COURTSHIP FEEDING AND OSPREY REPRODUCTION

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ABSTRACT.—A female Osprey (*Pandion haliaetus*) usually is fed exclusively by its mate between pair formation and egg-laying. Laying dates and courtship periods—but not clutch size, egg size, breeding success, or female weight reserves—were correlated (negatively) with the prelaying feeding rates of 12 females breeding in a coastal Massachusetts colony. However, the age of a pair and of its bond influenced laying dates and courtship periods more than food intake. Older and more experienced pairs arrived earlier and laid eggs more quickly than younger pairs. As an independent test of food limitation in Ospreys producing eggs, supplemental food was provided to 4 nests during courtship. Supplemental food did not influence a female's reproductive output or timing, but males at nests receiving extra food showed reduced rates of foraging. Egg production boosted the daily energy expenditure of female Ospreys by only about 20% and females gained little weight during courtship, suggesting that egg-laying is not a demanding process in this species. Because age and mate retention had a greater effect on the reproductive output and timing of female Ospreys than rates of food consumption during courtship, and because there was evidence that poorly fed females were less willing to copulate and less faithful to their mates than well-fed females, it is argued that Osprey courtship feeding may function primarily to ensure mate fidelity.
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THE influence of food supply on the timing of avian breeding and the amount of energy a female bird commits to any single reproductive effort has been debated. Lack (1948, 1954) originally emphasized ultimate factors, suggesting that clutch size and laying date were adjusted to produce, on average, the greatest number of surviving young. Others (von Haartman 1971, Jones and Ward 1976, Drent and Daan 1980) have suggested that food supply also functions as a proximate limit to avian breeding, with shortages of food or nutritional reserves prior to laying often preventing females from reaching optimal clutch sizes or laying dates. Because egg-laying does not place similar demands on all birds (Ricklefs 1974), however, food availability cannot be expected to limit the formation of eggs to the same extent in all species.

In this paper, I examine the extent to which female Ospreys (*Pandion haliaetus*) are limited by food during egg production. Prior to egg-laying, female Ospreys usually are fed exclusively by their mates (Poole 1983). Such courtship feeding—the transfer of food from male to female before and during egg-laying—provides a female with the food she needs during egg formation, a time thought to be potentially stressful (Ricklefs 1974, Drent and Daan 1980). Many birds engage in courtship feeding (Brown 1967, Krebs 1970, Nisbet 1977, Newton 1979, Tasker and Mills 1981), and because of its potential influence on a female's nutritional reserves, this feeding has been thought to influence reproductive performance (Lack 1966; Royama 1966; Nisbet 1973, 1977; Newton et al. 1983). Others have suggested that variation in rates of courtship feeding could influence a female's choice of mate (Nisbet 1973, Halliday 1983).

Few quantitative studies of avian courtship feeding have attempted to measure its actual impact on reproduction. Nisbet (1973) showed a significant, positive correlation between the courtship-feeding performances of male Common Terns (*Sterna hirundo*) and the clutch and egg weights of their mates, as well as the chick-feeding performances of those males. Terns in colonies with higher rates of courtship feeding also bred earlier (Nisbet 1977). Clutch size, egg size, and laying dates of Herring Gulls (*Larus argentatus*), however, were not correlated with rates of courtship feeding by males, although male chick-feeding performances were (Niebuhr 1981).

In a preliminary study of courtship feeding in Ospreys (Poole 1983), neither the quantity nor quality of fish delivered to females by their mates was associated with differences in the body weights, clutch sizes, or egg sizes of those females. However, this preliminary study was limited by small sample sizes; did not consider the influence of the age of pairs, or of the number of years a pair had bred together, on rates of courtship feeding and most aspects of reproduction; and did not consider the timing of breeding in Ospreys. Age, mate retention, and laying dates often are associated with differences in reproductive effort and success within a species (Coulson 1966, Mills 1973, Davis 1975, Bird and Lague 1982, Newton et al. 1983), but no studies of the relationship between courtship feeding and reproduction in birds have considered these potentially confounding variables. Here I present data from a study of courtship feeding and breeding performance in coastal Massachusetts Ospreys that does consider such variables. My objective was to answer several questions related to the reproductive ecology of Ospreys: (1) Does the amount or type of food delivered to a female during courtship influence her clutch or egg size, laying date, breeding success, or weight reserves? (2) What accounts for variation in the rates of food consumption by females during courtship? (3) What is the influence of age and mate retention on clutch size, egg size, and laying dates? (4) What factors might have selected for courtship feeding in this species?

STUDY AREA AND METHODS

I conducted this study in the Westport River estuary of southeastern Massachusetts (40°32'N, 71°05'W) from 1979 to 1982. Reproductive data were gathered during each of these years; rates of courtship feeding were measured during April–May in 1980 and 1982. Westport Ospreys began courtship feeding in late March, most birds laid eggs by mid-May, and most young fledged by mid-August. Fifteen nests were active (i.e. with eggs) and were accessible for study in 1979, 17 in 1980, 24 in 1981, and 27 in 1982. Most nests were located on platforms 3–7 m high in open salt-marsh habitat (see Poole and Spitzer 1983).

Perch scales (Poole and Shoukimas 1982) at nest platforms provided accurate and repeated weights of Ospreys when the birds perched on them, which they usually did several times a day. During 1982 I temporarily set up perch scales at 18 nests 1–4 days after a pair of Ospreys first appeared at a nest site (= "pair formation"), with a second weighing at each of these nests about the time females laid their first egg (= "laying date"). Perch scales were installed for at least 24 h, and repeated weights (range = 4–13) of individuals over this time period were averaged. This reduced variations in weight due to changes in the contents of a bird's crop. The weight of an egg was not added to a bird's weight at laying because weight changes due to feedings were considerably greater than changes due to the laying of an egg.

