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FIGHTING BEHAVIOR IN BALD EAGLES: A TEST OF GAME THEORY[1]

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

Abstract. Seven predictions of evolutionary game theory were examined in field studies of foraging behavior of Bald Eagles (*Haliaeetus leucocephalus*) wintering in the Chilkat Valley, Alaska. A cost/benefit analysis revealed that the frequencies of two foraging strategies (hunting and stealing from conspecifics) were balanced such that the payoffs of the two were nearly equal. Asymmetries in probable correlates of fighting ability (size and, possibly, spatial position [being in the air vs. on the ground], but not age) and expected gain in victory (hunger level) influenced the outcome of contests over food. Individuals used conditional strategies: small or young birds appeared to hunt (rather than steal) relatively more often than others. Pirating eagles often assessed the size and hunger level of food defenders and attacked those most likely to retreat. Contrary to prediction, ritualized displays served to advertise expected gain in victory and were good indicators of subsequent behavior. The level of escalated fighting was inversely related to resource availability. Finally, a graphical model shows that pirating frequency may or may not be influenced by changes in food abundance. The results generally support the predictions of game theory and explain several aspects of Bald Eagle foraging behavior.

Key words: Alaska; Bald Eagle; evolutionarily stable strategy; evolutionary game theory; fighting behavior; Haliaeetus leucocephalus; *kleptoparasitism.*

INTRODUCTION

Evolutionary game theory (Maynard Smith and Price 1973) has become a widely accepted paradigm in ecology. Adapted from models of human economic behavior, game theory examines evolutionary problems where the currency is not money but Darwinian fitness. Like optimization theory (see Krebs and McCleery 1984), the theory of games considers the costs and benefits of resource procurement options open to organisms and identifies "best" strategies. Game theory is unique, however, in addressing 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, parental investment in offspring, sex ratios, and plant growth (Maynard Smith 1982*a*). However, basic predictions of many published ESS models have not been rigorously tested. Here I examine seven predictions of game theory applicable to the feeding behavior of Bald Eagles (*Haliaeetus leucocephalus*).

Bald Eagles are good subjects for such studies because they have probably undergone strong selection for efficient foraging (Hansen 1984, Stalmaster and Gessaman 1984), and because their foraging behavior is poorly understood. Naturalists have long noted the eagle's proclivity for robbing food from other birds (Forbush 1927), but scientists have failed to ascertain why pirating is common even when food is abundant. Stalmaster and Gessaman (1984) found that 84% of second eagles coming to food patches kleptoparasitized conspecifics, while Knight and Knight (1983) observed that 58% of all arrivals at occupied patches chose to steal. Kleptoparasitism occurs in numerous bird species (Brockmann and Barnard 1979). A cost/benefit analysis in Great Egrets (*Casmerodius albus*) revealed that stealing offered less reward than other foraging tactics when food was abundant (Kushlan 1978). Both Kushlan (1978) and Stalmaster and Gessaman (1984) concluded that pirating may be adaptive when food is scarce but is suboptimal at other times.

Another intriguing aspect of foraging in Bald Eagles is the high frequency of turnover among food owners. Even the most aggressive pirates, after winning food, are themselves soon displaced. Knight and Knight (1983) found that owners won <17% of contests over food. This situation is unusual among animals; resource defenders typically enjoy a substantial advantage over challengers.

A third feature of feeding eagles is a high rate of display (A. Hansen, *personal observation*). The function of the stereotypic postures and calls is unknown.

The Foraging Game

The food acquisition problems of Bald Eagles can be represented in a game theory model. In the *Foraging 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 exclusively (capture live prey or scavenge unclaimed carrion) or steal exclusively. Or they

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[2] Present address: Centre for Resource Ecology, Department of Botany, University of the Witwatersrand, Johannesburg 2001, South Africa.

TABLE 1. Predictions of the *Foraging Game* examined in this paper.

Variable A: Frequency of hunting and stealing
1. The population-wide frequencies of hunting and stealing have stabilized at the ESS point where payoffs of the two strategies are equal.

Variable B: Differing roles
2. Size, age, position, and hunger level serve as cues to settle contests with little escalated fighting.
3. Individuals choose strategies contingent upon their phenotypes or roles.
4. Eagles assess the relative fighting ability or expected gain of opponents and act accordingly.
5. Ritualized displays advertise an individual's fighting ability but not its expected gain in victory.

Variable C: Food availability
6. Fighting intensity increases as food becomes scarce.
7. The ESS point is (is not) affected by resource abundance.*

* Which outcome is predicted depends on the payoffs and costs of each strategy under the different food regimes.

may use mixed strategies where they hunt at times and steal at others. The strategies may be either innately determined or learned (Harley 1981). The objective of each player is to find the strategy that maximizes fitness, i.e., the ESS. Conditions may change during the game, however, so strategies may have to be modified. The population-wide frequency of the strategies, the attributes of players, and food abundance all vary through time.

