



## Short Communications and Commentaries

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### Ospreys Use Local Enhancement and Flock Foraging to Locate Prey

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Two social-foraging behaviors used to exploit patchily distributed prey are local enhancement and flock foraging. Usually, local enhancement involves an individual or individuals joining one or more conspecifics that have indicated in some manner that they have located prey (Thorpe 1963). Consequently, the newcomer(s) discovers a food source previously unknown to it (Barnard 1980, Waite 1981, Knight and Knight 1983, Brown 1988a). Birds that forage in flocks can search more effectively by avoiding repeated searches of the same place, and by decreasing the chance of missing patches of prey (Krebs 1973, Barnard and Stephens 1983, Grubb 1987). Flock foraging is distinct from local enhancement because it refers to birds that forage as a group for an extended period of time, rather than to birds forming temporary groups as a consequence of responding to the food discoveries of conspecifics. The most apparent benefit of these two foraging strategies is the enhancement of the mean rate of ingestion (Pulliam and Millikan 1982, Clark and Mangel 1984, Brown 1988a, b). Another benefit may be a reduced variance in foraging success, and a reduced risk of starvation of the individual, its dependent offspring, or both (Ekman and Hake 1988).

In Nova Scotia, Ospreys (*Pandion haliaetus*) that nest close to the coast often do so in colonies. Males provide nearly all of the food for their mates and offspring. They forage alone or in flocks, usually in estuaries (Prevost 1977, Greene 1987). Most fish species taken as prey are abundant, but only are available periodically and are distributed patchily (Prevost 1977, Greene 1987). Knowledge by males about the location of prey could reduce the risk of nestling mortality. Food-related facultative brood reduction is an important mortality factor in nestling Ospreys (Poole 1982).

Greene (1987) found that Ospreys in a Nova Scotia colony transferred information (cf. Ward and Zahavi 1973) to conspecifics about the location of large schools of fish, but not about winter flounder (*Pseudopleuronectes americanus*). The winter flounder is the most common prey of Ospreys nesting in Nova Scotia, and

comprises about 90% of their diet (Prevost 1977, Greene 1982). Given the importance of this fish, it is plausible that other social-foraging strategies might be used by Ospreys to locate winter flounders (Flemming and Greene 1990).

Winter flounders are periodically available in schools during tidal surges (Tyler 1971), and they are likely to be patchily distributed in the intertidal zone because of the clumped distribution of their prey (Wells et al. 1973). Because detection of one flounder may provide information about the location of others, joining one or more conspecifics via local enhancement and/or flock foraging would allow an individual Osprey to locate a fish more readily than if the bird had remained solitary. Arrival at the foraging area with conspecifics would enhance the utility of these foraging behaviors. We tested the hypothesis that a population of Ospreys in Nova Scotia used these social-foraging behaviors to hunt for winter flounders.

The study area was an estuary in Antigonish County (45°38'N, 62°54'W), Nova Scotia, Canada. This shallow estuary drains a 750-km<sup>2</sup> watershed and empties into the Northumberland Strait in the Gulf of St. Lawrence. Ospreys nest colonially on utility poles along powerline corridors, as well as solitarily on dead or living trees. Mean interest distance for colonial nesters was 0.7 km. However, many colonial birds nested within 0.3 km of conspecifics (Flemming et al. 1991). Males of 29 breeding pairs that nested within 6 km of the estuary regularly foraged at the study site.

Observations (380 h) of foraging male Ospreys were made from either an elevated blind or from a boat. Observation bouts of 3 h were made during the period 0501-2000 AST, 1 May-27 August 1984-1985 and 8 June-8 July 1986. We counted the number of foraging Ospreys in a specified census area at 10-min intervals in 1985 ( $n = 588$  counts) and 1986 ( $n = 528$ ). The time of arrival was also recorded for each bird that entered the foraging area.