I checked for dates of pair formation and egg-laying in 1981 and 1982 by censusing nest sites in the colony every 2–3 days from the time pairs first arrived until there were no longer any pairs laying. Westport Ospreys appeared to form pairs only at established or potential nest sites and usually did so within a few days of arriving in the colony; there was no obvious tendency for one sex to arrive earlier than the other.

Banding data were used to analyze the effects of age on feeding and reproduction. Since 1979, many of the Ospreys breeding in the Westport population have been trapped, aged from banding data, and given individual color-band combinations for recognition in subsequent years. By 1982, 76% (44) of these Ospreys were color-banded, and the ages of 30 individual birds were known. These sample sizes were too small for adequate analysis of the separate effects of male and female age on feeding and reproduction. To analyze the effects of age, therefore, I either took the mean age of the pair when the ages of both male and female were known or estimated a pair's age from the age of the known member of the pair. This was possible because there was a significant tendency for Westport Ospreys to pair with birds of about their own age, i.e. a significant correlation between the ages of pair members ($n = 11$, $r = +0.71$, $P < 0.01$).

Because breeding Ospreys show low mortality and great year-to-year fidelity to nest sites (Spitzer et al. 1983), by 1981 it was possible to classify banded pairs on the basis of the number of years (0, 1, or 2+) they had mated together. This allowed analysis of the effects of mate retention on feeding and reproductive performance during the 1981 and 1982 studies.

During courtship, male Ospreys hunt fish for themselves and their mates, usually bringing their catch back to the nest area before starting to feed. A male generally eats parts of the head and anterior portion of the fish at a perch near the nest, and then delivers the remainder to its mate at the nest. With the help of two other observers, I measured rates of fish delivery by male Ospreys and food intake of both males and females at 12 nests during April 1982. Two methods were used. Length estimates of identified prey species (Poole 1982) were converted to weight using formulae appropriate to the most common species: Lux (1969) for winter flounder (*Pseudopleuronectes americanus*) and Clayton et al. (1978) for alewife (*Alosa pseudoharengus*). Caloric content of herring and flounder was calculated from available values (Sidwell et al. 1974, F. Steimle pers. comm.), which suggested energy equivalents of 0.9 kcal/g (wet weight) for winter flounder and 1.5 kcal/g for alewife.

Weight estimates of prey provided a measure only of the amount of food available to Ospreys. As a second measure of feeding, and to calculate actual food intake, we counted the number of "bites" of fish eaten$\cdot$bird$^{-1}\cdot$feeding^{-1}. Ospreys rip pieces of fish from a carcass in discrete bites that are easily counted. Because nests in the Westport colony are clustered, we could observe 2-3 nests at the same time. Simultaneous feedings often occurred at nests, so we recorded data as bite-counts/min every 2-3 min until feeding stopped. Feedings ranged from 9 to 61 min in duration. I assumed that males and females took bites of equal size because their culmens are roughly equal in size (Prevost 1982). Each nest was observed for 10 4-h watches covering equal portions of the daylight hours over a period of 4-11 days using 20-60× telescopes from a distance of 20-80 m. Watches took place 0-14 days before the first egg was laid, after a pair had been established at a nest site for at least 5 days.

To increase the food available to females prior to egg-laying, I provided supplemental food [400 g fresh fish (alewife) placed in nests once a day at about 1200] to 4 nests in 1980. Although these nests were not chosen randomly (accessibility was a factor), their reproductive rates in other years were similar to the colony's mean (Poole unpubl. data). Feeding started 2-3 weeks before egg-laying and continued through the laying of the final egg. Food delivery rates of males were monitored at the same time to determine the effect of the supplemental food. Fish-bites were not counted at nests in 1980. Four nonfed nests that also were monitored for delivery rates during 1980 served as feeding controls. All other nests accessible in the colony during 1980 ($n = 13$) were controls in comparisons of reproductive performance. It is unlikely that daily visits to nests to leave fish were a critical disturbance for the experimental pairs because the birds usually returned to their nests quickly after our visits, and Ospreys generally habituate easily to human disturbance (Poole 1981).

During 1979-1982, I visited all active nests 1-2 weeks after the onset of laying to record clutch sizes and egg dimensions. Egg volume was determined using Hoyt's (1979) length-breadth formula. Once hatching began, nests were visited weekly to determine egg loss, chick hatching sequence, initial brood size, loss of nestlings, and fledgling brood size (cf. Poole 1982).

To determine the influence of courtship feeding on mating success, in April 1982 I recorded whether or not males attempted copulations while their mates fed or shortly (<10 min) thereafter during 52 feedings in the Westport colony. Copulations were judged successful if a female tipped forward just prior to mating in a copulation-soliciting display (see Cramp and Simmons 1980: 273, Figs. B, C) and her mate appeared to achieve cloacal contact.

Results in text are shown as mean ±1 SE.

RESULTS

Prey species and measures of food consumption.—Seventy-six percent ($n = 114$) of the fish delivered to nests by male Ospreys during 1982 could be identified to species. Of the fish identified, 95% were winter flounder or alewife (Table 1). The total numbers of bites taken by Ospreys to consume whole fish of these two species were similar (Table 1). Ospreys nearly always ate the entire fish, discarding only the intestines. I assumed that Ospreys discarded similar amounts of intestine from herring and flounder of equal weight. A single bite from a carcass of each of these species weighed about the same (ca. 0.60 g/bite; Table 1); thus, no matter which species of fish an Osprey ate, the rate (bites/min) at which it fed was a fairly reliable measure of its food intake (g/min). The caloric content of bites from these prey species, however, differed by about 33% (Table 1).

