FORAGING BEHAVIOR, REPRODUCTIVE SUCCESS, AND COLONIAL NESTING IN OSPREYS

JOHN M. HAGAN III[1] AND JEFFREY R. WALTERS
Department of Zoology, Box 7617, North Carolina State University,
Raleigh, North Carolina 27695-7617 USA

ABSTRACT.—We tested several hypotheses about the evolution of colonial nesting in Ospreys. We examined foraging behavior and reproductive success of members of a dense colony in coastal North Carolina to test (1) if the colony functioned as a central place for exchanging information about the location of food patches (Information Center Hypothesis), (2) if the colony was located centrally relative to foraging sites, which would minimize foraging travel costs, (3) if the colony functioned to promote synchronized breeding, which would swamp predators with more young than they could consume, (4) if nesting in the center of a group decreased predation pressure, and (5) if safe nest-site distribution controls actual breeding distribution. The hypothesis that the colony functioned as an information center was supported by synchrony in departure, but contradicted by evidence of fidelity to foraging areas. The colony did not function as the geometric center of an individual's foraging locations. Colony members traveled 1.5-7 times as far as they would have traveled had they nested at their geometric centers. There was a negative correlation between the proportion of eggs lost in the colony and the number of eggs available to predators, suggesting some benefits to synchronous nesting in a close spatial group. However, there was no numerical response in predation relative to the total number of eggs available in the colony. Birds nesting toward the center of the colony produced significantly more fledglings than peripheral nesters, but strong nest-site fidelity prevented shifting to more central locations by peripheral nesters. Spatial distribution of nests reflected the distribution of potential nest trees, both within the lake and within the region. This and the plasticity of nesting density shown in Ospreys support Lack's (1968) Nest-site Hypothesis. We conclude that the spatial distribution of safe nest sites and advantages related to predation maintain coloniality in Ospreys. *Received 22 May 1989, accepted 15 January 1990.*

COLONIAL nesting in birds is a common yet poorly understood phenomenon. A *colony* may be defined as a group of animals that nest at a centralized location, from which they recurrently depart in search of food (Wittenberger and Hunt 1985). Members of a nesting colony of birds are constrained by the immobility of their clutch or brood. The costs of traveling to and from such a central location are obvious, but the benefits are not. Explanations of colonial breeding fall into three categories (Alexander 1974). Colonial breeding may enhance foraging (Crook 1965, Emlen 1971, Fisher 1954, Lack 1968, Ward and Zahavi 1973), reduce the probability of predation (Burton and Thurston 1959, Kruuk 1964, Horn 1968, Burger 1974, Hoogland and Sherman 1976), or result from resource constraints (e.g. nest sites, food distribution) (Horn 1968, Lack 1968). The first two explanations postulate that individuals nesting near others derive a higher fitness as a result of interaction. The third explanation postulates no such advantage. For most species it is not clear whether nesting near others is beneficial or is a by-product of a habitat constraint.

The Information Center Hypothesis (Ward and Zahavi 1973) relates colonial nesting to foraging success. Individuals may learn about the location of patchily distributed, ephemeral foods from other colony members. Information need not be exchanged actively. Simply following or cuing in on the return direction of an individual known to have been a successful forager qualifies as "exchange." Ward and Zahavi's Information Center Hypothesis has become widely cited (ISI 1983), but clear evidence that information transfer induces colonial nesting is lacking. It is a difficult hypothesis to test and involves distinguishing between successful and unsuccessful foragers, and then demonstrating

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[1] Present address: Manomet Bird Observatory, P.O. Box 936, Manomet, Massachusetts 02345 USA.

that unsuccessful foragers improve their success by obtaining information on food location from successful birds (Mock et al. 1988).

Nevertheless, evidence that information exchange seems to occur in colonies (or roosts) has recently been obtained for three avian species (Brown 1986, Rabenold 1987, Greene 1987). The role of the information exchange in the evolution of colonies remains debatable, however. Information centers could be widespread phenomena, critical to the evolution of coloniality, or they could simply be a secondary adaptation that sometimes occurs as a result of group living (coloniality having evolved for other reasons).

To address this question, we examined another colony of a species that has already been shown to exchange information. Demonstration of information exchange at an independent site would imply that it can be a widespread phenomenon, and therefore may be an important factor leading to, or at least maintaining, group living. Its relative importance to colony maintenance should be correlated to its commonness.

We tested the Information Center Hypothesis for an Osprey (*Pandion haliaetus*) colony in coastal North Carolina. This site is distant from the colony in Nova Scotia where Greene (1987) documented information exchange, and the strong natal-site fidelity of Ospreys makes it extremely unlikely that individuals of these colonies would mix (Poole 1989: 137). Male Ospreys supply nearly all of the food for the female and nestlings. Males in the North Carolina colony must travel long distances to any of several foraging locations, and exploit schools of marine fish, which fluctuate spatially and temporally. The colony is large (50-60 pairs) and dense, and returning foragers are readily visible. If information exchange is a prominent feature of group living in Ospreys, it should be evident at this site, where conditions theoretically conducive to information exchange are nearly ideal.

We tested other hypotheses related to predation reduction as a result of group living in Ospreys by examination of spatial and temporal patterns of reproductive success in the colony. Detection of predators is improved by flocking (Powell 1974, Siegfried and Underhill 1975, Kenward 1978, Lazarus 1979, Caraco et al. 1980, Barnard 1980, Bertram 1980, Jennings and Evans 1980, Thompson and Barnard 1983), and it seems likely that detecting predators would be similarly enhanced by grouping among nesting birds. Nests in the center of colonies suffer less predation than those on the periphery in many species, which is consistent with the proposed effects of group mobbing or predator detection (e.g. Patterson 1965, Tenaza 1971, Siegfried 1972, Feare 1976, Siegel-Causey and Hunt 1981).

Synchronous breeding of an avian assemblage can also produce benefits to members. By swamping potential predators with a synchronized production of young, colony members can reduce the probability that their offspring will be preyed upon (Patterson 1965, Nisbet 1975, Feare 1976, Veen 1977). Emlen and Demong (1975) suggested that synchronous breeding in Bank Swallow (*Riparia riparia*) colonies increased opportunities for social foraging, thereby increasing foraging efficiency. We tested this hypothesis by relating breeding chronology to reproductive success in the colony.

Finally, we tested two hypotheses related to resource constraints. Horn's Geometric Center Hypothesis holds that colony formation could be due to food distribution (Horn 1968). By nesting in the center of the distribution of a patchy, ephemeral food supply, birds can minimize overall foraging distance traveled. No benefit of sociality is implied; rather, foraging considerations that act on many individuals in an identical way lead to colony formation. The evidence to support this hypothesis comes from Horn's (1968) study of Brewer's Blackbird (*Euphagus cyanocephalus*).

The Nest-site Hypothesis (Lack 1968) holds that coloniality is related to the distribution of safe nest sites. If safe nest sites are clumped, nests will also be clumped. For those colonial species that feed solitarily, Lack (1968) maintained that safe nesting sites—rather than feeding habitats—are the critical determinants of nesting distribution. It has never been demonstrated that nest-site limitation alone can induce coloniality.