A mathematical analysis of the *Foraging Game* could determine the ESS for each player if all pertinent parameters were quantified. Unfortunately, such information is seldom obtainable. Thus my approach was to examine qualitative rather than quantitative predictions. Seven predictions of the *Foraging Game* were analyzed (Table 1); each was compared to the null model that evolutionary constraints (e.g., evolutionary lag) result in maladaptation (see Maynard Smith 1978). In this paper, predictions on each of the three variables of the *Foraging Game* are derived, tested against field observations of the feeding behavior of Bald Eagles, and discussed.

METHODS

Observations were done in the Chilkat Valley, Alaska, where >3000 Bald Eagles gather in autumn to feed on the carcasses of chum salmon (*Oncorhynchus keta*) that have spawned (Hansen 1984). Subjects were monitored from a blind or automobile at distances of 20–150 m using a 20–45 power spotting scope and 10 × 40 binoculars. Data were entered onto cassette tapes in the field and later transcribed. Four types of observations were completed in fall 1980 and 1981 and winter 1983 and are described below.

Variation about a mean value is expressed as $\bar{X} \pm$ SD throughout the paper.

Contests at focal salmon carcasses

Interactions occurring over 49 chum salmon carcasses were recorded in November and December 1980 and 1981. 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 deserted. A carcass weighed on average 4.3 kg and was fed upon by 2–18 ($\bar{X} = 7.8$) birds. For each of 467 observed displacement attempts, I recorded: 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 was not tallied. A contest is defined here as competitive interaction over food that is initiated when a pirate acts to displace a food owner and is concluded when one bird yields (at least temporarily). Most contests lasted only a few seconds. Behavior patterns are described in Table 2. Eagles were placed in one of three age classes based on plumage and beak color: juvenile (0.5–1.5 yr old), subadult (2.5 yr to maturation), and adult (after Sherrod et al. 1976 and Stalmaster and Gessaman 1984). When possible, relative sizes of opponents were ascertained by visual inspection. These data were used to assess 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: 4–27 November 1980 and 17 November to 9 December 1981; period three: 6–8 December 1980 and 17–23 December 1981). Food was considered limiting when carcasses appeared sparse and eagle numbers were declining (period two: 1–5 December 1980 and 10–16 December 1981). Later studies verified that eagle population size was closely related to food abundance (Hansen 1984).

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 they reached satiation. Soon after dawn, an eagle approaching a food patch from the direction of the night roosts was randomly selected as a focal subject and its behaviors and interactions with conspecifics were monitored. The lengths of searching/feeding bouts were measured with a stopwatch. A bout started when the subject landed at the feeding grounds or changed foraging tactics and ended when the bird again switched foraging methods or reached satiation. Food intake was approximated by counting the bites of fish consumed. The payoffs for hunting and stealing were calculated

TABLE 2. Partial ethogram of foraging behaviors by 14 focal Bald Eagles observed during 28 January to 11 February 1983. Frequencies of some behaviors are known to vary with local conditions.

Behavior	Description	Actor	Frequency of occurrence
Foraging tactics			Percentage of efforts to procure food ($n = 60$)
Hunt	pursue live prey or carrion 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 metres and drop towards feeder with talons extended	challenger	16
Walk (pirate)	trot towards feeder with slow deliberate steps while staring intently at feeder; neck is extended and neck and beak are held horizontally; if feeder does not Retreat, actor strikes with talons or beak	challenger	8
Defensive behaviors			Percentage of times attacked ($n = 39$)
Retreat	move rapidly from prey (by running or flying) as challenger approaches	feeder	74
Retaliate	jump slightly into the air and swing feet upwards to meet approaching challenger	feeder	26
Aggressive behaviors			Percentage of contests ($n = 73$)
Charge	while on the ground, run rapidly towards opponent and just prior to interception swing feet forward to strike opponent	feeder or challenger	12
Displays			Percentage of displays ($n = 97$)
Crouch-Vocalize	squat close to ground, retract neck while beak is held horizontally, and vocalize	feeder or challenger	41
Head Out/Up	while standing, extend neck with neck and beak held horizontally while raising and lowering tail and vocalizing and/or extend neck with neck and beak held vertically while raising and lowering tail and vocalizing; a single display consists of either Head Out or Head Up done in isolation or a single sequence of one followed immediately by the other	feeder or challenger	53
Wing Tip	while performing Head Out/Up, raise wings above the body at an angle of ≈45° from horizontal, and rapidly undulate wing tips (metacarpals)	challenger	6

by dividing the total food intake obtained through each tactic by the total time spent in search and consumption for each tactic. 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 28 January and 11 February, during which time a sample of 14 subjects was obtained. The effects of hunger level on behavior were examined 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 were more satiated (had eaten 50–100% of total).

