ASPECTS OF FOOD FINDING BY WINTERING BALD EAGLES

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ABSTRACT.—We examined three aspects of food location by Bald Eagles (Haliaeetus leucocephalus) wintering along the Nooksack River, Washington. First, eagles used intra- and interspecific local enhancement to locate food. Second, the time that eagles spent aerially searching for food, as indicated by the percentage of eagles flying or soaring, was negatively correlated with relative food availability. Third, eagles often followed others when departing from or arriving at communal night roosts. Following was most frequent when all food was eliminated by flood waters, suggesting a possible food-location function of this behavior. During the flood period, adult eagles were followed more often than immatures. Received 9 March 1982, accepted 24 November 1982.

ONE possible advantage of flocking behavior in birds is an improved foraging efficiency of individual flock members (Hinde 1961, Alexander 1974). An individual bird may learn locations of food sources through local enhancement, in which the searcher is attracted to actively foraging birds (Hinde 1961). Field and laboratory experiments have confirmed that social learning of food location by local enhancement occurs both intraspecifically (Turner 1965, Krebs et al. 1972, Krebs 1974, Barnard 1980, Waite 1981) and interspecifically (Krebs 1973; Kushlan 1976, 1977; Caldwell 1981), but this behavor has not been described in Falconiformes.

Another form of social learning of food location may occur on a larger scale. The Information Center hypothesis (see Ward and Zahavi 1973) predicts that communal roosts and breeding colonies have a food-information function, whereby unknowledgeable birds follow successful foragers to good feeding sites. Indirect evidence in support of this hypothesis has been presented by Krebs (1974), DesGranges (1978), and De Groot (1980), while alternative explanations for following behavior are discussed by Bayer (1982). Evans (1982) documented flock recruitment by Black-billed Gulls (Larus bulleri) departing a colony and proposed group foraging benefits as an expla-

nation. Other tests of the Information Center hypothesis have given equivocal or negative results. Loman and Tamm (1980) could not separate a food-information function of roosts of Eurasian Crows (Corvus corone) and Common Ravens (C. corax) from local enhancement. Andersson et al. (1981) refuted the information-center mechanism in Black-headed Gulls (Larus ridibundus) but found the presence of gulls at food sources made the sources more likely to be discovered.

Bald Eagles wintering along Pacific Northwest rivers are attracted to carcasses of spawned salmon (Oncorhynchus spp.), an abundant yet ephemeral food supply. Eagles feed, perch, bathe, and roost solitarily and in groups ranging in size to more than 100 individuals. In this study we examine the importance of local enhancement and following as food-finding mechanisms of wintering Bald Eagles.

STUDY AREA AND METHODS

Our study was conducted from December 1980 to March 1981 along a 25-km portion of the north and middle forks of the Nooksack River in northwestern Washington (48°54'N, 122°8'W). Eagles wintering within the study area are nonresident and vary considerably in number during the season (Stalmaster et al. 1979, Knight 1981). Recent evidence suggests that members of the population are transient (Hunt and Johnson 1981). Spawned bodies of chum salmon (Oncorhynchus keta) and coho salmon (O. kisutch), deposited along extensive gravel bars, provided the primary food source for eagles. Eagles regularly used five communal night roosts located within 1.5 km of the river.

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We examined food-finding strategies during 21 trials involving food-source manipulations in four feeding areas normally frequented by Bald Eagles. These sites were in the vicinity of salmon spawning areas and averaged 1.4 km (range 1.0–2.5) from eagle night roosts. Along gravel bars void of other food, spawned chinook (*O. tshawytscha*), chum, and coho salmon were arranged in two distinct piles or stations at the water's edge an average of 90 m (range 50–150) apart. At each station, salmon, averaging five in number (range 1–12) and 25.0 kg in weight (range 7.0–106.6), were placed 0.5–5 m apart and cut open to expose flesh and viscera. Within each trial the size, weight, condition (fresh or partly decomposed), and number of salmon placed at the two stations were equivalent, as were the distances of the stations from perch sites and surrounding vegetation. Views of the stations from major perch trees were unobstructed by vegetation. Stations were not repeatedly set up at exactly the same locations. We placed salmon on gravel bars during darkness so that eagles could not observe our activity.