We used a comprehensive approach to the study of colony formation and function in Ospreys, recognizing that many factors may operate to maintain colonial nesting. Although not commonly considered a colonially nesting species, Ospreys historically nested in colonies. Colonies became rare along the U.S. Atlantic seaboard in the 1950s and 1960s as a result of extensive use of DDT and its effects on eggshells (Ames and Mersereau 1964, Ames 1966, Hickey and Anderson 1968). Before this time, colonies

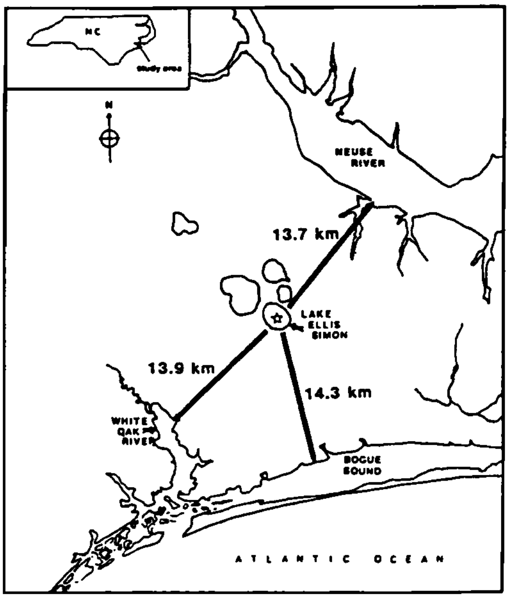

Fig. 1. Lake Ellis Simon and vicinity.

were common. One on Gardiner's Island, New York, supported approximately 300 nesting pairs of Ospreys (Puleston 1977). Ospreys are remarkably flexible in their nesting density, from remote and solitary nesting to colonies in which active nests are only 20 m apart (Poole 1989).

STUDY AREA AND METHODS

We studied an Osprey colony located at Lake Ellis Simon in coastal North Carolina (Craven County, 35°50'40"N, 76°59'06"W) (Fig. 1) from March through August, 1983 to 1985. This 600-ha, shallow, marshy lake contains hundreds of live cypress trees over water, in which 50-60 pairs of Osprey's nested each year. The density and number of nesting pairs has increased steadily from the 17 nests in 1967 (Henny and Noltemeier 1975).

Activity budgets.—From 15 May to 9 August in the 1983 breeding season, we sampled activity budgets of 23 nesting pairs. We restricted observations primarily to the nestling and postfledgling stages of the breeding cycle. From the pool of breeding birds, we randomly chose pairs for observation, excluding those whose nests had already failed. We took observations in 0.5-day samples (ca. 7 h duration, depending on day length), each of which involved focal samples of a single pair, unless two nests were close enough that adults of both pairs could be watched simultaneously. We observed birds from a portable blind on stilts, located ca. 100 m from the nest, and we completed the equivalent of one day of observation (sunrise to sunset) before we moved to a different nest. Afternoon samples were followed by subsequent morning samples to obtain this equivalent of a full day of sampling of a pair. We sampled three pairs twice (two days for each pair), but at different times during the breeding cycle.

We observed pairs for a total of 170 h, and assigned behaviors only to broad categories because we were interested in qualitative patterns in foraging by the males, which provide most of the food for their mates and young until fledging. The categories included (1) perched over nest, (2) perched on nest (includes incubation), (3) perched in territory (not nest tree), (4) away from territory, (5) flying within territory, (6) fishing in lake, and (7) other. Category 4 included all foraging away from the lake. Because foraging males ranged far, we could not subdivide this category further.

Foraging patterns.—During the incubation and nestling stages of the breeding season (April through June) in 1984 and 1985, we observed foraging patterns from a blind 12 m high, constructed of scaffolding, near the center of the lake. Arrivals, departures, and the foraging success of males were recorded every 15 min from sunrise to sunset, for each nest that could be seen from the tower. Sampling was done in two full (dawn to dusk) consecutive day sessions. Intervals of this span were unlikely to result in missed arrivals and departures because males typically spent 30 min to several hours perched in the nest territory after an arrival, and several hours away after a foraging departure. Although we could monitor 15-20 nests for fish deliveries with an 83× spotting scope, we could determine male presence/absence for only 10 nests in 1984, and 11 nests in 1985. Other nest territories had visual obstructions between the tower and the male's perch tree.

In 1985 we attached transmitters to 16 males so that vanishing and returning directions could be observed accurately. Only 8 provided consistent data; the other 8 males bit off the antennas, which drastically reduced signal range. We attached transmitters of 2-3% of the male's body mass to the base of the two central retrices with hot-melt glue. The height of the transmitter on a flying Osprey and of the 14-element receiving antenna atop the blind produced signal ranges of 6-14 km. We deduced foraging location from vanishing and return directions, and used these azimuths to compute geometric centers of foraging. We determined optimum nesting locations for each individual by calculating the geographic point where foraging travel distance, based on telemetry data, would have been minimized.

We tested the Information Center Hypothesis by comparing probabilities of departures of successful and unsuccessful foragers. When male Ospreys returned to their nests after being away for a minimum of 45 min (3 sample intervals), we classified them as being "successful" or "unsuccessful" foragers based on whether or not they returned with a fish. We chose

45 min as the criterion because observation indicated that a foray outside the lake could not be accomplished in less time.

Greene (1987) found that unsuccessful birds cued on the arrival of a successful bird. We examined the distributions of departures of unsuccessful birds (DEP_U) and departures of successful birds (DEP_S) relative to the distribution of arrivals of successful birds (ARR_S) among 15-min sampling intervals. If departures (or arrivals) were independent, their distribution among intervals should fit a Poisson distribution whose mean ($\bar{x}$) equals the number of departures divided by the number of intervals. If departures of unsuccessful birds were triggered by arrivals of successful birds, but successful birds departed independently of arrivals, then the following should hold:

1. The distributions of DEP_U among intervals with at least one ARR_S and among intervals with no ARR_S should both fit a Poisson distribution, but $\bar{x}$ will be greater for the former distribution.
2. The distributions of DEP_S among intervals with at least one ARR_S and among intervals with no ARR_S should both fit a Poisson distribution, and $\bar{x}$ should be the same for both distributions.
3. The distributions of DEP_U among intervals with at least one unsuccessful arrival (ARR_U) and among intervals with no ARR_U should fit a Poisson distribution, and $\bar{x}$ should be the same for both distributions. Differences in $\bar{x}$ were evaluated using *t*-tests.

Unsuccessful birds might *follow* successful birds when they leave the colony rather than depart in response to the arrival of a successful bird. If this was the mechanism of information exchange, then the following predictions should hold:

1. The distributions of DEP_U among intervals in which at least one DEP_S and among intervals with no DEP_S should both fit a Poisson distribution, but $\bar{x}$ will be greater for the former distribution, and
2. the distribution of DEP_S among intervals with at least one DEP_U and among intervals with no DEP_U should both fit a Poisson distribution.

