcass-to-eagle index (Fig. 1).

We used hierarchical, stepwise logistic regression (Dixon 1983) to (1) analyze the importance of body size and age on success of pirating attempts (or inversely, on success in keeping food during a pirating attempt), and (2) to determine how these factors influenced whether an eagle scavenged or pirated when presented with a choice. At each step in the selection procedure, the variables were evaluated for entry into or deletion from the current model. We considered interactions only if the corresponding main-effect variables were already in the model. The deviance chi-square statistic was used to evaluate the fit of the current model against the model that predicts each observation exactly. A large P value indicated that the

TABLE 1. Results of pirating attempts on feeding eagles. PSIZE (size of pirating eagle); PAGE (age of pirating eagles); FSIZE (size of feeding eagle).*

Variables used in regression equation			Success of pirating attempts	
PSIZE	PAGE	FSIZE	%	(*n*)
Large	adult	large	71	(24)
Large	adult	small	100	(29)
Large	immature	large	63	(27)
Large	immature	small	100	(20)
Small	adult	large	8	(12)
Small	adult	small	94	(16)
Small	immature	large	0	(28)
Small	immature	small	25	(4)

* Age of feeding eagle was not significant (Table 2), therefore, it was dropped from the analysis.

explanatory variables in the current model provided an adequate fit to the data (see Johnson and Temple 1986).

RESULTS

Effects of size, age, posture, and position

On 160 occasions we were able to determine age and relative body size of both the attacking and feeding eagles (n = 56 before the flood) (Table 1). The interaction of age and body size of the pirating eagle and body size of the feeding eagle were significantly related to contest outcome. Large eagles, regardless of age, were usually successful in pirating from feeding eagles. Small pirating eagles were generally unsuccessful unless they were adults attempting to supplant other small eagles. Body size of the attacking eagle was more important than age in explaining the success of pirating attempts (Tables 1 and 2).

Size of a feeding bird was important in explaining the outcome of an attack (Table 2). Small eagles almost always lost their food, except when attacked by a small immature. Large feeding birds almost always kept their food when attacking eagles were smaller, but lost their food about two-thirds of the time to large attacking birds (Table 1).

TABLE 2. Results from stepwise logistic regression analysis for variables in the food-pirating model against contest outcome (Table 1). PSIZE (size of pirating eagle); PAGE (age of pirating eagle); PSIZE × PAGE (interaction of size and age of pirating eagle); FSIZE (size of feeding eagle).*

Variables examined in regression equation	Coefficient	SE
PSIZE	3.46	1.13
PAGE	NS†	· ·
PSIZE × PAGE	3.66	1.63
FSIZE	−5.43	1.36
FAGE	NS	·
FSIZE × FAGE	NS	
CONSTANT	−0.90	0.45

* Deviance chi-square for the model was χ^2 = 5.20, P = .88 The nonsignificant goodness-of-fit test for this model indicates that the explanatory variables provide an adequate fit to the data (see Dixon 1983).

† Not significant (P > .05).

TABLE 3. Results showing which foraging strategy an eagle chose when a choice existed between scavenging and pirating

Variables used in regression equation		Strategy chosen			
		Pirating		Scavenging	
Eagle age	Eagle size	%	(*n*)	%	(*n*)
Adult	large	80	(41)	20	(10)
Adult	small	21	(10)	79	(38)
Immature	large	51	(38)	49	(36)
Immature	small	7	(3)	93	(43)

On 219 occasions we were able to determine age and relative body size of eagles in our foraging-preference experiments (Table 3). Age and body size were both important in determining which foraging mode was chosen, with body size being the more important variable (Table 4). Large adult eagles were most likely to pirate, while small adults rarely did (Table 3). Large immatures were as likely to pirate as scavenge whereas small adults were three times as likely to scavenge as to pirate.

On 243 occasions we determined (1) whether feeding eagles had their heads raised (i.e., the beak was horizontal to the ground or higher) during a pirating attempt, (2) for those with their heads up, how long the head had been up prior to the attack, and (3) whether the feeding eagle displayed (i.e., wing and talon displays, beaking, mantling: Stalmaster 1981:109–112) to the attacking bird. Feeding eagles that looked up during pirating attacks were more successful (40.8%, n = 169) in keeping their food than eagles that had their heads down (16.2%, n = 74)(P < .001, χ^2 = 14.1). Feeding eagles that had their heads up during an attack and kept their food, looked up ($\bar{X}$ ± SD: 8.6 ± 8.6 s, n = 69) significantly longer (P < .001, t = 3.8) than eagles that had their heads up and were displaced ($\bar{X}$ ± SD: 4.4 ± 3.8 s, n = 100). Feeding eagles that displayed to an attacking eagle were more successful in keeping their food (75.8%, n = 91) than were feeding eagles that did not display (5.3%, n = 152) (P < .001, χ^2 = 131.2).