Foraging tactics at experimental food patches

Before dawn on 12 mornings between 30 November and 23 December 1981 two to five ($\bar{X} = 3.0 \pm 0.8$) salmon carcasses, all similar in size and quality, were linearly arranged on a gravel bar at intervals of ≈4 m. When a food patch contained carcasses claimed by eagles as well as unoccupied carcasses, the foraging tactic of each new arrival was recorded. These obser-

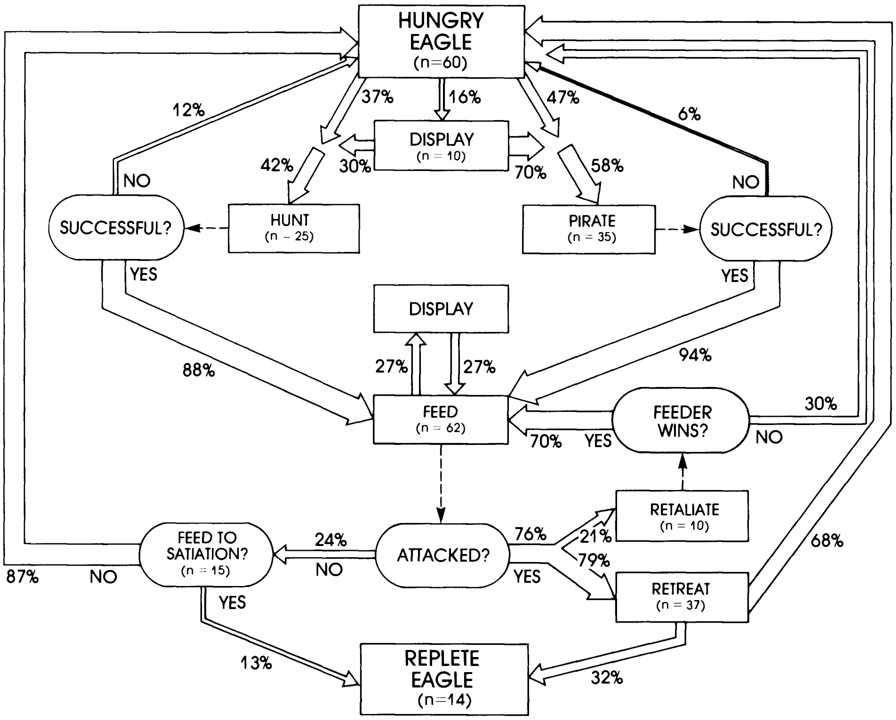

FIG. 1. Kinematic diagram of foraging by 14 focal Bald Eagles observed during 28 January to 11 February 1983. Arrow width is proportional to transition frequency. Frequencies of some behaviors are known to vary with local conditions.

vations were subdivided into periods when food was abundant 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 14 and 25 February 1983 to assess if displays correlate with subsequent supplanting attempts. Observations were made when both occupied and vacant carcasses were present. The display behaviors of each new arrival were tallied from the time the bird landed until it either settled at unoccupied carcasses, tried to steal, or flew away.

DESCRIPTION OF BEHAVIORS AND PATHWAYS

A repertoire of foraging behaviors and behavioral pathways is presented in Table 2 and Fig. 1. Foraging eagles hunted or pirated either directly or after first performing Head Out/Up or Wing Tip displays. Displacement attempts were initiated from the air or the ground. Birds that were successful in gaining access to a fish fed while scanning for attackers and occasionally performing Crouch-Vocalize or Head Out/Up. If attacked by a pirate, feeders either yielded or acted to defend their food. Physical contact could occur if feeders failed to respond to attackers, if feeders retaliated, or if opponents Charged. Such contact was sometimes violent, with the talons of one bird embedded in the body of another. Birds still not satiated after losing possession of a fish or eating all remaining flesh returned to foraging. When replete, the birds generally took a perch and became inactive.

VARIABLE A: FREQUENCY OF HUNTING AND STEALING

Prediction 1: pirating—suboptimal or ESS?

The best strategy for a player of the *Foraging Game* depends upon the population-wide frequencies of hunting and stealing. Barnard and Sibly (1981) developed a foraging model where some individuals (producers) invest in securing a resource which other individuals (scroungers) parasitize. Payoffs to scroungers are frequency-dependent; the fitness of scroungers is higher than that of producers when scroungers are rare, but lower when scroungers are common. Where the payoff curves intersect, the two types do equally well. A population containing producers and scroungers should converge on this ESS point. Therefore, the first prediction of the *Foraging Game* was: *the population-wide frequencies of hunting and stealing will stabilize at the ESS point where payoffs of each are equal.*

Results

1. *Rewards.*—The 14 focal eagles pirated more frequently (58%) than they hunted (42%) but derived similar amounts of flesh per unit search and consumption time through each tactic. Pirates gained 4.2 bites/min