In the case of joint departures, it is not possible to determine whether DEP_S depends on DEP_U or DEP_U depends on DEP_S, only that they are not independent. We tested for independence of distributions in two ways. First, we performed standard Chi-square tests of independence. Second, to better illustrate where deviations from independence occurred, we determined an expected joint distribution based on the assumptions that each distribution was Poisson, and that the two distributions were independent. We tested for deviations from this predicted distribution using the Chi-square analysis. These analyses were performed for the joint distributions of DEP_U and DEP_S, DEP_U and ARR_S, DEP_U and ARR_U, and DEP_S and ARR_S.

Birds that departed the colony at the beginning of the first day of a 2-day sampling session could not be classified as successful or unsuccessful. This biased the analysis toward synchronous departures because some intervals in which no departures were recorded actually included departures, but of unclassified birds. Therefore, we repeated all analyses using only data from the second of two consecutive days of sampling. On the second day, all initial departures could be classified based on success of the final foray on the previous day.

Temporal and spatial patterns of fledging success.—From 1983 to 1985, we checked all nests in the colony at weekly intervals for eggs, nestlings, or fledglings (from before breeding began to after all young had fledged). All nests were less than 9 m above the water and could be checked from a boat with a mirror attached to the end of a telescoping aluminum pole. Checking all nests required 1–3 h (depending on water level and weather conditions). Parent Ospreys were displaced from their nests for only 1–2 min during a check.

We designated all active nests as "central" or "peripheral" according to their location within the colony. We considered a nest peripheral if no other active nests stood within 200 m of either side of a line connecting the nest to the nearest point on shore.

We plotted the locations of all nests and potential nest sites on aerial photographs. Potential nest sites were identified subjectively as cypress trees that appeared to be physically able to support a nest. To examine whether Osprey nests were distributed in a pattern similar to available nest sites, we compared Morisita's index of dispersion (Morisita 1959) for actual nests with that for potential nest sites.

For each clutch, we recorded the week that eggs first appeared in the nest relative to the week that eggs first appeared in the colony that year (i.e. week of laying, where week of laying of first nesting attempt = 1). Laying was sufficiently asynchronous that we could employ regression techniques to examine the relation between reproductive success and week of laying. We used the mean reproductive success for all pairs laying in a given week in the regression analysis (GLM procedure in SAS [SAS 1985]). So as not to give undue weight to weeks with low sample sizes, we weighted the regressions by weekly sample sizes (number of pairs that laid in a particular week of laying) using the GLM WEIGHT statement. To examine advantages of nesting synchronously, we correlated the number of eggs in the colony during a given week of the breeding season to the number of eggs lost during that week.

RESULTS

Activity budgets.—Male Ospreys spent 54% of their time away from the nest territory during the nestling phase of the breeding season (Table

TABLE 1. Hours spent in various activities and associated percentages of total time observed. Data are pooled from 23 different breeding pairs observed in the pre- and post-fledgling portion of the breeding season.

	Breeding males				Breeding females			
	Prefledgling		Postfledgling		Prefledgling		Postfledgling	
Activity	Total	%	Total	%	Total	%	Total	%
Away from territory	61.76	53.9	24.74	40.1	13.44	13.5	17.41	22.8
Fishing in lake	0.10	0.1	0.02	0.0	0.00	0.0	0.00	0.0
Flying in territory	1.00	0.9	2.07	3.4	1.82	1.8	3.40	4.5
Perched on nest	5.52	4.8	0.07	0.1	51.53	51.8	14.48	19.0
Perched over nest	2.44	2.1	0.28	0.4	16.97	17.1	13.25	17.4
Perched on tree	42.65	37.2	34.39	55.7	15.27	15.4	27.43	36.0
Other	1.17	1.0	0.12	0.2	0.39	0.4	0.22	0.3

1). They rarely foraged in the lake itself, but instead foraged in 1 of 3 estuaries, each ca. 14 km away (Fig. 1). If weather conditions were suitable, males kettled in thermal air currents over the lake, and then glided toward the foraging area of choice. When thermals were not available, they used powered flight. Rarely, males flew to an open section of the lake, foraged there for a few minutes, and then proceeded to the estuaries.

Males typically made 1-3 forays during the half-day samples. They tended to make only 1 trip per sample after the young fledged, which reduced the amount of time spent away from the lake and increased time spent perched on a tree in the nest territory (Table 1). Of 27 forays that began and ended within the half day sample, the mean time away was 2.25 ± 0.98 h ($\bar{x}$ ± SD; range = 1.15-5.33 h). Most forays lasted between 1.5 and 2.5 hours. When a male returned to the colony, he typically delivered the fish to the female at the nest; he then perched on a nearby tree, where he usually remained until the next foray.

Because of the nesting density, territorial intrusions by other Ospreys were common. Intrusions within 100-150 m of the nest rarely elicited a chase, but nearly always provoked a characteristic vocal response by the resident. During the 170 h of observation, we recorded 761 vocalizations resulting from territorial intrusions (4.48 per hour). Often, intrusions appeared to be not agonistic but rather incidental (as a result of normal movements). To determine if these intrusions were related to fish deliveries by the males, we calculated an intrusion rate for time intervals after a fish was delivered to the nest, and compared it with intrusion rates for an equal interval before fish delivery. For each period, intrusion rates were significantly higher after fish delivery than before (Table 2). These data indicate that conspecific intrusions were related to food deliveries.

Foraging patterns.—In 1984 and 1985, we spent 28 days (14 two-day sessions) in the tower sampling presence/absence and foraging success data. For 144 forays in which we obtained both departure and arrival directions, the difference in direction averaged 15.2 ± 15.1°. When we missed departure directions, we used return directions to indicate foraging location. Telemetry produced 211 directions of forays on 8 individuals. We recorded 68 directions for other birds before their antennas were detached (a total of 279 observations).

Fish deliveries were not spread uniformly over the day (Fig. 2). Instead, there were four peaks in deliveries separated by 2-3 h intervals. This pattern probably resulted from the mean foray length of 2.46 h (SD = 1.49, n = 659 for tower data), and the fact that dawn imposed an initial foraging synchrony each day. By projecting these departure directions to the foraging areas, we determined that Ospreys used

TABLE 2. Rates of conspecific intrusion before and after fish delivery. Rates represent the mean for 22 fish deliveries.

	Conspecific intrusion rate (per hour)		
Time span (min)	After delivery	Before delivery	P^a
10	5.45	1.68	0.012
20	5.27	2.52	0.029
30	5.38	2.41	0.002
40	5.18	2.24	0.001
50	5.03	2.07	0.001
60	4.97	2.13	0.001

[a] Significance level for differences between rates for Wilcoxon two-sample test.

Fig. 2. The frequencies of fish deliveries at 15-min intervals throughout the day (Eastern Daylight Time).

the White Oak River, Bogue Sound, and the Neuse River intensively as foraging sites (Fig. 3).

Geometric Center Hypothesis test.—Lake Ellis Simon is geographically central relative to foraging areas used by the colony as a whole. However, for this site to function as a geometric center, each individual would have to exploit all three of the major foraging areas equally. Preference for a given area would cause a shift in the optimum location for placement of the nest away from the lake and toward that foraging area. Directions of departure for the eight transmitter-equipped individuals do not support the Geometric Center Hypothesis (Fig. 4). Individual males had strong preferences for one or the other of the two broad directions available for foraging. Individuals that foraged in a northeasterly direction (Neuse River) rarely or never departed toward Bogue Sound/White Oak River (southwest), and vice versa.