Flocks were categorized by the number of members and their density. An Osprey was considered to be a single forager unless a conspecific(s) began foraging within 200 m of it. At this point, the two or more

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birds were considered to be a flock of  $X$  members at distance interval  $Y$ . We used intervals of 0–50, 51–100, 101–150, and 151–200 m. A flock's distance interval was determined by comparison with measured natural reference points at the foraging area. The interval that we recorded was the smallest diameter that described a circle around all flock members. Flock density was estimated using the circular surface area of the interval (using mean interval diameters of 25, 75, 125, and 175 m) divided by the number of flock members. We designated flocks as high (members in the 0–50 m interval) or low (> 50 m) density in order to analyze search time/dive as a function of flock density.

A flock was timed from the moment it formed until a member dove, or until an Osprey joined or left the flock. Search time was only analyzed for flocks where a member dove because we were sure that these birds were foraging, as opposed to birds possibly flocking for nonforaging reasons, which was also common in our study area. This biases against flocks with zero success, but provided a common currency to investigate whether or not search time varied with flock size and density. For each dive, search time was multiplied by the number of flock members to obtain a mean individual search time for that flock. This compensated for the proportional increase in dive probability that would occur with an increase in flock size.

We recorded environmental conditions that foraging Ospreys would have experienced. We partitioned: the diurnal period into five 3-h periods (0501–2000); tidal amplitude into low, middle, and high tide; water clarity into clear (substrate clearly visible), hazy (objects < 10 cm in diameter were not visible), or murky (objects < 20 cm were not visible) at a depth of 1 m; and cloud cover as clear (< 10% cloud cover), cloudy, or raining. It was not always possible to collect data for all variables during each observation period; hence, sample sizes vary.

We used programs from SYSTAT 4.0 (Wilkinson 1989), or statistical methods presented in Zar (1984) to analyze data. Tests are two-tailed unless specified, in which case response direction was predicted *a priori*. The chi-square test and analysis of variance were used on normally distributed data. The Kruskal-Wallis test was used when distributions were not normal, and a nonparametric analog for the Student-Newman-Keuls test was used for multiple comparisons. For the chi-square tests of the distribution of times between successive arrivals versus the negative exponential, degrees of freedom varied because of variation in sample size and subsequent number of legal cells (expected  $\geq 5$ ).

Local enhancement was used by Ospreys that foraged in Antigonish estuary. Hunting Ospreys frequently hovered over sites while scrutinizing the water below. Those that eventually dove for prey usually spent 1 to 3 min hovering over a specific site before making the dive. This highly visible behavior was

exploited by other Ospreys, as hovering Ospreys often were joined by conspecifics (4.9 single birds joined/h,  $n = 380$  h). We considered an Osprey to have joined another bird or flock when it approached within 200 m. It seems unlikely that newcomers would have seen the patch of flounders from beyond that distance. Thus, the newcomer appeared to be joining conspecifics, rather than approaching the prey independently.

Flock foraging usually occurred when there were two or three Ospreys at the estuary. Individuals in foraging flocks stayed within 25 m of each other for as long as 10 min. Although Ospreys followed one another within the flock, the order of following continually changed.

We investigated the possible influence of environmental conditions on the use of flock foraging (Fig. 1). Both the counts of numbers of foragers and estimates of flock densities were analyzed using the Kruskal-Wallis test, with multiple comparisons made with a nonparametric analog to the Student-Newman-Keuls test. Below, we report which groups were significantly different from one another by separating their group number by a dash. Numbers following probability values indicate groups (histogram bars) from left to right in Fig. 1.