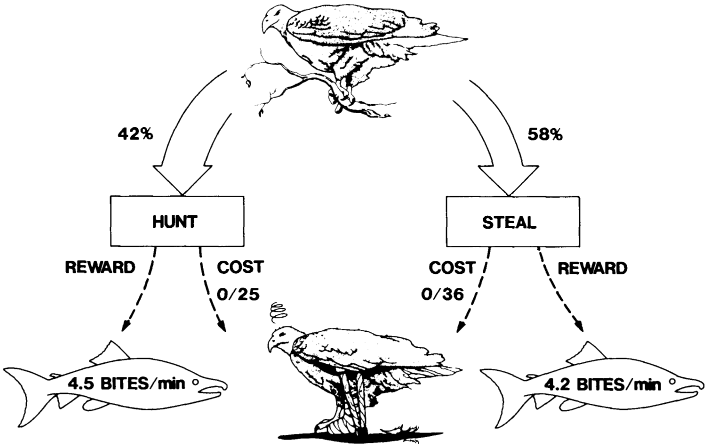

FIG. 2. The frequencies of hunting and stealing, and respective payoffs in feeding rate (bites per unit search and consumption time) and costs in incidence of injury (injuries/attempts) for 14 Bald Eagles monitored over full feeding periods.

and hunters 4.5 bites/min (Fig. 2); differences were not significant (Matched-pair signed-ranks test, $N = 14$, $T = 40$, $P \gg .05$). Thus, the rewards of each tactic were nearly equal.

2. *Risks.*—The costs of each tactic were also equal; none of the 14 focal eagles suffered injury during 36 pirating and 25 hunting attempts (Fig. 2). Undoubtedly, though, both hunting and pirating are performed with some risk of 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, but such blows are potentially dangerous. Hunters may be injured while trying to subdue or retrieve prey. I witnessed two occasions in summer where birds pursuing fish were swept downstream and submerged by fast water; both survived but surely such incidents occasionally result in drowning. Hunters are at risk also because some food items are possibly associated with danger (e.g., predators such as wolves or humans) 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, $t = 3.1$, $P < .0025$).

Discussion.—Why do Bald Eagles steal from conspecifics even when food is abundant? Is the behavior suboptimal except during times of food shortage (Stalmaster and Gessaman 1984), or are the foraging tactics at an ESS where the payoffs of the two tactics are equal (Barnard and Sibly 1981)? My data strongly support the latter explanation. The payoffs for hunting and stealing were very similar. The 14 focal eagles ingested nearly equal amounts of food per unit of searching and consumption time through hunting and stealing, and incidence of injury was zero for each tactic (Fig. 2). Based on these observations, the foraging strategies of the population seem to be at an evolutionarily stable state where the cost/benefit ratio of the two tactics is similar.

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 will hold so long as feeding rate minus cost of injury is the same for hunting and stealing.

VARIABLE B: DIFFERING PHENOTYPES AND ROLES

Prediction 2: cues for contest settlement

The *Foraging 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). They predicted 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 may 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. Subadults are only slightly lighter than adults (Imler 1941). Age is thought to correlate with plumage until maturity is reached at 4–6 yr (Southern 1964, Servheen 1975). Whether a bird is positioned above or below an op-

TABLE 3. Effect of relative size of Bald Eagles on supplanting success in pairwise interactions.

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

ponent 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.

The value of a prey item to each player 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 predicted, then, that *size, age, position, and hunger level will be used as cues to settle contests with little escalated fighting.*

Results.—Size differences were great enough to rank opponents in 40 contests. The larger of each pair won 85% of the time (Table 3) (Chi-square, $N = 40$, $\chi^2 = 18.6$, $P < .001$). 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). Older birds were no more successful in supplanting younger ones (70% of attempts) than were younger in displacing older (74% of attempts) (Chi-square, $N = 186$, $\chi^2 = 0.44$, $P > .5$). Juveniles attacking adults, however, won decidedly more frequently than adults pirating from juveniles (Chi-square, $N = 53$, $\chi^2 = 7.34$, $P < .01$).

The data were inconclusive on position effect. Evidence in support of a position effect is (a) efforts at supplanting by Aerial and Leap behaviors 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. Determining the positional advantage of aerial attackers, however, is confounded by: (a) the possibility of assessment (attackers may select inferior opponents) and (b) the observation that Walk displacements were more successful (80%, $N = 51$) than Aerial or Leap displacements (67%). The latter finding 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 or hunger state.

The value of the resource to each player also influenced contest outcome. The degree of satiation of contest winners (39 ± 34%) was less than that of contest losers (68 ± 35%) (Mann-Whitney U test, $N = 36$ and 38, $Z = 3.47$, $P < .0005$).

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. In addition to the records that feeders were struck seven times and an attacker only once 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%).

Discussion.—The data show that the outcome of contests between foraging eagles was influenced by size, hunger level, and possibly by position, but not by age. Large eagles won over small ones (Table 3), which suggests that most females are dominant over most males. Also, hungry eagles won over those 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 by an attacker of its likelihood of success causes this work to be inconclusive on the existence of a position effect.