We calculated where each of the eight individuals should have placed their nests, according to the Geometric Center Hypothesis, to minimize foraging costs (Fig. 5). For each bird, the optimum location was close to the foraging areas used, rather than the Lake Ellis Simon colony. If optimum points had been chosen, minimum round-trip distances of forays would have averaged 3.80–21.84 km. Observed minimum mean distances ranged from 27.56–33.96 km. The geometric center for all eight radio-equipped individuals combined occurred just south-southeast of Lake Ellis Simon (Fig. 5). Only 20 randomly selected azimuths from each individual were used in this calculation so that the value would be equally dependent on all eight.

Information Center Hypothesis test.—In the 2 yr of study, we recorded 402 successful bird foraging departures and 338 unsuccessful bird departures. The mean duration of absence from the territory for trips scored as unsuccessful re-

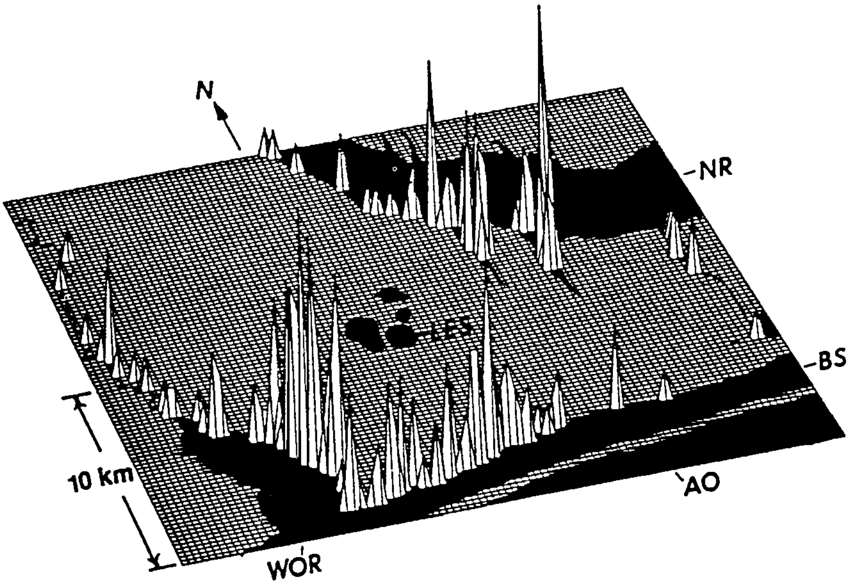

Fig. 3. The intensity of foraging use of the estuaries and rivers in the vicinity of Lake Ellis Simon (LES). Peaks represent usage intensity, based on departure and arrival azimuths obtained at the colony on all individuals. Dark areas are identified as NR (Neuse River), BS (Bogue Sound), AO (Atlantic Ocean), and WOR (White Oak River).

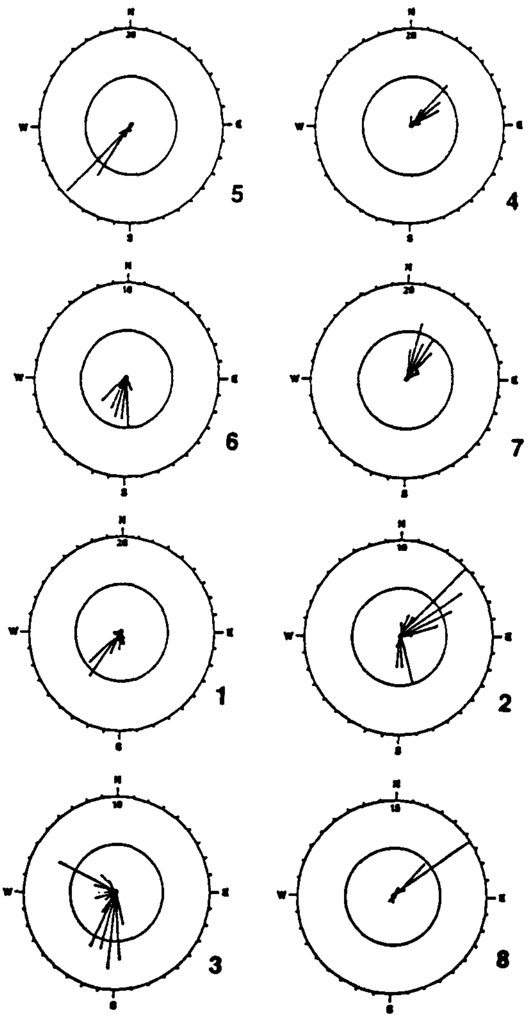

Fig. 4. Frequency of various foraging directions for each male providing consistent telemetry data (individual bird ID lower right of circle). The numbers below the north marker indicate the frequency represented by the outermost concentric circle. The inner circle represents half that value.

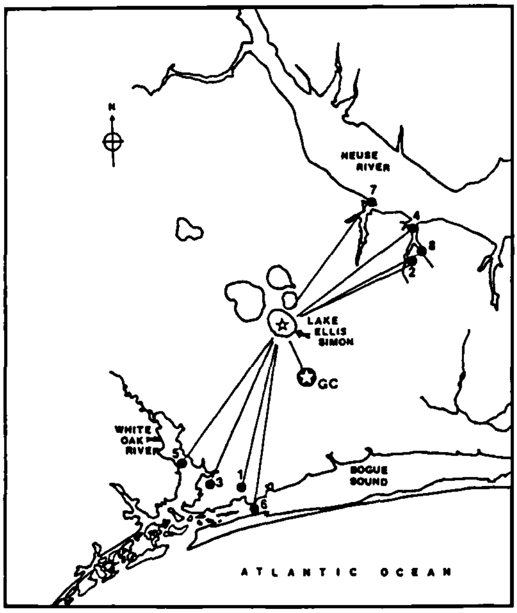

Fig. 5. The geometric optimum nesting locations based on known foraging locations of transmitter-equipped males. Dots represent geometric centers for males individually (associated number indicates male ID), and the enclosed star indicates the geometric center for all individuals combined (GC).

turns (2.39 h, SD = 1.45, n = 219) was very similar to that of successful returns (2.50 ± 1.50 h, n = 443), which indicates that these absences were also related to foraging behavior. Based on these sample sizes, foraging Ospreys returned to the colony without a fish 33.1% of the time.