There was an inverse relationship between the number of foragers and flock density. The number of foraging Ospreys was lower at midday ( $F = 10.18$ ,  $df = 4$ ,  $P < 0.001$ ; 1, 2–3, and 1, 2, 3, 4–5). At that time, flock density was greater ( $F = 3.43$ ,  $df = 4$ ,  $P < 0.01$ ; 1, 4, 5–2,3). There were fewer foragers at high tide ( $F = 3.83$ ,  $df = 2$ ,  $P < 0.05$ ; 1, 2–3), and flock density was higher for that tidal amplitude ( $F = 2.91$ ,  $df = 2$ ,  $P < 0.05$ ; 1–3). Fewer birds foraged when the water was murky ( $F = 3.06$ ,  $df = 2$ ,  $P < 0.05$ ; 1, 2–3), but flock density was higher then ( $F = 4.80$ ,  $df = 2$ ,  $P < 0.01$ ; 1, 2–3). The number of foraging Ospreys decreased with cloud cover, especially during rain ( $F = 4.63$ ,  $df = 2$ ,  $P < 0.01$ ; 1, 2–3). Flock density was greater during rain ( $F = 3.59$ ,  $df = 2$ ,  $P < 0.05$ ; 1–3). Ospreys formed higher-density flocks when there were fewer foraging conspecifics at the estuary.

A potential partner(s) was already at the foraging area and consequently available to newcomers as foraging partners only 33.5% of the time ( $n = 1,116$  counts). If foraging with others is advantageous, one might expect that Ospreys would join one another at the colony so as to arrive at the foraging area together. We evaluated this idea by comparing the frequency distribution of successive arrivals for each time interval with that predicted by the negative exponential, which assumes a random time of arrival. We found that the distribution of inter-arrival intervals was significantly different from the negative exponential for all time periods (0501–0800,  $X^2 = 21.59$ ,  $df = 7$ ,  $P < 0.005$ ; 0801–1100,  $X^2 = 43.51$ ,  $df = 10$ ,  $P < 0.001$ ; 1101–1401,  $X^2 = 26.35$ ,  $df = 3$ ,  $P < 0.001$ ; 1401–1700,  $X^2 = 41.16$ ,  $df = 9$ ,  $P < 0.001$ ; 1701–2000,  $X^2 = 41.23$ ,

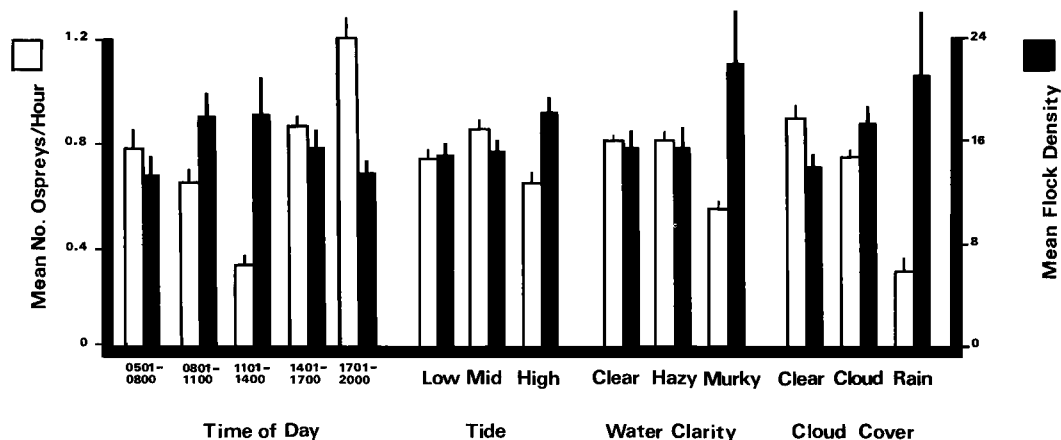


Fig. 1. Mean number of foraging Ospreys ( $n = 1,116$  counts; 1985–1986) and mean flock density (Ospreys/ha; 1984–1986) throughout day ( $n = 1,789$  flocks), as well as under different conditions involving absolute tidal phases ( $n = 1,789$ ), water clarity ( $n = 826$ ), and cloud cover ( $n = 1,472$ ). Error bars denote SE.

df = 11,  $P < 0.001$ ; Fig. 2), and for all tidal phases (low,  $X^2 = 40.27$ , df = 12,  $P < 0.001$ ; middle,  $X^2 = 89.47$ , df = 14,  $P < 0.001$ ; high,  $X^2 = 50.55$ , df = 11,  $P < 0.001$ ; Fig. 3). There were more short and long intervals between successive arrivals than expected, indicating that birds arrived at the foraging area together.