From a blind we recorded the arrivals of Bald Eagles and other species to the salmon stations and the frequency and success of supplanting attempts. Bald Eagles with white heads and tails were classed as adults and those with brown or mottled plumage as immatures. At 5-min intervals, the number, species, and ages of birds present at each station were recorded using a scan sampling technique (Altmann 1974). In addition, at 20-min intervals we recorded the number and ages of eagles perched in the vicinity. Trials were terminated when food was depleted or after 4–6 h if salmon were undiscovered. Intervals between trials ranged from 1 to 11 days.

We estimated the number of arrivals that may have been returning eagles that had left a station earlier (R) as

$$R = (a_{ad} - m_{ad}) + (a_{im} - m_{im}),$$

where a_{ad} and a_{im} are adults and immatures arriving at the stations during each trial, and m_{ad} and m_{im} are the maximum numbers of adults and immatures in the vicinity during each trial, determined from 20-min perch and feeding-site scans. Negative values of $(a_{ad} - m_{ad})$ and $(a_{im} - m_{im})$ were set equal to 0.

Bald Eagles were censused approximately every 7 days (range 4–17 days) between 0800 and 1300 PST from observation points providing views of nearly 90% of the study area. We recorded location by 0.8-km river section, age class, and activity (standing, feeding, perching, flying, or soaring) for each eagle sighted. Temperature, wind speed and direction, and percentage cloud cover were recorded during each census period.

We assessed the relative food abundance weekly by walking linear transects along five sloughs, which supported most of the chum salmon spawning in the study area. This censusing provided a reasonable estimate of the available food. The transects were 20 m wide; lengths (determined by pacing) averaged 442 m (range 270–698). Using a method originated by Servheen (1975), we recorded the species, accessibility to eagles, and percentage of remaining flesh of all salmon carcasses within the transects. Because river levels fluctuated, not all transects were the same length week to week. Therefore, we pooled salmon counts from all areas, standardized the results, and expressed relative salmon availability as the number of available salmon carcasses (whole or equivalent in partially eaten carcasses) per 1,000 m² of land and water surface.

We observed Bald Eagles departing and entering four night roosts on 47 mornings and 63 evenings. Morning observations began 30 min before and continued until 30 min after sunrise. We initiated evening watches 70 min before sunset and continued until dark. For all birds entering or leaving the roosts, we recorded time of day, age, flight direction (upriver, downriver, to or from river), and following behavior. We considered an eagle to be following another when it maintained the same flight path behind another eagle at a distance of less than 400 m until out of our view.

RESULTS

Local enhancement.—The first eagle arrived at the stations a mean of 35 min (±39 SD, n = 14) after sunrise and 21 eagles (±15 SD, n = 14) arrived within the next 30 min. Approximately 20% of 463 arrivals may have been eagles that left a station and later returned (see Methods). After the first eagle landed, subsequently arriving eagles often faced a choice. They could land at a salmon station with one or more eagles already feeding or enter the unattended station. During 30-min time periods beginning with the arrival of the second eagle, we recorded 191 arriving eagles that chose between the unattended station and the one with eagles present. In 182 cases eagles went to the attended station, which was significantly different from a random pattern ($z = 12.54$, df = 190, $P < 0.005$). We documented a high incidence of food robbery. In 57.9% of the arrivals, eagles attempted to supplant an eagle already present; 83.2% of these attempts were successful.

American Crows (*Corvus brachyrhynchos*), Common Ravens, and Glaucous-winged Gulls (*Larus glaucescens*) often fed alongside Bald Eagles, but Great Blue Herons (*Ardea herodias*) and Red-tailed Hawks (*Buteo jamaicensis*), which also fed on spawned salmon, did not.
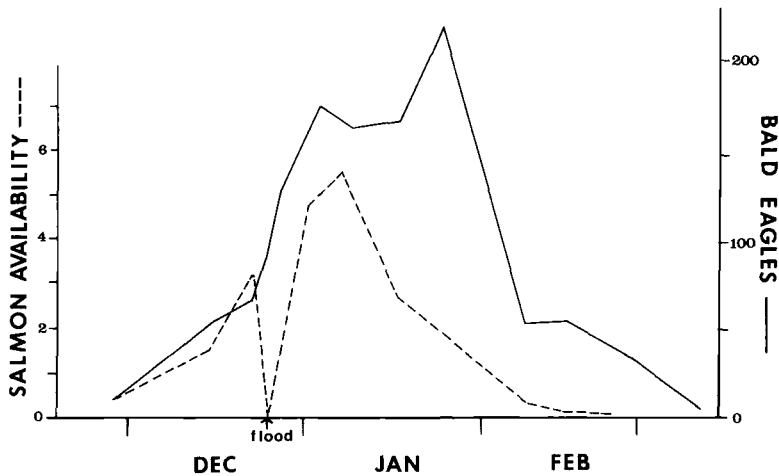
Fig. 1.   Number of Bald Eagles and relative salmon availability within the Nooksack River study area, 28 November 1980 to 12 March 1981. Salmon availability = number of available salmon carcasses per 1,000 m^2.