Departures of unsuccessful birds clearly were unrelated to arrivals of successful birds. Results of analyses of second days' data were contrary to predictions (Table 3). For DEP_U, the mean was not higher in intervals with at least one ARR_S than in intervals with no ARR_S. In fact, the trend was in the opposite direction, although the difference was not significant. The distribution of DEP_S was similarly related to the distribution of ARR_S, as was DEP_U to ARR_U. The distributions of DEP_U and ARR_S, DEP_S and ARR_S, and DEP_U and ARR_U were all independent by Chi-square analysis ($P > 0.05$). However, only the joint distribution of DEP_S and ARR_S was accurately predicted by assuming independent Poisson distributions (Chi-square, $P < 0.05$ for DEP_U and ARR_S, DEP_U and ARR_U). This was due primarily to a tendency for intervals with multiple DEP_U to have no other departures, and intervals with multiple departures to have no DEP_U. Overall, the analyses indicate that departures tend to be asynchronous relative to arrivals rather than synchronous as predicted, and that relationship is unaffected by the status (successful or unsuccessful) of either departing birds or arriving birds. The only change that resulted from including all the data was that for DEP_U, the mean was much greater in intervals with at least one ARR_U than in intervals

TABLE 3. Summary of analyses to test the Information Center Hypothesis. Second day's data only. DEP_U = unsuccessful bird departure, DEP_S = successful bird departure, ARR_S = successful bird arrival, ARR_U = unsuccessful bird arrival. "Mean" is the mean number of indicated events per 15-min sampling period.

Distribution	Fits Poisson[a]	Mean[b]
DEP_U	no***	0.203
DEP_S	no**	0.242
ARR_S	no**	0.348
ARR_U	yes	0.285
$DEP_U \| DEP_S = 0$	no**	0.225
$DEP_U \| DEP_S \geq 1$	no**	0.377A
$DEP_S \| DEP_U = 0$	yes	0.311
$DEP_S \| DEP_U \geq 1$	yes	0.442
$DEP_U \| ARR_S = 0$	no**	0.289
$DEP_U \| ARR_S \geq 1$	no***	0.206B
$DEP_S \| ARR_S = 0$	yes	0.366
$DEP_S \| ARR_S \geq 1$	yes	0.263B
$DEP_U \| ARR_U = 0$	no***	0.283
$DEP_U \| ARR_U \geq 1$	no***	0.212B

[a] Tested by Chi-square, ** = $P < 0.01$, *** = $P < 0.001$.

[b] For pairs of means compared using *t*-tests, "A" indicates those that differed ($P < 0.01$), and "B" indicates those that did not differ ($P > 0.05$).

with no ARR_U. This, too, is contrary to the predictions of the Information Center Hypothesis.

The data were consistent with the hypothesis that unsuccessful birds follow other birds leaving the colony. Using second days' data only, two predictions were realized. First, the mean was significantly greater for DEP_U in intervals with at least one DEP_S compared with intervals with no DEP_S. Second, DEP_S had a Poisson distribution both among intervals with at least one DEP_U and among intervals with no DEP_U (Table 3). However, contrary to prediction, DEP_U did not have a Poisson distribution either in intervals with DEP_S or intervals with no DEP_S. The unsuccessful birds followed both successful birds *and* other unsuccessful birds from the colony, whereas successful birds departed independently of one another. This conclusion is also evident from analysis of DEP_S relative to ARR_S (see Table 3).

That DEP_U and DEP_S were not independent was confirmed by Chi-square analysis ($P < 0.01$), and by our inability to predict their joint distribution based on assumed independent Poisson distributions ($P < 0.01$). Both intervals with multiple departures (especially intervals with 3 or more departures) and intervals with no departures were much more common than expected. If all data are included in the analysis, DEP_S no longer has a Poisson distribution, either in intervals with at least one DEP_U or intervals with no DEP_U ($P < 0.05$ in both cases). Otherwise results were unaffected by including the first day's data.

Temporal patterns of reproductive success.—In the three years of study 130 nesting attempts produced at least one egg. We excluded from regression analysis five renesting attempts which produced no fledglings. There was a significant difference between years in clutch size and number of fledglings, but not brood size (Table 4). The lack of difference in brood size (at hatching) is likely due to a large variance resulting from including brood sizes of 0 (nests where no eggs hatched). The differences in fledglings per nest resulted from a dramatic increase in survival of nestlings in 1985.

Ospreys began to arrive at Lake Ellis Simon in late February, and most had returned by mid-March. The earliest breeders laid eggs by 20 March, and one pair laid a single egg as late as early June (Fig. 6). Most pairs laid 2 weeks after the first pair(s), whereas only two pairs laid as late as 10 weeks after the first pair (Fig. 7). There was a strong negative linear relationship between the week of laying (WOL) and clutch size ($r^2 = 0.784$, $P = 0.0007$) (i.e. early nesting pairs laid significantly more eggs than late nesters). Regression of brood size on WOL indicated a similar trend ($r^2 = 0.788$, $P = 0.0006$). Week-1 layers did not produce as many nestlings as those that laid in the two subsequent weeks, but this pattern was not sufficiently strong to warrant a quadratic regression. The negative

TABLE 4. Summary ($\bar{x} \pm$ SD) of reproduction for each year of study. *P*-values represent the probabilities that there was no difference between years for the indicated parameter. Sample sizes are in parentheses after year.

Year	Clutch size	Brood size	Fledglings
1983 (41)	2.59 ± 0.745	1.65 ± 1.277	0.90 ± 0.860
1984 (41)	2.75 ± 0.537	1.78 ± 1.173	1.02 ± 0.961
1985 (48)	2.86 ± 0.461	1.98 ± 1.082	1.48 ± 1.111
P	0.039	0.850	0.016

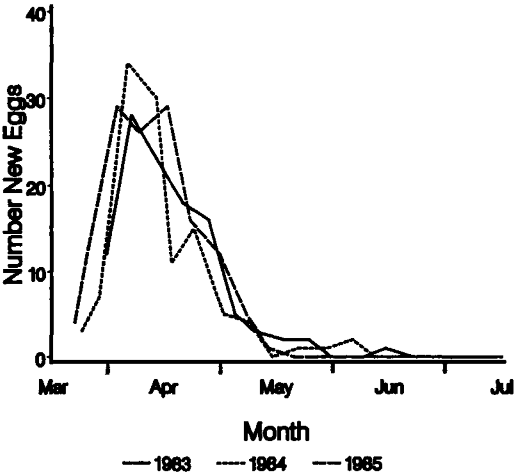

Fig. 6. New eggs laid in the colony relative to the time of year, for each year of study.

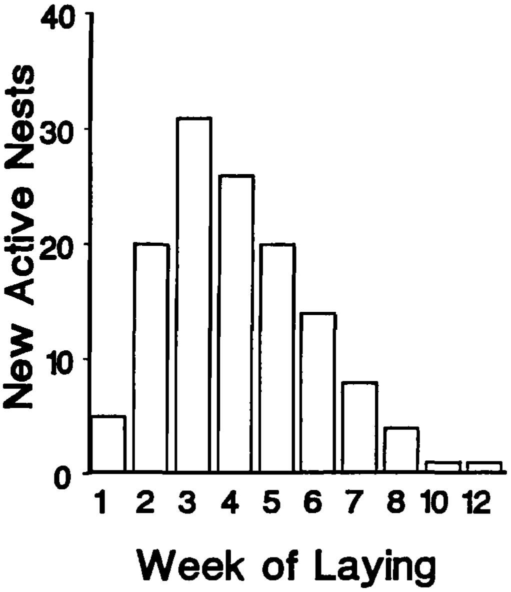

Fig. 7. Newly active nests for each week of the laying season. Week of laying is relative to the week eggs first appeared in the colony.

relationship between WOL and numbers of fledglings produced was also significant ($r^2 = 0.755$, $P = 0.001$).