Incidental observations provided evidence for three patterns of behavior that may have contributed to synchronous arrival. Newcomers were joined by conspecifics that had been perched at the periphery of the estuary. Ospreys were also observed forming small flocks (2–11 individuals) while they were riding thermals. Usually, this occurred in the vicinity of the Osprey colony. Finally, we observed small flocks of two to four male Ospreys circling and/or hovering over nests in an Osprey colony, while vocalizing (36/164 intraspecific interactions). This may have been an attempt to recruit foraging partners. Resident males were usually at nearby perches when this happened. However, they never chased these "soliciting" birds; rather, they remained at perches and vocalized. On 8 of 36 observations of this behavior, the resident males joined the soliciting males, and the group flew to the foraging area.

Assuming that the dive of an Osprey reflects the presence of prey, we explored how search time and dive success were affected by the number of flock members and flock density. Table 1 shows that mean search time/dive was significantly lower for individuals that were members of a flock. An individual's search time/dive also was significantly shorter in higher-density flocks (Table 2). However, the percentage of successful dives was unaffected by flock size or density (ANOVA,  $F = 0.87$ , df = 5,  $P = 0.50$ ;  $F = 0.52$ , df = 12,  $P = 0.36$ ).

Increased flock size and density reduced the risk of taking an excessively long period of time to locate

prey. The coefficient of variation of search time/dive significantly declined with increased flock size ( $Y = 1.44 - 0.0985X$ ,  $n = 9$  flock sizes,  $n = 675$  search times/dives,  $r^2 = 0.51$ ,  $P < 0.05$ ), and increased flock density ( $Y = 99.9 - 2.341X$ ,  $n = 18$  densities,  $n = 309$  search times/dives,  $r^2 = 0.17$ ,  $P < 0.05$ ).

Winter flounders, the principal prey of Ospreys in this study, were patchily distributed in the Antigonish estuary (Tyler 1971, Wells et al. 1973). Perhaps as a consequence, Ospreys often responded to the food discoveries of conspecifics in a manner consistent with local enhancement. Furthermore, when there were few foragers, Ospreys searched for winter flounders in flocks. These social-foraging behaviors were beneficial, as reflected in the reduced time required by a group member to find prey, and especially while in a dense group as opposed to a dispersed one. However, dive success was unaffected by either flock size or density, suggesting that being a member of a flock did not influence the ability of an individual to capture prey.

Caraco et al. (1990) have shown that variance in food ingestion is an important component in determining a bird's foraging strategy. Social foraging is one means of controlling variance (Ekman and Hake 1988). We found that Ospreys foraging in flocks reduced their variance in the time required to locate prey. Still, there may be a cost to flock foraging once a patch of prey is found. Unless patches are large enough to satisfy the requirements of all flock members, foraging solitarily may often be a better strategy (Ekman and Rosander 1987, Hake and Ekman 1988). Since winter flounders occur in small groups (Tyler 1971), one would expect that there is an upper limit to cost-effective flock foraging.

Ospreys could "fine tune" the benefit/cost tradeoff by altering flock size or density. Flock size was usually small in our population, so altering it would have