In 7 of 7 trials, the first eagle arriving chose a station attended by crows and/or ravens over an unattended station. This was significantly different from a random pattern (z = 2.65, df = 6, P < 0.01). Although two stations were concurrently available during the experimental trials, Bald Eagles and American Crows occurred together more frequently than expected in 1,026 scan samples (Cole's index; C_7 = 0.17; χ^2 = 10.36, df = 1, P < 0.005; Cole 1949, 1957).

Flight behavior associated with food finding.— On 26 December 1980, flood waters inundated feeding areas and eliminated all salmon in the study area (Fig. 1). As the water level dropped, salmon again became available. Eagle numbers in the study area increased after the flood, increasing from 90 eagles on 26 December 1980 to 179 eagles on 4 January 1981 (Fig. 1). During three censuses prior to the flood no eagles were seen soaring, whereas on the first day of the flood 67.8% of the eagles recorded were soaring over the river or along adjacent ridges. During the eight censuses after the flood, only 6.8% of all observed eagles were soaring. No eagles were observed feeding during the flood.

A negative curvilinear relationship occurred between the percentage of birds in the air (flying or soaring) and relative salmon availability (F = 9.87, df = 2,10, P < 0.01; Fig. 2). When salmon availability declined, the percentage of birds in the air increased exponentially. No correlation was detected between the

percentage of eagles in the air and weather variables such as wind speed, percentage cloud cover, and ambient temperature.

Following during roost departures and arrivals.— Of 473 eagles departing roosts, 31.3% left within 1 min of the preceding bird(s), and 73.1% left within 5 min. Of 771 eagles arriving at roosts, 24.7% entered within 1 min of other eagles, and 65.0% within 5 min. To assess whether or not eagles were departing or arriving independently of one another, we examined data from one roost (Kenney Creek), where we were able to distinguish all flight directions of eagles. If eagles leave or arrive independently, the joint probability of birds flying in the same direction is equal to the product of the individual probabilities for each direction. For example, if 20.0% of 30 eagles depart upriver, 16.7% fly to the river, and 63.3% fly downriver, the probability of two birds flying in the same direction is $0.20^2 + 0.167^2 + 0.633^2 = 0.469$. Eagles departing and entering roosts within 1 min of each other chose the same direction more frequently than expected (Table 1).

If an average flight speed of 80 km/h (Brown 1976: 84) is assumed, eagles that followed others by our definition (see Methods) left or entered roosts within 18 s of the lead bird. Therefore, we feel our definition provided a conservative estimate of following behavior.
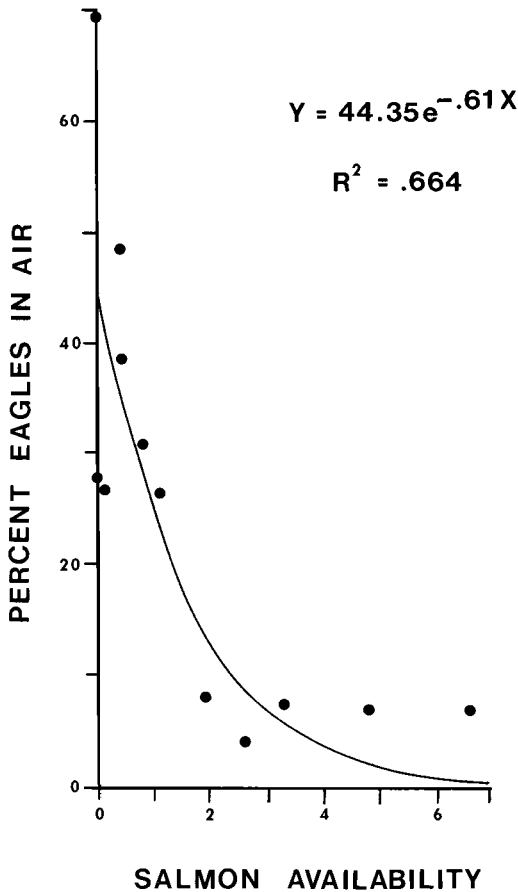
Sixty-nine (14.6%) eagles followed other ea-

$$Y = 44.35e^{-.61X}$$

$$R^2 = .664$$

SALMON AVAILABILITY

Fig. 2. Relationship between percentage of eagles in the air and salmon availability during weekly censuses, 16 December 1980 to 19 February 1981.