Although decrease in clutch size was an obvious factor in the seasonal decline in fledglings, other factors affected egg or nestling loss. We defined *egg failure* as the number of eggs that failed to hatch (clutch size minus brood size at hatching). There was a significant positive relationship between week of laying and egg failure ($r^2 = 0.628$, $P = 0.006$). Later layers had smaller clutches, and more of their eggs failed to produce nestlings, which exacerbated the seasonal decline in offspring production.

Eggs may fail to hatch because of predation, accidents in the nest, or inviability due to infertility, overheating, or overcooling. To distinguish between egg loss due to predation or accident and loss due to inviability, we defined an *inviable egg* as one that remained in the nest for 6.5 weeks or longer, and a *lost egg* as one that disappeared before that time. The normal incubation period for Ospreys is 4.5-5 weeks. No significant relationship was found between mean number of inviable eggs and week of laying ($r^2 = 0.146$, $P = 0.276$), or the mean proportion of the clutch that was inviable and week of laying ($r^2 = 0.293$, $P = 0.106$). However, a significant relationship was found between the mean number of lost eggs per nest and week of laying ($r^2 = 0.456$, $P = 0.032$). Thus the increased egg failure for later nesters was due to egg predation or accidental loss rather than inviability. Although later nesters lost more eggs, comparison of nestling loss and week of laying indicates that they did not lose more nestlings ($r^2 = 0.003$, $P = 0.899$).

Lost eggs, represented as the proportion of total eggs in the colony during a given week, was significantly negatively correlated with the absolute number of eggs in the colony ($r^2 = -0.46$, $P \ll 0.01$). This indicates that the more eggs available to predators, the less the probability any single egg would be lost. However, the absolute number of eggs lost in a given week was not related to absolute number of eggs available ($r^2 = 0.02$, $P \gg 0.10$) (i.e. there was no evidence of a numerical response of predation in relation to the number of eggs available).

If reproductive success is measured on a proportional scale, losses are measured in terms of proportion of reproductive effort (clutch size) rather than in absolute terms. The proportion of eggs that became nestlings significantly decreased with week of laying ($r^2 = 0.727$, $P = 0.002$) (i.e. late nesters lost a significantly larger proportion of their smaller clutch size). Similarly, later nesters fledged a significantly smaller proportion of their clutches ($r^2 = -0.696$, $P = 0.003$). The later nesters produced fewer

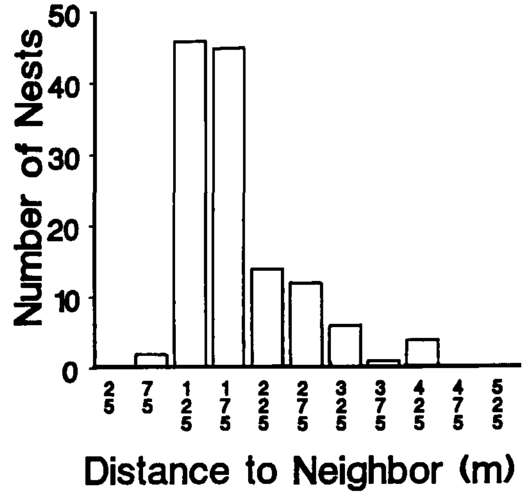

Fig. 8. Number of nests with its nearest active neighbor falling in the indicated distance category. Values on the abscissa represent the midpoint of the distance category.

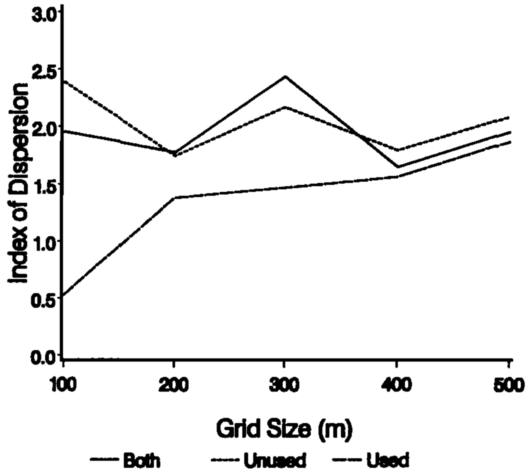

Fig. 9. Morisita's Index of Dispersion for used, potential, and both used and potential nest sites combined, at various quadrat sizes. Grid size value represents the length of the quadrat edge in meters.

fledglings and achieved less reproductive success per unit effort than early nesters.

The number of pairs that initiated laying at Lake Ellis Simon was greatest in week 3 (Fig. 7), while reproductive success expressed as mean number of young fledged peaked at week 2. A Wilcoxon two-sample test did not indicate any difference in reproductive success between week-2 and week-3 breeders ($P = 0.218$), but week-2 pairs produced significantly more young than week-5 pairs ($P = 0.050$), even though the same number of pairs initiated laying in both weeks (Fig. 7). We suggest that the number of pairs at a similar stage of the breeding cycle was unrelated to reproductive success, but rather time of year had an overriding influence.

Spatial patterns of reproductive success.—The mean distance to nearest active neighbor was 183.9 ± 75.254 m, and the range was 89-435 m. The modal distance fell in the 101-150 m category (Fig. 8), and the median distance was 158 m. The mean distance to a nest's nearest four active neighbors was only 280.7 m, which indicates that most nests were surrounded by other active nests. We used exact distances between nests and found no relation between week of laying and distance to nearest active neighboring nest ($r^2 = 0.028$, $P = 0.641$). This indicates that early nesters were not any closer to, or farther from, other active nests than late nesters. There was no significant relationship between reproductive success and mean distance to nearest four active neighbors ($r^2 = 0.13$, $P = 0.307$) (i.e. proximity to neighbors did not enhance or diminish fledgling production).

Because used sites are members of both "used" and "potential" sites, we calculated Morisita indices for three categories: used sites, unused sites, and all sites (used or unused). Index values for both "used" and "unused" sites were both above 1, which indicates clumping. However, the ratio of the "used" site index to the "all" site index is the important value because this reveals whether actual nests are more clumped or less clumped than available nest sites. The index for "used" sites tended to be slightly lower than the indices for "all" sites or "unused" sites (Fig. 9). The great disparity between the indices at quadrat sizes of 100 m may reflect a minimum inter-nest distance threshold for this population. Although "used" sites are slightly less clumped than "all" sites, the pattern is not sufficiently strong to suggest avoidance of conspecifics (other than that some minimum inter-nest distance exists).

The dispersion indices show used sites and potential sites to be similarly dispersed, but they do not indicate whether the locations of the two distributions are in the same space. The nest sites could all occur on one edge of an area of available sites, yet still be dispersed similarly to available sites. To examine this possibility, we used a multivariate regression with the x

TABLE 5. Summary statistics ($\bar{x}$ ± SD) and comparisons of reproductive variables of central and peripheral nests. Wilcoxon two-sample tests were used for all comparisons. Sample sizes are in parentheses. Means shown are on a per nest basis.