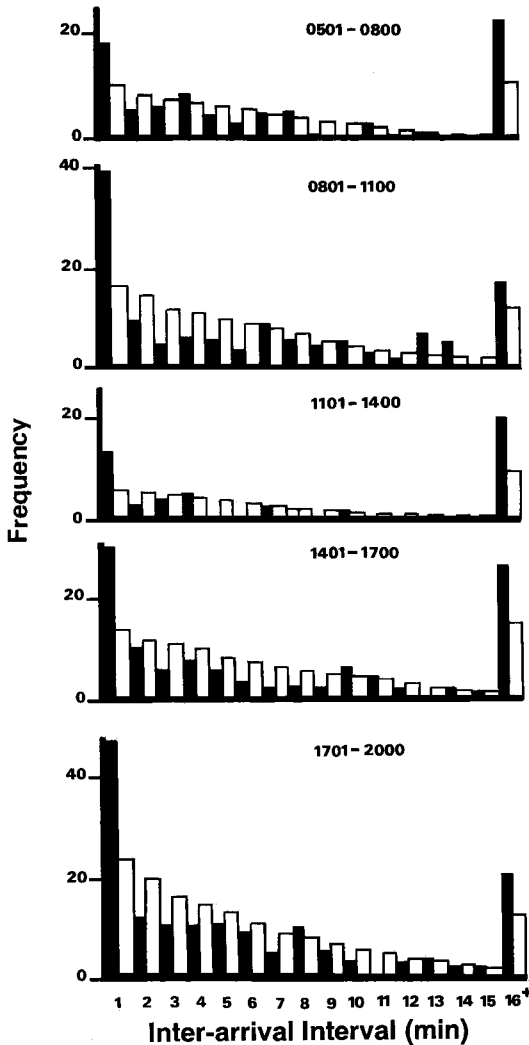


Fig. 2. Distribution of time intervals between successive arrivals throughout day (1985-1986). Solid bars are observed, and open bars are expected based on negative exponential.

been of limited value. However, flock density could have been readily changed. By maintaining a large distance between foraging neighbors, while still keeping them in sight, an individual could essentially forage on its own, but have the option of using local enhancement during good foraging conditions. In contrast, flock foraging might occur during those foraging conditions that resulted in fewer foraging Ospreys, because foraging by local enhancement would be less viable then. This is because fewer conspecifics would be available to be exploited, and prey would be especially difficult to locate (Flemming and Smith 1990). Consequently, the variance in the time required to locate prey would be higher. To minimize

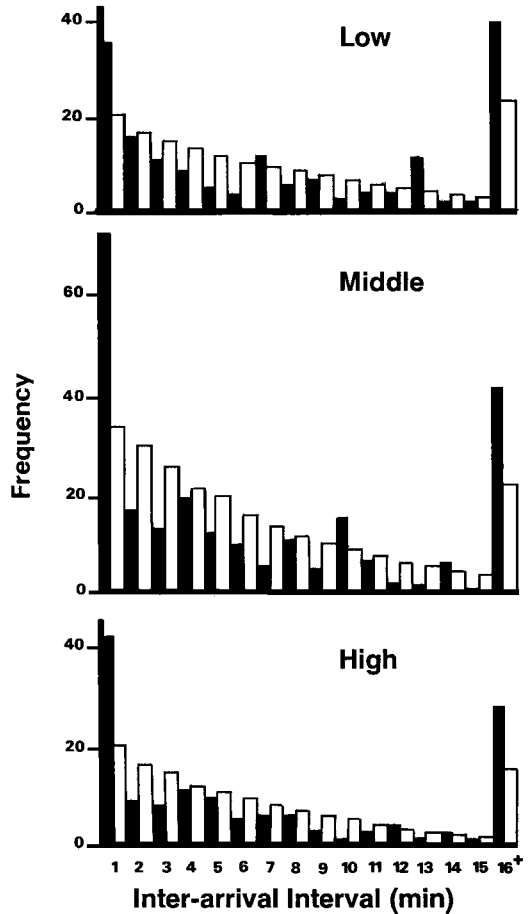


Fig. 3. Distribution of time intervals between successive arrivals during low, middle, and high absolute tidal phases (1985-1986). Solid bars are observed and open bars are expected based on negative exponential.

variance, Ospreys could more frequently seek opportunities to form foraging flocks, thereby increasing the mean flock density relative to times when foraging conditions are good. We found strong evidence for compensatory use of flock foraging during adverse environmental conditions, when the premium was on minimizing the variance in the time required to locate prey.