Variation in food intake during courtship.—Three pairs of Ospreys were observed for only short periods of time (4 days) relative to their entire courtship period (number of days between pair formation and egg-laying) and to other pairs. It was important to know, therefore, if there were significant variations in rates of food delivery and intake for a pair as the courtship period progressed. For 7 pairs observed over longer periods (9-11 days), the numbers of fish delivered by males during the first and second half of this period were the same, as was the actual consumption of food by females (Table 2). Likewise, females observed up to egg-laying ate as much food as those for which observations stopped 7-10 days before they laid eggs (Table 2). Thus, the delivery rates of male Ospreys and the food intake of their mates were constant during the courtship period, and there was no reason to suspect any bias due to differences in the timing of feeding observations.

During 1982, male Ospreys delivered 0.25 ± 0.02 fish/h to their mates (= 3.4 fish/day). The mean duration of these hunting trips was 17.3 ± 1.3 min, so males spent, on average, 59 min/day foraging (= 7.3% of the day). However, there was no significant correlation between the number of fish delivered to females per 4-h period and the amount they actually

TABLE 1. Primary species of fish eaten by Westport Ospreys during courtship, and calculations of the weight of bites taken from fish carcasses by these birds. Means ± SE shown. $n = 114$ identified deliveries. Data from 1982.

	Alewife	Flounder	t	P^a
Percentage of identified deliveries	40%	55%		
Total number of bites needed to consume whole fish	496 ± 29	526 ± 40	0.65	NS
Weight of whole fish (g)	285 ± 12	330 ± 17	2.02	*
Weight of average single bite (g)	0.58	0.63		
kcal/bite	0.87	0.57		

[a] NS = $P > 0.10$, * $P < 0.05$.

ate (i.e. the number of fish-bites/female; $n = 11$, $r_s = +0.30$, $P > 0.10$). Similarly, the number of bites consumed by pair members was not significantly correlated ($n = 11$, $r_s = +0.43$, $P > 0.10$), suggesting that males were not sharing fish equally with their mates. Males, on average, ate 1.41 ± 0.14 times as much as females, but some males consumed a greater proportion of the shared fish than others (Fig. 1). Females with older mates (5+ yr), and those that had bred with the same male for 2 or more years, consumed the most fish (Fig. 1). Thus, the food intake of female Ospreys depended primarily on how fish were shared between mates, rather than how many fish were delivered to a nest, and the better-fed females were those with older, more familiar mates.

Courtship feeding and reproductive effort and success.—Examination of natural variation in rates of feeding by female Ospreys during courtship (Table 3) permitted an analysis of the associations between a female's food intake and her breeding effort and success. Rank correlation analysis was performed to test the significance of these associations (Table 4). Variation in the amount of food consumed by females was not correlated significantly with egg size or clutch size (Table 4, row 1), nor did females laying 4 eggs eat more fish than those laying 3 eggs (Table 5). Likewise, neither egg failure nor brood size at fledging, both measures of breeding success, correlated significantly with the amount of food eaten (Table 4, columns 7 and 8).

Expressing courtship feeding as calories rather than fish-bites did not alter the conclusion that feeding rates were unrelated to egg size, clutch size, and breeding success (Table 4, row 2). Such results are to be expected, however, because there was a strong correlation between the number of fish-bites consumed by females per hour and their caloric intake ($n = 12$, $r_s = +0.74$, $P < 0.01$).

Supplemental feeding.—All 4 pairs receiving food supplements accepted and eventually ate the extra fish. Males at nests provided with supplemental food hunted only when the extra food had been consumed; these birds foraged only about half as much as males at nonfed nests (Table 6, rows 1 and 2). Although the experimental feeding did make more food available to females than to controls (Table 6, row 3), it did not change clutch or egg sizes, nor

TABLE 2. Delivery and consumption of fish by Ospreys observed early and late in the courtship period. (A) Pairs ($n = 7$) observed over a period of 9–11 days; early = 1st half and late = 2nd half of this period. (B) Pairs observed up to egg-laying (= late; $n = 4$) vs. those for which observations stopped 7–10 days before laying began (= early; $n = 4$). Means ± SE shown. df are the number of 4-h watches during which feeding was measured.

	Early	Late	df	t	P^a
	A				
Number of fish delivered by male/h	0.21 ± 0.03	0.27 ± 0.04	61	1.62	NS
Food consumption by female (bites/h)	82 ± 9	68 ± 8	61	1.11	NS
	B				
Number of fish delivered by male/h	0.22 ± 0.03	0.29 ± 0.03	72	1.84	*
Food consumption by female (bites/h)	66 ± 7	71 ± 7	56	0.30	NS

[a] NS = $P > 0.10$, * $0.05 < P < 0.10$.

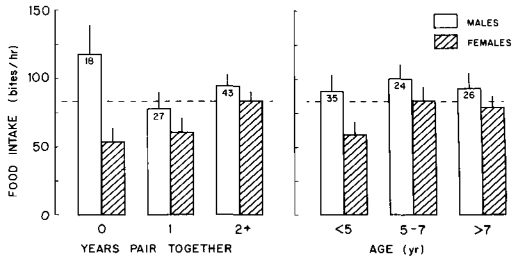

Fig. 1. Food consumption (bites/h ± SE) for male and female Ospreys in the Westport colony during the 1982 courtship period in relation to the number of years a pair had bred together (left) and the age of a pair (right). Sample sizes (the number of 4-h observation periods during which food consumption was measured) are shown for each group in the upper section of open histograms. Dotted lines show equal male/female division for the 3 groups combined. In the left figure, females in pairs that had spent 2+ years together received more food than other females ($z = 2.32$, $P = 0.02$). In the right figure, food consumption for the youngest group of females was significantly lower than for older females ($z = 2.40$, $P = 0.02$).

the timing or success of breeding efforts relative to unfed controls (Table 6, rows 4-7). Moreover, the clutch and egg sizes of females that were fed in 1980 did not differ from their efforts in 1979 and 1981, years when they were not fed (ANOVA average egg size: $F_{2,11} = 0.30$, $P > 0.10$; ANOVA clutch volume: $F_{2,11} = 1.02$, $P > 0.10$).