TABLE 1. Results of tests for independence of eagles departing and entering Kenney Creek roost within 1 min of other eagle(s).[a]

Dates[b]	Total number of eagles departing (A) or arriving at (B) roost	Number of simultaneous departures (A) or arrivals (B)	χ^{2c}
A. Roost departures			
16, 18–21 Dec	41	12	16.80***
26–28 Dec	28	10	6.84**
29–31 Dec	26	11	10.82***
1–2 Jan	29	6	0.83 (N.S.)
3–4 Jan	31	11	4.80*
10, 13 Jan	39	10	23.85***
24–25 Jan	32	8	4.94*
10–13 Feb	30	7	7.94**
B. Roost arrivals			
29–30 Dec	28	9	6.67**
31 Dec, 1 Jan	46	12	5.28*
2–3 Jan	40	8	4.78*
22–23 Jan	27	7	2.44 (N.S.)
24–26 Jan	38	16	13.09***
3–4 Feb	30	9	3.94*

[a] Null hypothesis: Eagles departing or entering roost within 1 min of other eagle(s) choose flight direction independently. Alternative hypothesis: Eagles flying within 1 min of other eagle(s) do not choose direction independently of one another.

[b] Days were combined to provide adequate sample sizes.

[c] Significance levels (df = 1): *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, N.S. = not significant.

gles when departing night roosts. In addition, 36 (7.6%) flew side by side. In five instances of following, we confirmed that flights terminated at feeding sites. When arriving at night roosts, 78 (10.1%) eagles followed other eagles and 8 (1.0%) flew side by side. As many as 10 eagles were seen flying in line during roosting flights. The relative frequency of following incidents during roost departures was not correlated with roost size ($F = 1.56$, df = 1,46, $P > 0.20$), the maximum number of eagles entering or departing being used as an estimate of roost size.

During roost departures, immature eagles followed other eagles more frequently than did adults ($\chi^2 = 3.44$, df = 1, $P < 0.10$). When departing roosts, 17.6% of immatures followed others, whereas only 11.2% of adults followed other eagles. Age relationships of eagles in-

volved in these following incidents varied discernably between a 5-day time period corresponding with the flood (26–31 December 1980) and the remainder of the season. Adults departing roosts were followed with a greater probability than were immature birds during the flood ($\chi^2 = 10.14$, df = 1, $P < 0.005$; Fig. 3); the two age groups were followed equally during the rest of the season, however. A higher proportion of both adult ($\chi^2 = 5.30$, df = 1, $P < 0.05$) and immature eagles ($\chi^2 = 4.06$, df = 1, $P < 0.05$) leaving the roosts followed other eagles during the flood period than during the remainder of the season (Fig. 3). The tendency to follow decreased toward the end of the season.

Immatures enroute to roosts in the evening followed other eagles more frequently than did adults ($\chi^2 = 10.89$, df = 1, $P < 0.005$). Fifty-one (13.7%) immatures followed others, whereas 25 (6.7%) adults followed other eagles into
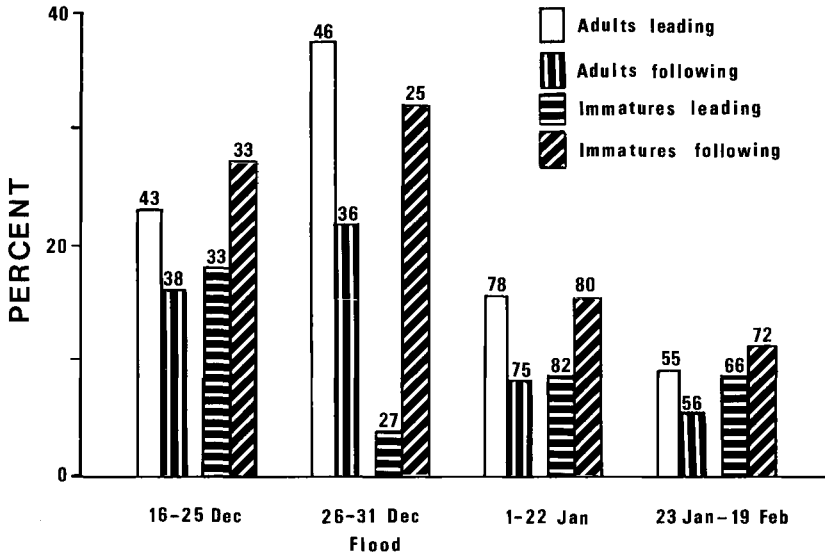
Fig. 3. Percentage of adult and immature eagles that were leading and following other eagles during roost departures. Numbers denote sample sizes.