Age had surprisingly little influence on contest outcome. The only difference between age classes was between juveniles and adults. Juveniles displaced adults more than adults supplanted juveniles (Table 4). In contrast, Stalmaster and Gessaman (1984) found, in Washington State, that younger age groups were subordinate to older age groups. The only possible explanation I can offer for the discrepancy between the two studies is that an age effect was strongly countered in Chilkat eagles by another asymmetry. For example, subadults may have been, on average, hungrier than adults, and this would have improved their success in winning contests.

Escalated fighting was uncommon. Charge was done

TABLE 4. Outcomes of supplanting attempts by Bald Eagles, partitioned by age. Age groups listed above the horizontal lines attacked the age groups listed below the horizontal lines.

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

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 in size, hunger level, and possibly in position and age are used by eagles to settle contests, usually without escalated fighting.

Prediction 3: winning strategies for specified phenotypes and roles

How might asymmetries in RHP or resource value influence the "best" combination of hunting and stealing for a player in the *Foraging Game*? 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-scrounger model, the ESS will be a conditional pure strategy—e.g., play producer if relatively large, otherwise play scrounger (Parker 1984). Accordingly, *players of the* Foraging Game *should choose a strategy contingent upon their phenotypes or roles (e.g., hunt if small, steal if large).*

Results.—The relationship between foraging strategy and phenotype was properly quantified only for hunger level. Contrary to prediction, there was no significant difference in pirating rates among focal subjects when hungry (65%) vs. when more than half satiated (50%) (Chi-square, $N = 60$, $\chi^2 = 1.5$, $P > .1$).

Less direct data suggest that foraging strategy may be influenced by age and size. At experimental food patches juveniles and subadults were first feeders more often than expected by the proportion they comprised of all feeders (Chi-square, $N = 21$, $\chi^2 = 7.4$, $P < .01$) which implies that they hunt more than adults. Also, one focal eagle that was very small went to unclaimed prey seven times but did not try to steal from others during a feeding period. Casual observations suggest that this behavior is typical for very small eagles.

Discussion.—The results show that foraging strategy was not influenced by an individual's hunger level but may have been by its age or size. Juveniles and subadults appeared to hunt more often than adults, as indicated by the fact that the young birds were first feeders at food patches disproportionately often. Stalmaster and Gessaman (1984) found a similar pattern. Also, limited observations suggest that small birds may hunt almost exclusively.

The best strategy for a player in the *Foraging Game*, then, may depend upon its RHP. Mathematically determining the ESS for an individual, however, is a very complex problem involving relative size, age, and position. The evolution of strategies for contests with multiple asymmetries is 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.

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. Stalmaster and Gessaman (1984) concluded that subadult eagles wintering in Washington suffered greater food stress than adults.

Prediction 4: assessment—sizing up the competition

The prediction that asymmetries serve as cues for settling contests is based on the assumption that both contestants have knowledge of the asymmetries. How is such knowledge gained? Animals may assess the attributes of opponents relative to their own. Maynard Smith (1982*a*) showed that an assessor strategy can be an ESS if assessment is cheap relative to the cost of escalated fighting. It follows for the *Foraging Game* that *eagles should assess the relative fighting ability or expected payoffs of opponents and act accordingly.* If so, small or nearly satiated feeders will 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 3) (Chi-square, $N = 40$, $\chi^2 = 6.4$, $P < .02$). 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 more than half satiated (1.7 ± 0.99 attacks) than when they were less than half satiated (1.1 ± 0.92 attacks) (Matched-pairs signed-ranks test, $N = 8$, $T = 3.5$, $P < .025$).

Discussion.—Eagles apparently assessed the relative attributes of conspecifics and often chose to displace the individuals most likely to yield (small or 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 loss of a possible positional advantage enjoyed by aerial attackers.

Several studies show that animals assess the traits of opponents that correlate with fighting ability such as size and strength (e.g., Davies and Halliday 1978, Riechert 1978, Clutton-Brock et al. 1979). However, documented cases of animals assessing expected payoff are rare. How is relative hunger level judged by eagles? A bird's hunger status may be revealed by its crop size; empty, half-full, and full crops can be distinguished by a human observer. Another possibility is that time spent feeding is the cue, since intake is a function of time.

These data make apparent why even the most aggresssive birds, after displacing a feeder, were generally

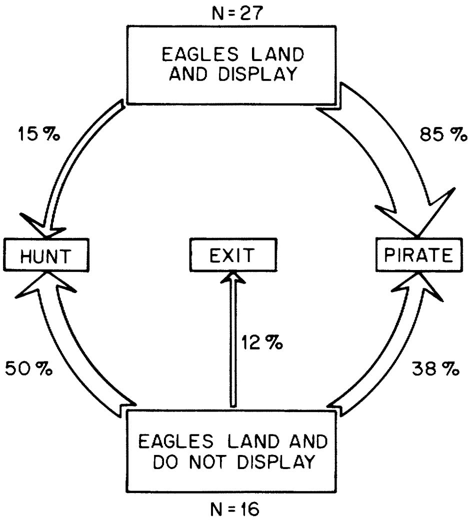

FIG. 3. Relationship between display and subsequent behavior of Bald Eagles arriving at experimental food patches in early morning. "Exit" means the eagle flew from food patch.

themselves soon displaced. Simply stated, food holders had the odds against them. First, a position effect possibly favored attackers. Second, as feeders ate more, their payoff for defending a carcass fell and thus their 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 approaches the infinite regress envisioned by Parker (1974) a decade ago.