Weight change in female Ospreys during courtship and the energy demands of egg-laying.—There was no significant correlation between the feeding rates of females and their body weights at laying (Table 4). Most female Ospreys gained little weight during courtship. Although the 17 females weighed during the 1982 study were heavier at laying than when they formed pairs (1,868 ± 15 g vs. 1,933 ± 15 g, paired $t = 4.00$, $P < 0.01$), this increase was only a 3% change in weight over 16.5 ± 1.6 days. Females, therefore, returned from migration close to the weights at which they initiated laying.

If egg-laying were an energetically demanding process for Ospreys, one would expect clutch and egg size to be closely linked to female condition, as reflected by body weight. Yet the weights of females were not well correlated with either their clutch or egg sizes (Table 4, rows 3 and 4). Similarly, at the start of laying, females with clutches of 4 eggs had weights that were similar to females with 3 eggs (Table 5). Breeding success (percentage of eggs hatched and fledging brood size) also correlated poorly with female weight (Table 4, row 5), and females failing to hatch eggs were not lighter at laying than females that hatched at least 1 egg ($t = 0.17$, df = 14, $P > 0.10$). Although females laying in the first half of the laying period (12–26 April) were heavier than those laying in the second half (27 April to 10 May; 1,897 ± 19 g vs. 1,818 ± 20 g, $t = 2.74$, df = 13, $P < 0.02$), factors other than weight appeared to explain

TABLE 3. Rates of food consumption and various indices of breeding performance for female Ospreys whose feeding was observed in 1982. ND = no data.

Pair	Food intake[a]	Mean egg size (ml)	Clutch volume (ml)	Female weight at laying (g)	Laying date[b]	Courtship period (days)	Eggs failing (% of clutch)	Fledging brood size
A	89 (56)	66.9	201	ND	17	24	0	2
B	87 (55)	62.4	250	1,965	8	24	25	1
C	83 (53)	57.3	229	1,905	0	17	25	3
D	80 (46)	67.7	203	1,875	6	18	0	3
E	74 (47)	69.9	210	1,930	14	26	0	1
F	74 (57)	69.0	207	2,000	11	22	0	3
G	70 (54)	64.8	259	1,900	10	18	50	2
H	67 (52)	59.5	238	1,865	17	28	ND	ND
I	56 (36)	66.2	199	1,870	23	28	0	3
J	52 (31)	68.6	274	2,110	28	26	25	1
K	47 (36)	ND	ND	1,950	15	25	100	0
L	45 (34)	62	186	1,910	21	31	100	0

[a] Fish-bites (kcal)·$\text{female}^{-1}\cdot\text{h}^{-1}$.

[b] Number of days after first egg in colony.

TABLE 4. Spearman rank correlation coefficients (×100) between the various indices of feeding and breeding performance listed in Table 3.[a]

	Number of pairs	Mean egg size	Clutch volume	Female weight at laying	Laying date	Courtship period	Egg loss	Young fledged
Feeding								
Bites/h	12	−4	+45	−2	−66*	−63*	−38	+49
kcal/h	12	−1	+10	−5	−57[b]	−56[b]	−34	+37
Mean egg size	27		+53**	+8	−15	−4	−37[b]	+28
Clutch volume	27			0	−1	+32	−23	+27
Female weight at laying	18				+11	+10	−12	−21
Laying date	27					+84***	+43	−45
Courtship period	27						+10	−51**
Egg loss	26							−88**
Young fledged	26							

[a] * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.
[b] $P < 0.10$.

much of the variation in laying dates and courtship periods (discussed below). Thus, the weight differences among females were not related to the courtship-feeding performances of their mates, nor were these differences reflected in their clutch or egg sizes.

The mean weight of a fresh egg from the Westport population was 68 ± 1 g ($n = 29$), about 3.5% of the mean body weight of an adult female at laying. Thus, a 4-egg clutch, the largest laid, was only about 14% of a female's weight. Substituting a basal metabolic rate (BMR) of 3.2 $\text{kcal} \cdot \text{h}^{-1} \cdot \text{kg}^{-1}$ (Wasser *in* Prevost 1982) into Ricklefs's (1974: Table 12) calculations for the energy requirements of egg-laying for hawks and owls, I found that egg-laying increased the daily BMR of a female Osprey by about 18%. Thus, laying did not appear to be demanding for Ospreys.

Variation in clutch and egg sizes.—There was a colony-wide tendency for clutch size to remain stable throughout the 4 yr of this study [3.23 ± 0.09 (low in 1981) vs. 3.33 ± 0.13 (high in 1979)] and, historically, within the larger geographical region of the coastal northeastern United States (Poole 1982). Because food supply varied among colonies in this region (Poole 1982), there is no reason to suspect that such stability was food related.

Only 3 females were known to have changed mates in the years 1979–1982, but for these birds total clutch volume changed little in the year they were fed by a new male (1.3 ± 0.9% change). For 9 males known to have changed mates during this same period, however, there were large differences in the volumes of clutches produced by their new mates (20 ± 19% change). These data suggest that clutch volume varied among individual females, but that it was relatively constant year-to-year for

TABLE 5. Characteristics of females laying 3- vs. 4-egg clutches in the Westport colony, 1979–1982. Weight and feeding data are from 1982 only. Laying dates from 1981 and 1982. Means ± SE shown. NS = $P > 0.10$.