Variables	Nests		P-value[a]
	Central	Peripheral	
Clutch size	2.79 ± 0.543 (78)	2.61 ± 0.661 (52)	0.120
Brood size	2.06 ± 1.097 (78)	1.44 ± 1.194 (52)	0.003*
Brood size[b]	2.47 ± 0.640 (65)	2.14 ± 0.772 (35)	0.023*
Fledglings	1.30 ± 1.308 (78)	0.92 ± 0.967 (52)	0.032*
Egg failure	0.73 ± 0.832 (78)	1.17 ± 1.004 (52)	0.011*
Inviable	0.38 ± 0.540 (78)	0.73 ± 0.866 (52)	0.029*
Nestling loss	0.91 ± 0.896 (65)	0.77 ± 0.942 (35)	0.383
Egg loss	0.35 ± 0.718 (78)	0.44 ± 0.725 (52)	0.275
Week of laying	4.10 ± 1.592 (78)	4.15 ± 2.304 (52)	0.625

[a] * = significant at alpha = 0.05.

[b] Adjusted brood size (brood sizes of 0 excluded).

and y coordinates of the nest sites (used and unused) as the dependent variables, and a class variable with the value of "used" or "unused" as the independent variable. This analysis tests for statistically similar centers of gravity between points representing used and unused sites, regardless of dispersion pattern. No significant differences were indicated by this multivariate comparison (Wilk's criterion = 0.99356, $P = 0.435$, $F_{2,258}$) (SAS 1985). Thus the two sets of points occurred in the same space.

Central nests produced clutch sizes similar to peripheral nests (Table 5). However, peripheral nests produced significantly smaller brood sizes, and consequently fledged fewer young (Table 5). The relatively poor success of peripheral nests could be attributed to higher egg inviability, because egg loss was otherwise similar. Thus, brood sizes of peripheral nests were smaller than central ones (Table 5). Peripheral nests did not lose more nestlings than central nests. Once an egg hatched, the nestling had as good a chance of surviving in a peripheral as in a central nest. Spatial effects thus contrasted with chronological effects, which were related to egg loss rather than egg inviability. Consistent with this, peripheral nesters did not lay any later than did central ones (Table 5). The decreased productivity of peripheral nests appeared to be independent of the overall seasonal decline in productivity.

DISCUSSION

The mean length of time Lake Ellis Simon breeding males spent away from the nest on a foraging trip (2–5 h) was unusually long compared with foraging durations reported previously for Ospreys. This appeared to be a result of the substantial distance males flew to acquire food. Stinson (1978) reported that foraging trips of Ospreys in the Chesapeake Bay region typically lasted <1 h, as did Greene (1987) for Ospreys in Nova Scotia, and Poole (1982) for widely separate populations in Florida and New York. The consequences of conditions at Lake Ellis Simon were an unusually low rate of fish delivery and extensive manifestation of brood reduction through sibling aggression (Hagan 1986). Under these conditions, food location information should have been at a premium to Ospreys nesting at Lake Ellis Simon. In addition, the apparent central location of Lake Ellis Simon relative to foraging sites presented an equally suitable condition to test Horn's Geometric Center Hypothesis.

Foraging patterns and colonial nesting.—Mean flight distances are less for average colony members than for average members of a dispersed population, as long as the colony is displaced from the center of a circular foraging area, with random patch location, by no more than 70% of the radius (Wittenberger and Dollinger 1984). By using known foraging location data, as in this study, rather than a theoretical distribution, the cost of acentric location can be measured directly. The travel distances of Lake Ellis Simon males were from 1.5 to more than 7 times as great as birds could have achieved by nesting in the geometric center of their own foraging locations. This implies that substantial increase in foraging costs resulted from colony membership over the study period.

One does not expect the computed optimum locations of nests to correspond exactly with nest sites. The former are subject to sampling errors. Sampling considerations aside, an individual cannot predict his optimum nest location before the breeding season because he has no way of knowing what his exact foraging locations will be. Furthermore, some of the individual geometric centers did not fall in suitable nesting habitat. However, the general location of the optimum nest site may be predictable. Given the restricted distribution of male Ospreys' individual foraging sites that we found, it seems that individuals anticipated the general vicinity where they would forage. From males outfitted with transmitters in 1984 and 1985, it appeared that general foraging-site preference remained constant year to year. A more realistic determination of optimum nest-site location might be to calculate each individual's geometric center, and then choose the nearest location to that point which represents suitable nesting habitat. Without exception, that point would lie near the foraging sites, not near Lake Ellis Simon (see Fig. 5).

Because successful and unsuccessful foragers were identified, our study represents a direct approach to testing the Information Center Hypothesis. We found only weak evidence for information exchange. It was clear that departures of previously unsuccessful foragers were not influenced by arrivals of successful foragers. Unsuccessful birds tended to depart with other birds, but did not discriminate between previously successful and previously unsuccessful birds. The nonrandom distribution of departures may have been due to independent responses to environmental factors rather than due to interactions between birds. For example, wind conditions favorable to gaining the altitude necessary to accomplish long flights to the foraging areas may have triggered departures. Also, dawn and dusk may have imposed a weak diurnal rhythm on departures. Departures of successful birds were distributed randomly, which indicates that interactions among birds, rather than environmental factors, were responsible for the nonrandom distribution of departures of unsuccessful birds. However, among successful birds, there was a trend toward an excessive number of intervals with no departures or with multiple departures ($0.05 > P < 0.1$). The pattern was the same among both successful and unsuccessful birds, but it was stronger among the latter.

It is possible that departures of unsuccessful birds were influenced by interactions with other birds not included in the sample. We sampled only interactions within a neighborhood of 10 to 11 pairs. We expected patterns consistent with information exchange to be stronger than they were, despite this constraint. The departure data are arguably inconclusive. The data obtained from radio-equipped males are more difficult to reconcile with the Information Center Hypothesis. The lack of variation in each male's departure direction indicates that information on food location was not used. Rather, familiarity with a specific site apparently was of greater importance. Moreover, males that foraged northeasterly had reproductive success similar to those that foraged southwesterly, which indicates that these two foraging areas were equally capable of supplying food during the breeding period. Differences among individuals for preferred foraging sites have been documented for other central-place foragers (e.g. Cook 1978, Morris and Black 1980, Gorke and Brandl 1980), and among communally roosting species (Caccamise and Morrison 1986). Many species may lack the variability in individual foraging locations assumed in the Information Center Hypothesis. A postulated explanation for such behavior is that spatial memory decreases with increasing quantity of information for processing (Olson et al. 1981). When a large foraging radius is necessary (as for Ospreys nesting at Lake Ellis Simon), minimization of spatial information (i.e. a narrow departure arc) may enhance foraging efficiency. This reasoning does not offer an explanation for colonial nesting.

These results contrast with Greene's (1987) study of a small colony of Ospreys (11 pairs) in Nova Scotia. In that study birds foraged primarily within visual range of the colony (<2 km), and foraging trips were of short duration (most <30 min). At Lake Ellis Simon, where an average foraging trip was longer than 2 h in duration, food location information may be of little value, as food patches may have shifted spatially in that interval. Birds in the Nova Scotia colony may have received more precise, current information on food location because the colony was near the foraging areas. This is particularly true if arrivals were used as a cue, as in Nova Scotia. At Lake Ellis Simon, arrival direction provided imprecise information about location of food 10–15 km distant. Perhaps Lake

Ellis Simon functions as an information center only when foraging conditions are worse than during our study. Fledgling success was lower (Table 4), brood reduction more common, and fewer foraging trips were successful (60% vs. 74%) in 1984 than in 1985. However, two males in two seasons showed the same affinity for particular foraging locations.