Prediction 5: information transfer—attributes or intentions?

The use of the assessor strategy by Bald Eagles has implications for interpreting the function of ritualistic displays. If eagles choose to steal from the conspecifics most likely to retreat, then food owners that are willing to fight will benefit by advertising this fact to dissuade attackers. Ethologists have long asserted that displays can serve to signal threat (see Caryl 1979 for a review). More recently, Maynard Smith (1982*b*) offered a more precise explanation. He suggested that animals may display to signal their fighting ability but not their intentions (i.e., what they intend to do next). This follows because cues of RHP (e.g., size) are inherently reliable and thus are evolutionarily stable. Signals of intentions are susceptible to deception; there is nothing to prevent an animal from "lying" about whether it intends to attack. Such signals should lose their meaning and fall into disuse. In support of this hypothesis, Caryl (1979) found in several bird species that displays were poor predictors of subsequent attack. Maynard Smith (1982*b*) did not discuss the existence of cues advertising asymmetries in resource value, but according to his logic, displays of differences in hunger level would be unstable because they could easily be mimicked by replete birds. Consequently, I predict that *eagle displays advertise RHP but not expected gain in victory.*

TABLE 5. Rate of display (Crouch-Vocalize, Head Out/Up, and Wing Tip) by Bald Eagles competing over focal salmon carcasses during 1981. Criteria for judging food level are presented in Methods.

Period	Food level	Display rate* ($\bar{X}$ ± 1 SD)	Sample size†
one (17 Nov–9 Dec)	high	0.07 ± 0.06	17
two (10 Dec–16 Dec)	low	0.18 ± 0.17	9
three (17 Dec–23 Dec)	high	0.07 ± 0.05	8

* Number of displays per minute when eagles were present at focal salmon.

† Number of focal salmon observed.

Results.—Contrary to prediction 5, the data indicate that eagles use ritualized displays to advertise differences in expected gain and that the displays are good predictors of subsequent behavior.

The focal eagles performed the Head Out/Up and Wing Tip displays at higher rates when <50% satiated (0.20 ± 0.20 times/min) than when >50% satiated (0.05 ± 0.09 times/min) (Matched-pairs signed-ranks test, $N = 10$, $T = 6$, $P < .014$).

During observations of eagles arriving at experimental food patches, 16 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 (Fig. 3). Of the 27 arrivals that did display, 23 (85%) tried to supplant feeders. These data show a positive correlation between display

TABLE 6. Responses of feeding Bald Eagles to challenges by pirates under different food regimes. Period and food level as in Table 5.

Period	Food level	Displacement attempts	Retaliations		Successful retaliations	
		No.	No.	%	No.	%
one	high	205	56	27	45	80
two	low	155	64	41	60	94
three	high	107	31	29	29	94
Total	···	467	151	32	134	89

and attack (Contingency coefficient, $N = 43$, $C = 0.44$, $P < .01$).

Discussion.—The fact that display rate decreased as eagles ate indicates that Head Out/Up and Wing Tip displays are used by individuals to advertise that they are hungry (have much to gain in victory) and thus are likely to win contests. Furthermore, it is clear that these displays convey not only assessment information but also information about the intentions of the actor. Head Out/Up and Wing Tip predicted with an accuracy of 85% what would follow. These displays presumably alter the behavior of signal recipients. A potential pirate is often prudent to avoid attacking a feeder that displays. Similarily, feeders often benefit by yielding to displaying pirates.

How could signals of hunger level and intentions be reliable? These displays draw attention to the throat region and a distended crop is sure sign of a cheater; thus they are reliable by their form. The displays have become ritualized signals of resource value over evolutionary time precisely because they are reliable yet cheap to produce. Thus, this work shows that displays can reliably signal not only RHP, but also expected payoff and intentions, contrary to Maynard Smith (1982*b*).

The validity of the results are supported by Enquist (1985), who showed mathematically that signals of intentions can be evolutionarily stable. Additionally, Hansen (1984) presents a logical argument that reliability may be insured either by a potential cheater's inability to perform the display or by the high cost cheaters may pay in escalated fighting.

VARIABLE C: FOOD AVAILABILITY

Fish stocks and hunting conditions for eagles may change rapidly in southeast Alaska (Hansen 1984). How do fluctuating prey levels affect the *Foraging 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, the influence of differences in expected gain between players on individual foraging strategy was examined. I now explore how population-wide changes in resource value affect contest intensity and pirating frequency.