	3 eggs	4 eggs	P
Number of clutches (%)	57 (71%)	23 (29%)	
Average egg size (ml)	64.8 ± 0.8	62.8 ± 1.1	NS[a]
Laying date	23 Apr. ± 2 days	22 Apr. ± 3 days	NS[b]
Food intake of female (bites/h)	72 ± 7	69 ± 6	NS[c]
Weight of female at laying (g)	1,917 ± 23	1,965 ± 43	NS[d]
Age of female (yr)	7.8 ± 1.1	6.8 ± 0.8	NS[e]

[a] Mann-Whitney test, $z = 0.99$.
[b] $z = 0.44$, df = 32.
[c] $t = 0.23$, df = 93.
[d] $t = 0.63$, df = 15.
[e] $t = 0.05$, df = 15.

TABLE 6. Feeding rates and breeding performance of Westport Ospreys provided with supplemental food during the 1980 courtship period, compared to control pairs that were not fed. Means ± SE shown. Pairs fed: $n = 4$; pairs not fed: $n = 4$ for feeding comparisons (rows 2 and 3), $n = 13$ for reproductive comparisons (rows 4-7). NS = $P > 0.10$.

	Pairs fed	Pairs not fed	P
Percentage of day male was hunting	3.6%	7.5%	
Amount of food delivered by male (g/h)	34 ± 7	70 ± 7	***[b]
Food available·pair^{-1}·day^{-1} (g)[a]	1,150 ± 90	940 ± 93	*[c]
Mean egg size (ml)	62.5 ± 2.2	64.6 ± 1.6	NS[d]
Clutch volume (ml)	188 ± 3	218 ± 12	NS[e]
Laying date	24 Apr. ± 4 days	28 Apr. ± 2 days	NS[f]
Hatching success (%)	50 ± 19	82 ± 6	NS[g]

[a] Includes supplemental fish given to pairs fed; daily delivery rates calculated from g/h figures.

[b] Mann-Whitney $Z = 3.75$, df = 59 (number of 4-h periods during which feeding was monitored), $P < 0.001$.

[c] $Z = 1.78$, df = 59 (as above), $0.05 < P < 0.10$.

[d] $t = 1.01$, df = 16 (number of pairs).

[e] $t = 1.51$, df = 16 (number of pairs).

[f] $t = 0.93$, df = 16 (number of pairs).

[g] $U = 39$, df = 16 (number of pairs).

a particular female, no matter which male fed her.

To determine better the sources of variation in Osprey clutch and egg sizes, the clutches and eggs of 14 banded females were measured for 3-4 consecutive years (data from Poole 1983: Table 4, unpubl. data). Clutch- and egg-size variance then were partitioned into between-individual and within-individual components (Hartl 1980: 245, Findlay and Cooke 1983; Table 7). The between-individual component accounted for a significantly larger share of this variance; approximately 90% of the variance in Osprey egg size and 60% of the variance in clutch size arose from differences between individuals (Table 7). Thus, despite variation within the population, there was a significant tendency for individual females to lay clutches and eggs of the same size year-to-year.

Although mean egg size was highly repeatable for female Ospreys in the Westport colony, there was a significant positive correlation between female age and egg size ($n = 23$, $r = +0.63$, $P < 0.01$). In addition, the 14 females whose eggs were measured between 1979 and 1982 laid somewhat larger eggs in 1982 than in 1979 (3.1% increase: paired $t = 2.31$, $v = 13$, $P < 0.05$). There was a significant negative correlation, however, between the ages of females and changes in their egg sizes ($n = 11$, $r = -0.64$, $P < 0.05$), suggesting that age exerts an increasingly weaker influence on egg size in Ospreys. While individual factors control initial egg size in Ospreys, therefore, eggs got somewhat larger as birds aged. Age, however, was apparently not an important influence on clutch size (Table 5).

Variation in laying dates and courtship periods.—Only laying dates and courtship periods were correlated significantly with the rates at which

TABLE 7. Components of egg and clutch size variance in the Westport Osprey colony. R_I is the intraclass correlation coefficient, a measure of how much of the total variation is due to differences between individuals, as opposed to within individuals. $n = 14$ females sampled for 3-4 consecutive years (i.e. 50 clutches).

Source of variation	Sum of squares	df	Mean square	F[a]	R_I
Egg size					
Between individuals	1,449	13	111.5		
Within individuals	102	35	2.9	38.45***	+0.91
Clutch size					
Between individuals	7.94	35	0.61		
Within individuals	3.17	13	0.09	6.77**	+0.62

[a] ** $P < 0.01$, *** $P < 0.001$.

TABLE 8. Spearman rank correlation coefficients (×100) between the age of Osprey pairs, their breeding experience (number of years together), and various indices of the timing of breeding in the Westport colony, 1981-1982.[a]

	n	Pair experience	Pairing date	Laying date	Courtship period
Pair age	31	+83***	−52**	−80***	−57***
Pair experience	46		−45**	−52***	−11
Pairing date	46			+75**	+3
Laying date	46				+63***
Courtship period	46				

[a] ** $P < 0.01$, *** $P < 0.001$.

female Ospreys fed (Table 4, row 1). Although females that ate more fish did lay eggs earlier, laying dates also were correlated with the age of a pair, the number of years a pair had bred together, and its pairing date (Table 8, Fig. 2). Older pairs, and pairs that retained the same mate, generally bred earlier (Fig. 2, left and middle). Stepwise multiple regression analysis (Dixon 1981) of laying dates on age, mate retention, and pairing dates of pairs showed that together these three variables explained 84% of the variance in the timing of egg-laying by Ospreys (Table 9). Mate retention alone accounted for two-thirds of this variance (Table 9).