We have interpreted our results from the standpoint of inherent advantages. However, an alternative explanation must be considered. Flocks, especially high-density ones, may simply be concentrations of birds associated with high prey abundance. This argument cannot be refuted and, indeed, may explain part of our observations. However, it does not explain all of the results. Nonforaging area flocking, synchronous arrival, and compensatory changes in flock structure suggest an active "choice" of strategies. It

TABLE 1. Mean individual search time/dive as a function of solitary versus flock foraging, 1984-1986.

Flock size	Mean search time/dive (s)	No. dives
1	163.6 <sup>a</sup>	366
2	100.2	163
3	120.0	76
4	153.4	26
5	101.5	24
Flocks of 2-9 members	114.1 <sup>a</sup>	309

<sup>a</sup> One-tailed *t*-test of search time for flock size 2 or more being less than that for flock size 1 ( $P < 0.001$ ).

is apparent that Ospreys in our study benefitted from an active form of social foraging.

Greene (1987) reported that Ospreys used a Nova Scotia colony as an information center to exploit large schools of fish. Hagan and Walters (1990) rejected the hypothesis that information was transferred in a North Carolina Osprey colony on the basis that departures of unsuccessful foragers were not influenced by the arrival of successful foragers, and that males showed strong fidelity to particular foraging areas. In the population we studied, individual Ospreys used local enhancement and flock foraging while hunting for winter flounders. Moreover, we observed behaviors suggestive of flock members being recruited at the nesting colony: either passively, by joining other Ospreys riding thermals; or actively, via what appeared to be soliciting behavior. On these occasions, Ospreys left the colony in groups and also arrived at the foraging area in groups. Hagan and Walters (1990) have noted synchronous departure of Ospreys from an Osprey colony. They reported that birds which were unsuccessful in returning with prey on their previous foray, more frequently departed from the colony in those 15-min intervals during which others departed.

In addition to transfer of information (Greene 1987), another function of nesting in colonies might be for Ospreys to form foraging flocks. Nesting in a colony would enhance the probability of finding potential flock mates to allow social foraging to occur (Evans 1982). This would be especially important when environmental conditions mitigated against successful foraging. At such times, foraging in flocks would be beneficial due to an enhanced ability to compensate for poor foraging conditions that would otherwise reduce the number of fish delivered to nestlings (Machmer and Ydenberg 1990). Hence, colonial birds could more readily reduce the impact of adverse foraging conditions. This might enhance fledging success. Flemming et al. (1991) examined the relative reproductive success of colonial versus solitary nesting Ospreys in this population. They found that colonial pairs fledged more young than solitary pairs.

TABLE 2. Mean individual search time/dive as a function of flock density, 1984-1986.

Flock size	Flock density	Mean search time/dive (s)	No. dives	<i>P</i> <sup>a</sup>
2	Low	57.1	98	0.05
	High	39.5	65	
3	Low	44.2	65	0.001
	High	15.1	11	
4	Low	43.6	21	0.01
	High	16.2	5	
2-9	Low	45.6	224	0.05
	High	34.3	85	

<sup>a</sup> One-tailed *t*-tests of search time for high-density flocks being less than that for low-density flocks.

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## Vocalizations in *Aptenodytes* Penguins: Application of the Two-voice Theory

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*Aptenodytes* penguins are colonial seabirds that have no nest but incubate a single egg on their feet. There are two species in the genus: the Emperor Penguin (*A. forsteri*) breeds during the harsh antarctic winter on the sea ice, and the King Penguin (*A. patagonicus*) breeds in subantarctic regions on beaches. Both sexes in each species produce a mutual display call that facilitates the search for a partner at the pairing period. When these penguins return from the sea to resume responsibility for the egg or chick, they use

the same call to achieve mutual recognition of the incubating partner and its mate (Stonehouse 1960, Prévost 1961, Jouventin 1982). King Penguins head towards the restricted area of the colony where their partners are incubating and call to be recognized. However, partner reunion would appear to be particularly difficult for the Emperor Penguin because these birds exhibit a wandering incubation that enables them to regulate the microclimate of the colony by gathering in dense huddles, thus withstanding the