Prediction 6: contest intensity

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

$$p = V/C,$$

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

Results.—During periods when food was scarce relative to eagle numbers, there was an increase in rates of display, rates of Retaliation of feeders against pirates, and instances of contact. Rates of display (Crouch-Vocalize, Head Out/Up, and Wing Tip) increased from 0.07 ± 0.05 times/min when food was plentiful to 0.18 ± 0.17 times/min when food was scarce (Mann-Whitney U test, $N = 9$ and 25, $Z = 2.19$, $P = .014$) (Table 5). 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, $N = 467$, $\chi^2 = 8.66$, $P < .01$) (Table 6). Seven instances of talon-to-body contact occurred during the 155 displacement attempts when food was scarce and 2 instances occurred during 312 contests when food was abundant.

Discussion.—As predicted by the Hawk-Dove model, escalation increased as resource value rose. Display rate, Retaliation 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 a mechanism of density-dependent population regulation. Resource shortages bring increased escalation, which forces low-status individuals to emigrate or die.

Prediction 7: pirating frequency

The effects of changes in food abundance on pirating frequency are difficult to predict. Stalmaster and Gessaman (1984) suggest 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 (Fig. 4); hunters find fewer carcasses and pirates find fewer victims. It is not clear, though, 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 *Foraging Game* because the payoffs and costs of each strategy under different food regimes are not well known.

Results.—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 7) (Chi-square, $N = 122$, $\chi^2 = 0.79$, $P > .30$). Supplanting success did vary with food abundance. Pirates won 61% ($N = 155$) of contests when feeding was poor and won 76% ($N = 312$) of

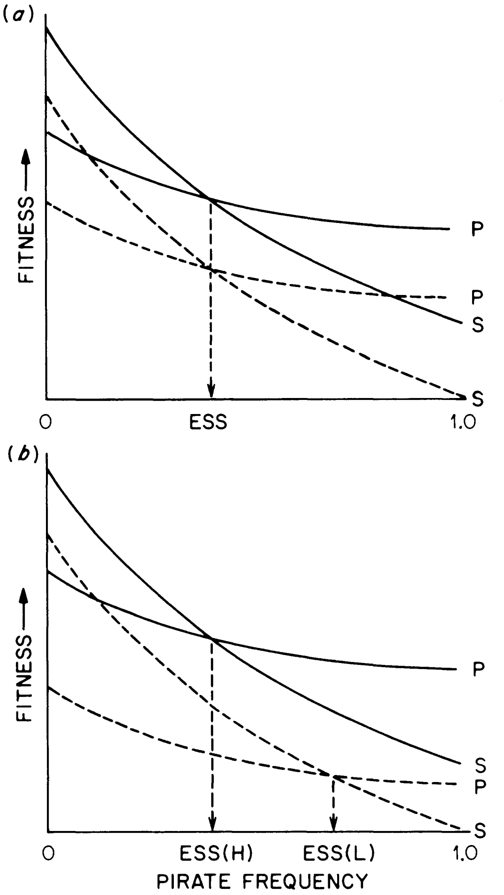

FIG. 4. Two possible effects of resource levels on the foraging ESS in producer-scrounger games. (a) The fitness curves of producers (P) and scroungers (S) for when food is scarce (- - -) are both shifted downward equal distances along the *Y* axis from when food is abundant (——), and the ESS point does not change. (b) The *Y*-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). (Modified from Barnard and Sibly 1981, Parker 1984.)

contests when feeding was good (Chi-square, $N = 467$, $\chi^2 = 11.2$, $P < .001$).

Discussion.—The data are inconclusive on the effect of food levels on the pirating frequency ESS point (Fig. 4). 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 was so is not clear. More observations over a wider range of food levels are needed to determine if the ESS point changes in the *Foraging Game* as food supplies vary. Fig. 4 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 (1978) and Stalmaster and Gessaman (1984) that pirating has high payoff when food is scarce but is maladaptive when food is plentiful.

TABLE 7. Frequency of Bald Eagle foraging tactics under differing food regimes. Period and food level as in Table 5.

Period	Food level	Hunt	Steal	% steal
one	high	21	47	69
two	low	10	16	62
three	high	8	20	71
Total	···	39	83	68

CONCLUSIONS

This study provides support for several predictions of evolutionary game theory. It offers the first direct evidence of a producer-scrounger-type population (Barnard and Sibly 1981) in an evolutionarily stable state. The work adds to existing knowledge that animals assess the fighting ability of opponents (e.g., Davies and Halliday 1978, Riechert 1978, Clutton-Brock et al. 1979) and provides somewhat unique findings that animals also assess the relative value of a resource to an opponent. It shows that animals may select behavioral strategies contingent upon their phenotype or role and that fighting intensity is correlated with the value of the contested resource.

Field observations demonstrated that assessment cues may carry information not only on RHP but also on expected gain and intentions. Results obtained with a graphical model of pirating frequency imply that the ESS point for a population may or may not change in response to resource dynamics depending on whether the rewards of different strategies vary proportionally.