Because the Nova Scotia colony was closer to foraging sites and because foragers were within visual range of the colony, the apparent exchange of food location information may have represented local enhancement. Local enhancement is described typically as unsuccessful foragers cuing on successful foragers *at the foraging site*. When the colony is in visual proximity to the foraging site, individuals can watch foraging birds without leaving the colony.

Whether information exchange occurs near or far from the foraging site represents an important distinction. The original Information Center Hypothesis (Ward and Zahavi 1973) was intended to explain assemblages of birds *away* from foraging sites, and thus a phenomenon distinct from local enhancement. Assemblages (colonies or roosts) near foraging sites could result exclusively from the location of the food resource, and not from the need to exchange information. Certainly local enhancement, which involves information transfer, is an important biological phenomenon through which birds can gain useful information. However, to explain colonies or roosts solely on the basis of the Information Center Hypothesis, as intended by Ward and Zahavi, requires that the assemblage be remote from the foraging sites. The Lake Ellis Simon colony satisfied this distinction. From our negative results, along with positive results from Greene's (1987) study, we conclude that information transfer is not likely a primary cause of coloniality in Ospreys, but rather a secondary capability that may be facultatively employed depending on geography of the colony in relation to foraging areas.

Reproductive success and colonial nesting.—Other socially derived benefits of nesting near other individuals can be obtained through synchronization of the group's breeding effort. The proximate mechanism Darling (1938) proposed was that of social facilitation, but the evolutionary basis of synchronized reproduction in a colony might be to reduce the probability of predation by swamping predators with more young than predators can consume (Hamilton 1971). Most birds breed over a 3-5-week period within a season (Perrins 1970), but Ospreys at Lake Ellis Simon laid over a 12-week range during the 3 years of this study. That breeding in Osprey colonies is more prolonged and less synchronous (see also Ames and Mersereau 1964, Ogden 1977, Judge 1983, Garber 1972, Kennedy 1977, Prevost et al. 1978) than in many species is in part a consequence of body size that makes predator swamping less likely. Regardless of the degree of synchrony achieved, the question is whether rate of egg or nestling loss is reduced by the presence of other nests. Our data indicate that benefits derived from swamping predators may have been realized because the rate of egg loss was lower when eggs were most abundant. However, the lack of a numerical response of predators (as measured by number of eggs lost) during this time indicates that the egg-loss rate had to do with lower egg loss of early-season breeders (and perhaps more experienced breeders), and not with predator-swamping effects due to synchrony.

If Ospreys obtained substantial benefits from information exchange about food patch location, later layers would be expected to fare best, as they would have more birds on which to cue when their young were at the critical 2-4 post-hatching week age (Hagan 1986). We found no such pattern. Rather, earlier breeders were more successful than late breeders.

Among Ospreys, later layers produced fewer young for two reasons. First, they laid smaller clutches, and second, they lost more eggs before hatching. Eggs may have been lost to Fish Crows (*Corvus ossifragus*), which were abundant locally. Also, intraspecific territorial encounters were frequent in the colony, and often resulted in momentary battles on the nest platform. Conspecific agonistic interactions in Ospreys are not well-documented, but a study of more solitary nesters in northeastern Nova Scotia recorded 99 conspecific encounters in 560 h of observation (0.17 per hour) (Jamieson and Seymour 1983). Conspecific encounters, usually manifested as vocal warnings, were 26 times more frequent at Lake Ellis Simon. Egg loss might result from occasional, more intense interactions (see Poole 1989). This seems more likely than predation, given the tenacious nest attendance by females during incubation. Intraspecific kleptoparasitism of fish at the colony also occurred, which represents an additional cost to colonial nesting. Such intraspecific interactions might be expected to increase gradually as the breeding season progresses, if interactions increase with the density of pairs involved in nesting.

Chronological patterns in reproductive success do not indicate any cause of colony formation, but spatial patterns may. Birds in the center of the colony produced more young than peripheral pairs. This was caused by an increase in number of inviable eggs produced by peripheral pairs. Though younger individuals of colonial species often occupy nest sites on the colony periphery (Coulson 1968, 1971; Tenaza 1971), peripheral nesters in our study did not initiate egg laying any later than central nesters, as would be expected if younger individuals occupied these sites. Moreover, Ospreys tended to return to the same nest year after year, regardless of age. Of 21 color-banded males, none switched nesting territories in 3 yr. Of 27 color-banded females, only 4 changed nest sites among years.

If a factor other than age produced higher egg inviability of peripheral nesters, then colony formation may be an evolved feature. This factor would have to be one which had an influence only on the viability of eggs, as reproductive success in peripheral and central nests was otherwise equivalent. Disturbance, displacing the parents from the nest too frequently or for excessive lengths of time during incubation, is a possibility. Sources of disturbance might include Fish Crows, other Ospreys, or human recreational fishing in the lake.

Nesting toward the center of the colony may represent a reproductive advantage, but pairs did not move gradually toward the center over the years. Perhaps what precludes nest-site shifts is the importance of nesting at a familiar site, of nesting with a familiar mate, or of retaining a prior resident's advantage in disputes over nest sites. Ospreys nest in a distribution that mirrors available nest-site distribution within the colony. This implies that central positions were not sought actively and that pairs did not seek to nest near other pairs on a within-colony scale. In fact, Ospreys are sensitive to encroachment into their nesting territory by other Ospreys. These results reduce support for the hypothesis that a primary benefit of colony formation is a socially mediated reduction in predation.

The Nest-site Hypothesis.—Ospreys apparently could nest near the foraging sites, but in trees unlike those of Lake Ellis Simon. Two active nests were found in these foraging areas, but in the tops of very tall trees rather than in trees over water. Trees over water occur abundantly only at Lake Ellis Simon. Ospreys appear to be equally successful nesting alone, or nesting near each another (Poole 1989: 138). This is consistent with the hypothesis that colonial nesting in Ospreys is a consequence of nest-site distribution. This hypothesis was not tested directly (except within the colony), and thus is only weakly supported by our study.

Colonial nesting Ospreys may benefit from predation reduction. The benefits appear to be restricted to effects on egg viability rather than on egg or nestling loss, and to spatial rather than temporal factors. This may be a primary or secondary benefit. Colony formation may also be explained by resource constraints (specifically the distribution of nest sites) but not food. Osprey colonies which exist today are located in trees over water, like Lake Ellis Simon, or on predator-free islands (Greene 1987). Thus, the Nest-site Hypothesis, perhaps combined with predation reduction, seems the most parsimonious explanation for colonial nesting in Ospreys, although the Nest-site Hypothesis needs to be tested directly. This conclusion does not contradict the fact that information about food location can be exchanged by Ospreys. We suggest that this is not crucial to the origin of colonial nesting in Ospreys, but is rather an interesting adaptation resulting from group living. Clear evidence that the Information Center Hypothesis is a general explanation of assemblages of birds is still lacking.

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