roosts. Adults led more often during these incidents than did immatures ($\chi^2 = 11.41$, df = 1, $P < 0.005$). There was no significant temporal variation in the rate adults followed other eagles, but immatures followed more frequently during the flood than at other times ($\chi^2 = 5.21$, df = 1, $P < 0.05$).

Of 22 cases of eagles flying side by side, 11 involved 2 adults, 6 involved 2 immatures, and 5 involved an adult and an immature.

To assess the frequency of following behavior during roost departures, we calculated a Following Index (FI) as:

$$\frac{\text{number of eagles following other eagles}}{\text{total number of eagles departing roost} - 1} \times 100.$$

Birds flying side by side were not used in this calculation. We calculated a Salmon-to-Eagle Index (SEI) as:

$$\frac{\text{number of available salmon carcasses/1,000 m}^2}{\text{number of eagles}} \times 100,$$

using results from Bald Eagle and salmon censuses. The 47 morning observation periods were placed into 11 time periods corresponding to eagle and salmon censuses.

Variation in SEI and morning roost depar-

ture FI values occurred between 16 December 1980 and 19 February 1981 (Fig. 4). Sharp declines in the SEI accompanied by high FI values occurred during the flood and again in mid-January. As food availability increased after the flood the FI decreased. Considering the entire season, we observed no correlation between the SEI and morning FI values. A negative correlation occurred ($r = -0.914$, $P < 0.05$), however, when the five time periods during and immediately after the flood, 26 December 1980 to 19 January 1981, were considered separately. The frequency of following behavior was highest when all salmon were eliminated by flood waters ($\chi^2 = 12.41$, df = 1, $P < 0.005$). No correlation was noted between the SEI and evening roost arrival FI, yet the frequency of following into roosts was also higher during the flood period than at other times in the season ($\chi^2 = 4.99$, df = 1, $P < 0.05$).

DISCUSSION

Local enhancement.—Through the process of local enhancement, "the attention of other members of the flock may be called to a new food source discovered by one individual" (Hinde 1961: 394). If Bald Eagles are individually adept at finding food and do not benefit from local enhancement, one would predict
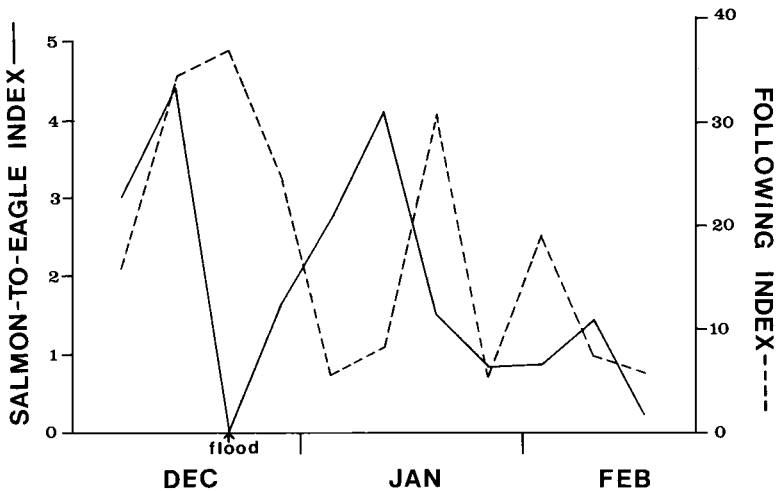
Fig. 4. Temporal variation in Salmon-to-Eagle and Following indices during night roost departures, 26 December 1980 to 19 February 1981.

that, when equivalent stations of salmon are available, both would be used, perhaps simultaneously. On the other hand, if food is more easily located when attended by other feeding birds, one would expect that the attended and unattended stations would attract eagles disproportionately.

Our data strongly suggest that Bald Eagles use the presence of other eagles as cues in locating food during the winter months. A Bald Eagle standing on the river bar is more easily visible to a searching eagle than salmon carcasses, which are difficult to see among driftwood and boulders.