TABLE 4. Results from stepwise logistic regression analysis for variables in the pirating vs. scavenging model (Table 3). SIZE (size of eagle); AGE (age of eagle).*

Varibles examined in regression equation	Coefficient	SE
SIZE	−2.74	0.40
AGE	−1.35	0.36
CONSTANT	1.41	0.32

* Deviance chi-square for the model was χ^2 = 5.11, P = .40. The nonsignificant goodness-of-fit test for this model indicates that the explanatory variables in the model provide an adequate fit to the data (see Dixon 1983).

Adult eagles displayed (36.5%, $n = 126$) no more than immatures (38.5%, $n = 117$) ($P > .75$, $\chi^2 = 0.1$).

We documented a total of 573 pirating attempts. More (75.0%) attacks were initiated from the ground than from the air ($P < .001$, $\chi^2 = 143.8$); however, there was no difference ($P > .75$, $\chi^2 = 0.05$) in pirating success between attacks from the air (65.8%) and the ground (66.7%).

Effects of food levels

Before the flood, when the salmon-to-eagle index was high (Fig. 1), 80.5% ($n = 77$) of the pirating attempts were successful; after the flood < 68% ($n = 496$) were successful ($P < .025$, $\chi^2 = 5.1$).

We examined four explanations for why feeding eagles were less likely to be displaced after the flood. It was not due to a higher frequency of eagles with heads up during pirating attempts; there was no difference between the number of feeding eagles that looked up during a pirating attempt before the flood (68.0%, $n = 128$) and after the flood (71.3%, $n = 115$)($P > .50$, $\chi^2 = 0.3$). The increased success was not due to eagles looking up longer; feeding eagles had their heads up no longer before the flood ($\bar{X} \pm$ SD: 6.3 ± 7.7 s, $n = 87$) than after the flood (5.9 ± 5.0 s, $n = 82$)($P > .50$, $t = 0.4$). Nor was it due to a higher frequency of eagles displaying during pirating attempts; feeding eagles displayed no more often prior to the flood (34.7%, $n = 121$) than following the flood (40.2%, $n = 122$)($P > .25$, $\chi^2 = 0.8$). There were, however, significantly more instances of physical contact (wings or talons of one bird striking the body of the other bird) between attacking and feeding eagles after the flood (82 cases of physical contact during 496 pirating attempts) than before (6 of 77) ($P < .05$, $\chi^2 = 3.9$).

When food was abundant and foraging eagles had the choice between an unoccupied and an occupied carcass ($n = 120$), they chose to scavenge almost as often as they chose to pirate (45.8 vs. 54.2%, respectively) ($P > .25$, $\chi^2 = 0.83$). When food was scarce and eagles had a choice ($n = 99$), they scavenged significantly more often than they pirated (58.3 vs. 41.7%, respectively) ($P < .025$, $\chi^2 = 5.6$).

Discussion

Individual differences, such as body size and age, have been shown to be correlated with contest outcomes, with larger or older animals dominant over smaller or younger individuals (reviewed by Wilson 1975). The relationships of position, size, and age and contest outcomes in Bald Eagles are not consistent among studies. Some authors have reported that eagles exhibit an age-determined dominance hierarchy (Griffin 1981, Harper 1983, Stalmaster and Gessaman 1984); others have shown no relationship with age (Sherrod et al. 1976, Fischer 1985). Stalmaster and Gessaman (1984) examined the role of position and reported that eagles pirating from the air were more successful than those attacking from the ground. Prior to our study only Hansen (1986) had looked at both age and size differences and position. He found that age and size were associated with pirating success, with size being more important; his results for a relationship between position and contest outcome were inconclusive. Our results indicate that eagles exhibit a dominance hierarchy correlated largely with differences in body size, and to a lesser degree by age. In addition, we found no relationship between position and contest outcome.

Apart from individual variation, there are at least three explanations for the relative differences we observed in eagle body size: sex, age, and geographic origin. First, Bald Eagles show reverse sexual size dimorphism (Imler and Kalmbach 1955, Bortolotti 1984, Harmata 1984, Garcelon et al. 1985), with females being the larger sex. Second, immatures, although lighter, have longer flight feathers (Imler and Kalmbach 1955, Orians 1980, Bortolotti 1984, Harmata 1984). Third, birds in higher latitudes are larger than those in lower latitudes (Friedmann 1950, Imler and Kalmbach 1955, Baird et al. 1974, Lish 1975, Bortolotti 1984, Harmata 1984). Because of these factors and because birds on any one wintering area may have come from several distant breeding areas (Griffin et al. 1980, Young 1983, Hansen 1984, Harmata 1984), we were unable to attribute the differences we observed in body sizes to any one factor.

Age has been considered important in determining eagle dominance hierarchies because food theft requires skill, which presumably increases with experience. As an individual gains experience its dominance status increases and it gains an advantage by signaling this change to conspecifics (i.e., adult vs. immature plumage: Rohwer 1977). Cheating may occur if birds alter their plumage to signal a dominance status that is higher than their true fighting ability (Orians 1980). The results of Hansen (1986) and our study suggest that body size, a cue less subject to cheating (but see Dawkins 1986:122), is of more importance than signaling dominance. Possibly the plumage variability in immature eagles has been selected for other reasons, such as improved crypticity in avoiding competitors and predators (Hansen 1984) or to allow individual recognition (Orians 1980).