Additionally, the work offers insights into several facets of Bald Eagle foraging behavior. Contrary to Stalmaster and Gessaman (1984), pirating appears to be adaptive even when food is abundant; eagles hunt and steal at rates which maximize fitness. The best foraging strategy for each eagle may depend upon its phenotype or role. Small or young birds probably do better by hunting, while large adults more often benefit from stealing. Interestingly, pirates assess the 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. Because of assessment 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 prey items.

These foraging behaviors of eagles have important ecological implications (Hansen 1984). First, a consequence of assessment is that contests are usually settled without escalated fighting and thus food supplies are divided with little injury to eagles. Second, these foraging behaviors are the mechanisms of endogenous population regulation. They collectively result in population size being adjusted to food supplies as a consequence of some eagles claiming a disproportionate share of the available food and thus forcing others to emigrate or starve.

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LITERATURE CITED

Barnard, C. J., and R. M. Sibly. 1981. Producers and scroungers: a general model and its application to captive flocks of house sparrows. Animal Behaviour **29**:543–550.

Brockmann, H. J., and C. J. Barnard. 1979. Kleptoparasitism in birds. Animal Behaviour **27**:487–514.

Caryl, P. G. 1979. Communication by agonistic display: what can game theory contribute to ethology? Behaviour **68**:136–169.

Clutton-Brock, T. H., S. D. Albon, R. M. Gibson, and F. E. Guinness. 1979. The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus* L.). Animal Behaviour **27**: 211–225.

Davies, N. B., and T. M. Halliday. 1978. Deep croaks and fighting assessment in toads *Bufo bufo*. Nature (London) **274**:683–685.

Enquist, M. 1985. Communication during aggressive interactions with particular reference to variation in choice of behavior. Animal Behaviour **33**:1152–1161.

Ewald, R. W., and G. H. Orians. 1983. Effects of resource depression on use of inexpensive and escalated aggressive behavior: experimental tests using Anna Hummingbirds. Behavioral Ecology and Sociobiology **12**:95–101.

Forbush, E. H. 1927. Birds of Massachusetts. Norwood Press, Norwood, Massachusetts, USA.

Hansen, A. J. 1984. Behavioral ecology of Bald Eagles along the Pacific Northwest Coast: a landscape perspective. Dissertation. University of Tennessee, Knoxville, Tennessee, USA.

Harley, C. B. 1981. Learning the evolutionarily stable strategy. Journal of Theoretical Biology **89**:611–633.

Imler, R. H. 1941. Alaskan Bald Eagle studies. United States Department of the Interior Fish and Wildlife Service, Denver, Colorado, USA.

Knight, S. K., and R. L. Knight. 1983. Aspects of food finding by wintering Bald Eagles. Auk **100**:477–484.

Krebs, J. R., and R. H. McCleery. 1984. Optimization in behavioral ecology. Pages 91–121 *in* J. R. Krebs and N. B. Davies, editors. Behavioral ecology: an evolutionary approach. Blackwell, Oxford, England.

Kushlan, J. A. 1978. Nonrigorous foraging by robbing egrets. Ecology **59**:649–653.

Maynard Smith, J. 1978. Optimization theory in evolution. Annual Review of Ecology and Systematics **9**:31–56.

———. 1982*a*. Evolution and the theory of games. Cambridge University Press, New York, New York, USA.

———. 1982*b*. Do animals convey information about their intentions? Journal of Theoretical Biology **97**:1–5.

Maynard Smith, J., and G. A. Parker. 1976. The logic of asymmetric contests. Animal Behaviour **24**:159–175.

Maynard Smith, J., and G. R. Price. 1973. The logic of animal conflict. Nature (London) **246**:15–18.

Parker, G. A. 1974. Assessment strategy and the evolution of animal conflicts. Journal of Theoretical Biology **47**:223–243.

———. 1984. Evolutionarily stable strategies. Pages 30–61 *in* J. R. Krebs and N. B. Davies, editors. Behavioral ecology: an evolutionary approach. Blackwell, Oxford, England.

Riechert, S. E. 1978. Games spiders play: behavioral variability in territorial disputes. Behavioral Ecology and Sociobiology **3**:135–162.

Servheen, C. W. 1975. Ecology of the wintering Bald Eagles on the Skagit River, Washington. Thesis. University of Washington, Seattle, Washington, USA.

Sherrod, S. K., C. M. White, and F. S. L. Williamson. 1976. Biology of the Bald Eagle on Amchitka Island, Alaska. Living Bird **15**:143–182.

Southern, W. E. 1964. Additional observations on winter Bald Eagle populations: including remarks on biotelemetry techniques and immature plumages. Wilson Bulletin **76**: 121–137.

Stalmaster, M. V., and J. A. Gessaman. 1984. Ecological energetics and foraging behavior of overwintering Bald Eagles. Ecological Monographs **54**:407–428.