Because mate retention was associated with both the laying dates of females (Table 8) and their feeding rates (Fig. 1), partial correlation analysis was used to test if the relationship between feeding rates and laying dates could have been the result of the co-correlation of these variables with the number of years a pair had bred together. Using partial correlation to remove the influence of mate retention, the relationship between the feeding rates of females and their laying dates was no longer significant ($r_p = -0.10, P > 0.10$). Earlier laying, therefore, was primarily a function of mate retention rather than of feeding rates.

Similarly, the duration of courtship periods was significantly negatively correlated with the feeding rates of females (Table 4, row 1), although the age of pairs also varied inversely and significantly with courtship periods (Table 8; Fig. 3, middle). Pairing dates and pair experience were not related to the length of courtship periods (Table 8; Fig. 3, left and right). Females in older pairs were thus quicker at initiating laying after pairing, regardless of when those pairs formed or how many years they had been breeding together. The association between the duration of courtship periods and the feeding rates of females was no longer significant, however, after removing the influence of a pair's age using partial correlation ($r_p = +0.01, P > 0.10$). Thus, both shorter courtship periods and higher rates of feeding by females were associated with age of pairs, although feeding rates alone were not critically related to how long pairs spent courting.

Courtship feeding and the decision to breed.—Copulations were attempted at only 48% of 52 feedings observed among courting Westport Ospreys. Of 93 copulation attempts, only 32% occurred during or shortly after feedings (within 10 min), so pairs appeared as likely to attempt matings when a female had not eaten recently as when she had. Furthermore, copulations appeared no more successful during or soon after feedings than at other times (47% vs. 48%).

TABLE 9. Stepwise multiple regression analysis of the effects of a pair's age (yr), breeding experience (number of years together), and date of pairing (number of days after 1 January) on the laying dates (number of days after first egg in colony) of Westport Ospreys, 1981 and 1982. $n = 18$ pairs, none sampled in more than 1 yr. Multiple regression equation: $y = 66.23 - 1.58x_1 + 0.65x_2 - 1.18x_3$, $F_{3,15} = 25.3$, $P < 0.001$.

Step	Variable	R^2	Increase in R^2	F	P[a]
1	Breeding experience (x_1)	0.67	0.67	35.14	***
2	Pairing date (x_2)	0.78	0.11	24.88	***
3	Age (x_3)	0.84	0.05	18.24	***

[a] *** $P < 0.001$.

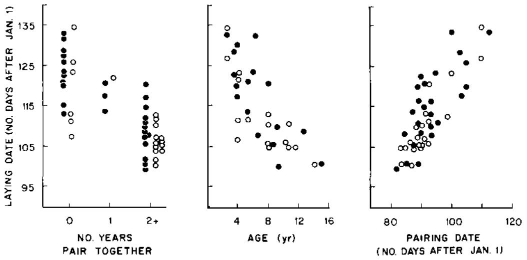

Fig. 2. Relationships between the laying dates of Westport Ospreys and the number of years a pair had bred together (left), a pair's age (middle), and the date on which a pair formed (right). Closed circles are data from 1982, open circles are from 1981. In the left figure, 1981 and 1982 data are separated for clarity. Correlation coefficients for Fig. 2 are shown in Table 8.

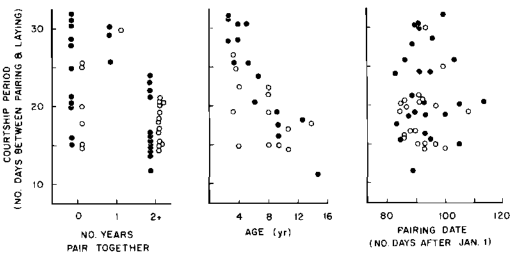

Fig. 3. Relationships between the duration of courtship periods for Westport Ospreys and the number of years a pair had bred together (left), the age of a pair (middle), and pairing date (right). Symbols are shown as in Fig. 2. Correlation coefficients for this data are shown in Table 8.

Among 10 pairs with more than 10 observed copulation attempts, new pairs ($n = 4$) had a lower success rate than pairs that had bred together in a previous year (37% vs. 72%; $t = 3.13$, $P < 0.02$), usually because females did not tip forward in a copulation-soliciting posture. Males with new mates tended to "mantle" food (protecting prey from mates by facing away from them and hunching over the prey; see Cramp and Simmons 1980: 273, Fig. A) for 5–30 min at the nest before eventually giving it to their mates. Such behavior was especially prevalent during the first 5–10 days after pairs formed. Among older established pairs, food transfers generally occurred quickly and smoothly, without such behavior. Although there were only 2 nonlaying pairs in 1982 (not included in the feeding study), these males were seen to delay delivery of food to their mates. Thus, feedings may not be an immediate stimulus for Osprey copulations, but efficient food transfers among courting Ospreys appear to be a requirement for successful copulations and perhaps for egg-laying.

DISCUSSION

The influence of age and mate retention.—Both the timing of breeding and the reproductive effort of Ospreys were associated more closely with the age of a pair, and the number of years they had bred together, than with the amount of fish a female received from her mate prior to egg-laying. Rates of food consumption by females during courtship also were related to age and mate retention. Studies of the relationship between courtship-feeding rates and reproductive effort seldom have considered the effects of age or mate retention. Nisbet (1977) suggested that differences in clutch and egg sizes between two separate colonies of Common Terns were not due to differences in the age structures of the populations. The mean laying date was significantly earlier in the colony with the larger eggs and clutches (Nisbet 1977), however, and numerous studies have shown that clutch and egg sizes decline with laying dates independently of a pair's age and experience (Perrins 1970, Mills 1973, Ankney and MacInnes 1978, DeSteven 1978, Murphy 1978, Birkhead and Nettleship 1982, Birkhead et al. 1983).