We found that feeding eagles that looked up while feeding and displayed to attacking birds were more successful in keeping their food. In a previous study (Knight and Knight 1986) we tested the hypothesis that eagles look up while feeding in order to detect pirates. We found that as group size increased, with a concomitant increase in pirating attempts (Ross and Schaael 1982, Stalmaster and Gessaman 1984 and R. L. Knight, *personal observation*), feeding eagles were more vigilant. Our finding that the head-up interval prior to an attack varied positively with a feeding eagle keeping its food provides additional support for our hypothesis. A longer head-up interval enables a feeding eagle to

assess the motivational state of the attacking bird as well as decide whether to retreat or display (Hansen 1986). Alternatively, the head-up posture itself may be associated with a greater ability to defend or inflict injury (i.e., a postural increase in resource-holding potential), and, perhaps as a consequence, the posture may signal a high motivation to fight.

Variations in resource abundance can influence foraging strategies and contest outcomes (Ewald and Carpenter 1978, Frost and Frost 1980, Davies and Houston 1981, Ewald and Orians 1983, Ewald 1985). Hansen (1986) examined the influence of food abundance on contest outcomes in Bald Eagles and found that pirating was less successful when food was scarce. He attributed this to an increase in both display and retaliation rates of feeding eagles as well as an increase in physical contact. Likewise, we found that eagles had a higher success rate of pirating when food was abundant. We found that only the increase in physical contact was correlated with the decrease in pirating success when food was scarce. This suggests that when food was scarce feeding eagles were more willing to escalate their aggressive behavior against an attacking eagle.

When eagles had a choice of foraging modes, and food was scarce, they preferred to scavenge. We suggest three explanations for this: (1) physical contact, and therefore the risk of injury, increases, (2) pirating is less successful, and (3) it takes more effort to displace a feeding eagle than to scavenge. Even though eagles may prefer to scavenge when food is scarce, they pirate more often because there are fewer unoccupied carcasses. For example, during 212 min of observation at feeding stations before the flood, there was at least one salmon carcass without a feeding eagle present 95.2% (n = 202 min) of the time; whereas, after the flood, carcasses without feeding eagles occurred only 19.9% (n = 518 min) of the time.

Considering the potential costs associated with pirating and the apparent benefits associated with scavenging, why do eagles pirate when salmon carcasses are abundant and the potential for scavenging is high (Knight and Knight 1983, Stalmaster and Gessaman 1984, Hansen 1986, this study)? Stalmaster and Gessaman (1984) suggested that pirating by wintering Bald Eagles was suboptimal during times of food abundance. Kushlan (1978, 1979) drew a similar conclusion for food theft by Great Egrets (*Casmerodius albus*). Hansen (1986), using game theory (Maynard Smith and Price 1973), concluded that pirating was adaptive even when food was abundant. He found that eagles that pirated ingested no more food and incurred no greater risks than eagles that scavenged. We suggest eagles pirate when food is abundant to gain experience that will increase their chances of successfully pirating when food is scarce. When food is abundant failure to pirate successfully would have less serious consequences; there is a lower risk of injury and if an eagle is unable to meet its energy requirements by pirating, there are abundant carcasses to scavenge. A much more detailed analysis of costs and benefits, both in terms of energy and risk, is necessary before these alternative explanations can be tested.

Gauthreaux (1978) suggested that social dominance is one mechanism that may influence differences in foraging modes by individuals during the nonbreeding season, and there is convincing evidence that sexual differences (which translates to body size and plumage differences) among birds of prey result in differences in foraging behavior, habitat use, and distribution (Mills 1976, Bildstein 1978, Stinson et al. 1981, Marquiss and Newton 1982, Bildstein et al. 1984, Collopy and Bildstein 1986, Temeles 1986).

Flight efficiency and striking power in aggressive interactions will depend on both age and body size of an eagle. Longer flight feathers coupled with a lower body mass (low wing loading) result in a more energy-efficient flight while shorter feathers and a heavier body mass (high wing loading) result in greater force in an attack (Andersson and Norberg 1981). Cade (1982) described raptors with high wing loading as "attackers" and those with low wing loading as "searchers."

Bald Eagles show a progressive decrease in feather length with increasing age (Bortolotti 1984, Garcelon et al. 1986). Therefore, small immatures will have the most efficient flight while large adults will have an advantage in aggressive interactions since larger birds can strike harder; small adults and large immatures fit somewhere in between (Hansen 1984:125, Harmata 1984:76). This precise argument was made and empirically confirmed by Ewald and Rohwer (1980) in nonbreeding hummingbirds. In summary, a dominance hierarchy based on size and age differences insures dominant birds access to resources through pirating (see also Hansen 1986), while increased flight efficiency of other individuals may allow them to exploit resources and habitats where other individuals are less efficient (Gauthreaux 1978, Ewald and Rohwer 1980, Morse 1980, Temeles 1986).

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