At least three possible alternative explanations of our data exist. First, although we attempted to arrange stations so that visibility and attractiveness to eagles were equivalent within each trial, other environmental factors not considered may have influenced the eagles' choice of stations. In only four trials we placed stations within 50 m of sites used the previous day. We could not separate the effects of site preference, memory, or attraction to crows and ravens on the choice of the first eagle to arrive in these four trials. Second, Bald Eagles may prefer feeding with other eagles because of the ease of consuming salmon torn open by others. Stalmaster (1981) documented a preference by eagles for partially eaten salmon. He suggested that this behavior may be adaptive, because it eliminates time and energy needed to rip open skin, and a partially eaten carcass may indicate

food suitable for ingestion. Third, eagles may feel more secure when feeding with other eagles due to a greater ability to detect disturbance or possible danger.

Crows and eagles occurred together at feeding stations more frequently than expected. Crows, if unable to tear the skins of carcasses, may benefit from such an association by feeding on partially eaten carcasses and scraps left by eagles. This association may also benefit members of both species by increasing their abilities to detect possible danger.

Flight behavior associated with food finding.— One method used by Bald Eagles to locate food may be visually searching for feeding birds and food sources while flying and soaring along the river and surrounding ridges. As available food decreases, eagles might spend more time aerially searching for food. Our findings support this contention. We did not detect any effect of weather conditions on the incidence of soaring, possibly because our censuses were conducted in the morning before thermals were generated and because of a narrow range in wind velocities. The increase in eagle numbers after the flood was most likely a result of regional flooding, which caused widespread elimination of salmon (Hunt and Johnson 1981). The Nooksack River was not as seriously affected as other drainages because of the later timing of spawning activity.

Following.—Here we examine four nonexclusive explanations for following behavior. First,

following may result from independent flights that are synchronous with extrinsic factors (Bayer 1981), such as light intensity or time of day. Second, because the probability of independent but simultaneous departures and arrivals increases with the size of the roost (Bayer 1981), following may be an artifact of roost size. We have shown, however, that eagles leaving or entering roosts within 1 min of each other were not flying independently, nor was the frequency of following behavior correlated with roost size. Third, birds flying in association may be socially bonded. Mates may remain together, young may follow parents, and eagles may be attracted to conspecifics because of age, relatedness, or prior experience. The nature of social bonds in Bald Eagles is unknown outside of the breeding season. Our observations of eagles flying side by side suggest that social bonds may persist and may thus account for a portion of the following behavior. Fourth, following may be a mechanism of information exchange in accordance with the Information Center hypothesis. To support this hypothesis unequivocally, data must show that unsuccessful birds follow successful foragers to the site used the previous day (Bayer 1982) or that leaders have a higher probability of finding new food patches than followers. We did not collect such data; thus, the evidence we present supports the hypothesis only indirectly.

The greater frequency of following incidents during the flood and the increased tendency for adults to be leaders are consistent with a food-information explanation. We may assume that adults, with more experience, are more successful foragers than are immatures and would be better to follow during food stress. The percentage of eagles flying in association (flying side by side or following) with other eagles into the roosts in the evening (11.2%) was substantially lower than those departing roosts in the morning (22.2%). This discrepancy in frequencies of following behavior between morning and evening lends support to there being a food-information function during roost departures in addition to other possible functions of following.

The negative correlation between the morning FI and SEI in the time periods during and immediately after the flood suggests a food-related function. During periods of resource limitation or extreme environmental stress, selection pressures may be intense, and popu-

lations may experience an "ecological crunch" (Wiens 1977). Thompson et al. (1974) demonstrated that flocking was more important to reduce the risk of not finding food than to maximize foraging efficiency. During food-stressed conditions, selection may favor any behavior that minimizes the risk of individual Bald Eagles not finding food and thus may favor a communal roosting habit. The salmon shortage during the flood of December 1980 may have been an example of such an ecological crunch.

Communal roosting in Bald Eagles may not have evolved to enable eagles to acquire information about food location; rather it may be due to the actions of several selective pressures. Information exchange may have developed as a secondary adaptation once communal roosting evolved for other reasons (Wittenberger 1981). Roosts may be selected because of favorable microclimatic conditions or proximity to feeding areas, thereby allowing for reduced energy expenditures (Hansen et al. 1980, Steenhof et al. 1980, Stalmaster 1980). Communal roosts may provide gathering points prior to long-distance movements and may facilitate formation and reuniting of pairs (L. Young pers. comm.). For an individual, these benefits may outweigh any potential costs.

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