Differences in laying dates may also explain much of the variation in breeding performance within colonies of Common Terns, otherwise attributed to differences in rates of courtship feeding by males (Nisbet 1973). Older terns often breed earlier and produce larger eggs and clutches (Hays 1978, Nisbet et al. 1984). If, like Ospreys, male Common Terns increase the amount of food they deliver to mates as pairs age or gain breeding experience, then the differences in clutch and egg weight found by Nisbet (1973) could be due primarily to older, experienced pairs breeding earlier and producing larger eggs and clutches, rather than to increased rates of feeding by females in older pairs.

This hypothesis suggests that courtship feeding may influence clutch and egg size only indirectly, by stimulating a female toward the final stages of egg development. Better-quality pairs (e.g. older birds, with more experience breeding together) would be expected to breed earlier, to lay larger eggs and clutches, and to be more proficient at finding food, although food supply alone would not necessarily be the critical determinant of reproductive effort. Clearly, studies of the influence of courtship feeding on avian reproduction also must consider the influence of a pair's age, of mate retention, and of laying dates if ambiguous results are to be avoided.

Variation in the laying dates of Ospreys during this study was modest and not related to differences in clutch or egg size (Table 4). When the laying season is more protracted, however, significantly smaller eggs and clutches are produced by Ospreys that lay late (Ogden 1977, Judge 1983, Poole 1984).

Older seabirds, it has been suggested, may lay larger clutches and eggs because they have an easier time finding food and hence building up reserves for egg-laying (Ryder 1981). Yet data on American Kestrels (*Falco sparverius*, Bird and Lague 1982) and on Ospreys show that age-related differences in clutch and egg sizes can be independent of food supply and nutrient reserves, as measured by body weight. Although there are theoretical reasons for expecting reproductive effort to increase with age in birds (Williams 1966, Pianka and Parker 1975), proximate regulation of age-related change in avian clutch and egg sizes remains obscure.

Retention of mates appeared to influence the feeding rates of females, suggesting that characteristics of the pair bond itself may determine the amount of food females eat. Males with familiar mates may be more responsive to female begging. My observations showed that only males with new mates appeared hesitant to make the food transfer. Breeding experience did not influence the rates at which females fed through increased or more efficient foraging, however. I found that rates of food consumption were not significantly related to differences in the actual number of fish delivered to nests, but rather to how fish were shared between mates.

Supplemental feeding.—The results of the supplemental feeding experiment were consistent with findings from the 1982 study on natural variation in rates of feeding during courtship. Additional food had no significant impact on the reproductive effort (clutch and egg sizes), timing, or success of female Ospreys. Supplemental feeding in other species prior to egg-laying often has resulted in earlier laying, with little change in clutch or egg size independent of laying date (Källander 1974, Smith et al. 1980, Dijkstra et al. 1982, Ewald and Rohwer 1982; but see Hogstedt 1981, Newton and Marquiss 1981). Such findings suggest that for some species food supply may affect clutch and egg sizes only indirectly through its influence on laying dates, with female condition playing a less critical role than it does, for example, in the egg production of many waterfowl (cf. Newton 1977, Ankney and MacInnes 1978, Drent and Daan 1980). Hogstedt (1981) argued that some factor other than food may determine the actual onset of laying, although individuals supplied with extra food may respond more quickly to a laying stimulus than less well-fed birds. Cavé (1968) found that the stage of ovarian development was more advanced prior to breeding in Eurasian Kestrels (*Falco tinnunculus*) provided with extra food than in those that were not, even though rapid ovarian development had not begun in any of these birds.

The onset of effective courtship feeding may stimulate rapid ovarian development in Ospreys. Supplementary feeding alone did not advance laying dates in this study, and rates of food consumption were not significant correlates of laying dates or courtship periods. However, dates of the initiation of courtship feeding (i.e. pair formation) were correlated with laying dates, suggesting that females were more responsive to when their mates began to feed them than to how much food they received.

That male Ospreys curtailed hunting with the provision of supplemental food suggests that males foraged only when hungry, or perhaps when their mates begged. To what extent female begging stimulates hunting by male Ospreys remains to be investigated. Reduced hunting by fed males suggests that there was little selective pressure on these birds for increasing food delivery to their mates beyond a certain, perhaps minimum, hunger or caloric threshold. If the reproductive effort and success of a pair of Ospreys increased with the amount of food delivered to females prior to laying, one might predict that all male Ospreys (fed or not) would provide surplus food to their mates as insurance against reproductive loss.

None, however, were seen to do this. Indeed, males are capable of foraging at much higher rates than they do during courtship. Males with young bring 3-4 times more food to their nests than courting males (Green 1976, Poole 1984).

There was significant year-to-year stability of clutch and egg sizes for individual females in this study even though they often were fed by different males in different years. Such repeatability suggests that there may be a strong heritable component to these aspects of breeding in Ospreys. Van Noordwijk et al. (1980) and Findlay and Cooke (1983) have shown significant positive relationships between repeatability and heritability of both clutch and egg sizes in several species of birds.

Female weight reserves.—In many bird species females gain significant amounts of weight before egg-laying, presumably allowing them to draw on stored reserves to meet the demands of egg-laying and/or incubation (Jones and Ward 1976; Newton 1977, 1979; Nisbet 1977; Ankney and MacInnes 1978; Raveling 1979; Krapu 1981; Newton et al. 1983). Among female Common Terns, it is unclear how much of their "excess weight" is actually gained during courtship, although most of it is subsequently incorporated into eggs (Nisbet 1977). Eurasian Sparrowhawk (*Accipiter nisus*) females (but not males) show significant weight gain during the courtship-feeding period but lose little weight in egg-laying; instead, they appear to use their weight reserves as a buffer against food shortage during incubation (Newton et al. 1983).

Ospreys, by contrast, gain little weight before laying eggs. This could be because Osprey eggs are small relative to female body weight and appear energetically cheap to produce compared to the eggs of other species (cf. Ricklefs 1974, Hunt 1980). Decreasing relative egg size with increasing female body weight is typical for raptors (Newton 1979: 115). Thus, a pattern of small gains in weight during courtship coupled with low costs of egg production may be common for large-bodied birds of prey like Ospreys, although such a pattern is not restricted to this group (see Ankney and Scott 1980). The fact that Ospreys can depend on dietary protein in forming their eggs also may help to eliminate a need for extra body reserves (cf. Jones and Ward 1976, Ankney and MacInnes 1978, Ankney and Scott 1980). Although female Ospreys lose weight during incubation (Poole 1984), variation in female weight was not an important factor in incubation success during this study.

The evolution of courtship feeding in Ospreys.—Female Ospreys are totally dependent on their mates during courtship, yet this feeding behavior also must benefit the genetic interests of males because foraging is energetically expensive for Ospreys (Poole 1984). Why has feeding, rather than some other less costly display, evolved as the primary courtship behavior of this species?

Courtship feeding is common among gulls and terns, birds that often have exceptionally heavy clutches with respect to adult body weight. Hunt (1980) suggested that courtship feeding may be an adaptation allowing females of these species to obtain the extra energy needed for the production of eggs without having to leave the nest for long periods to forage after their initial eggs have been laid. Similarly, Royama (1966) has shown that courtship feeding in Great Tits (*Parus major*) is restricted to a period after egg-laying has begun, a time of maximum energy demands when females are increasingly tied to the nest. Courtship feeding does not appear to serve such a critical nutritional function for Ospreys (nor perhaps for most other raptors), however, as egg production usually is not demanding in these species and males are effective incubators and guardians of the nest site.

Several studies (Nisbet 1977, Newton 1979, Wheeler and Greenwood 1983) have attempted to explain courtship feeding with the "gravid female hypothesis," namely that females hunting active prey and putting on extra weight prior to egg-laying lose maneuverability (and thus hunting efficiency), or become more vulnerable to egg damage as they carry better-developed eggs. Either situation could force them to depend increasingly on their mates for food. Yet female Ospreys in this study did not gain significant amounts of weight during courtship. Likewise, their dependence on the male usually began immediately after pair formation, rather than developing slowly as Wheeler and Greenwood (1983) hypothesized should happen in female raptors that are becoming increasingly heavy with eggs. Additional observations outside this study showed that females hunted successfully on their own when they were poorly fed by their mates. Thus, the gravid female hypothesis does not appear applicable to Ospreys.

Assessment of the quality of prospective mates, especially by females, is another possible function of courtship feeding (Nisbet 1973, Hunt 1980). Although the pair bonds of Westport Ospreys generally were stable during the early stages of courtship, it may be adaptive for females choosing new mates to assess the amount of food males deliver to them, if there is seasonal continuity to rates of food delivery by individual males as Nisbet (1973) and Niebuhr (1981) showed for other species. I did not measure the chick-feeding performances of enough male Ospreys to draw conclusions about continuity in rates of feeding by individuals. However, reproductive success (egg loss and fledging brood size), an indirect measure of a male's foraging ability after egg-laying, was not correlated with a male's courtship-feeding performance. Thus, female Ospreys may assess potential mates by more important criteria than variation in rates of courtship feeding. Nest sites, for example, are limited for most populations of coastal Ospreys (Poole and Spitzer 1983), and single males in possession of a nest, or a good potential site, are a scarce resource (pers. obs.). Females, which do not build nests on their own (pers. obs.), therefore could easily forfeit the chance to breed in any one season by readily deserting a mate because his delivery rates were low.

Males that fail to deliver fish, however, or that do so at a low enough rate that their mates sometimes are forced to hunt on their own, may suffer loss of fitness through cuckoldry, loss of nest sites, or reduced success of copulations. Generally, these are males that mantle food at the nest (pers. obs.). Although such poorly fed females were not seen in this study, limited data from studies in 1983 showed that these birds often begged from passing males that were not their mates, while well-fed females rarely did this. In addition, when her mate was absent, one consistently hungry female wandered repeatedly to a nearby nest where a single male was temporarily in residence. There she received food and was seen to copulate on several occasions with this male, a bird that did not become her mate. Males that refuse to deliver food may forfeit nest sites because well-fed females regularly defend nests against intruding birds during the courtship period, a time when nest-site competition can be intense in Osprey colonies (pers. obs.). The evidence indicates that there may be a food-delivery threshold below which female Ospreys lose faithfulness to mate and nest site.

These findings suggest that a key function of courtship feeding is to ensure mate fidelity. Tasker and Mills (1981) found that increased rates of courtship feeding among gulls coincided with increased success of copulations and a lower percentage of time a female was away from the nesting territory. By feeding its mate, a male bird may help to guarantee its exclusive access to the female when she is fertile. Such access appears to be of concern for male Ospreys; during courtship (only), males continually accompany their mates on flights away from the nest site (pers. obs.), probably a form of mate guarding (cf. Birkhead 1979, Beecher and Beecher 1979). Because females are left alone at nests while males forage, however, and because well-fed female Ospreys often defend their nests against intruding conspecifics (including males), courtship feeding may function in addition to mate guarding to reduce the extent of a female's wanderings and to increase a male's confidence of paternity (Fitch and Shugart 1984).

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