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FOOD SUPPLY AND REPRODUCTIVE PERFORMANCE OF THE AMERICAN OYSTERCATCHER IN VIRGINIA¹

ERICA NOL²

Department of Zoology, University of Toronto, 25 Harbord St.,
Toronto, Ontario M5S 1A1, Canada

Abstract. The relationship between food supply and reproductive performance was determined in a 3-year study of the American Oystercatcher, *Haematopus palliatus*, in Virginia. Clutch size, clutch-initiation dates, interclutch intervals, fledging success, distance to food, and quality and density of food were examined for 41 territories. Food supply varied more among territories than did clutch size, clutch-initiation dates, or interclutch intervals. Annual and interannual fledging success was extremely variable. Although no measure of food supply contributed significantly to variation in clutch size, the size of nearby feeding areas was positively correlated with average egg size and fledging success and was negatively correlated with the date of first clutch initiation. Earlier laying females had greater fledging success. Of the measures of food supply only the size of the nearby feeding area contributed significantly to variation in fledging success. Growth rates and rates of provisioning young were similar among broods of different sizes. In general, the match between food supply and reproductive performance was poor. As predation was the major cause of chick losses, I suggest that better territories for oystercatchers are those that allow parents to watch for predators of the young, and forage at the same time.

Key words: *American Oystercatcher*; *Haematopus palliatus*; food supply; reproductive performance; long-term reproductive success; provisioning rates; chick growth.

INTRODUCTION

Food-supplementation experiments have long been used to examine the relationship between various measures of reproductive success (mostly clutch size) and the supply of food on the territory (see Ewald and Rohwer 1982, Arcese and Smith 1988). These experiments have generally been tests of hypotheses from life-history theory (Lack 1968, Klomp 1970, Winkler and Walters 1983, Hussell and Quinney 1987). Although natural variation in food has been shown to affect seasonal reproductive performance in at least five species of birds (Hussell and Quinney 1987), absence of a relationship between food and reproductive performance has also been noted (e.g., Smith et al. 1980, Van Noordwijk et al. 1981, Bédard and La Pointe 1984, Arcese and Smith 1988) and may be more common except that "negative" results are often not reported. With an increasing number of tests for a "match" between food and reproductive output, generalizations may be made about the categories of

birds that should respond proximately to variation in food (e.g., Arcese and Smith 1988). For example, the presence of a match may depend on the relationship between clutch mass and/or chick mass and adult body mass, the magnitude of yearly environmental fluctuations (Boyce and Perrins 1987), or the presence of density-related seasonal reproduction (Arcese and Smith 1988).

Oystercatchers are large, conspicuous territorial shorebirds that feed mostly on large, visible prey. Hence, it is possible to measure the quality and availability of food with considerable precision (e.g., O'Connor and Brown 1977; Hockey 1981; Goss-Custard and Durell 1987a, 1987b, 1987c). In local populations the distances between territories and food sources and the densities of food vary greatly among individuals, but whether this natural variation among habitats influences reproductive success is largely unknown. The observed variations in nesting success are correlated with habitat differences among populations of the European Oystercatcher (*Haematopus ostralegus*) in some studies (Heppleston 1972, Briggs 1984, Safriel 1985), but not in others (Harris 1967). Herein I report on the relationship between food quality and availability with reproductive success for a population of

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² Present address: Department of Biology, Trent University, Peterborough, Ontario K9J 7B8, Canada.

American Oystercatchers (*H. palliatus*). I also report on the long-term variability in reproductive success for the study population.

STUDY AREA AND METHODS

The study was conducted on Chincoteague Island, Wallops Island, and Assawoman Island in coastal Virginia (37°50'N, 75°35'W) during the breeding seasons (March to July) of 1981 to 1983. From 1978 to 1983, 60 adults (from a total of 90 birds) were trapped at the nest with drop traps lined with fish net (Mills and Ryder 1979). The adults were banded with aluminum bands and unique color-band combinations. Usually both birds of the pair were identifiable by color-band combinations.

All pairs in the study area had both a nesting territory and a regular feeding area 100 m to 3 km distant (hereafter called "distant feeding areas"). However, some pairs also fed on their nesting territories (hereafter called "nearby feeding areas"). The distant feeding areas included: (1) large mud flats containing common razor clams (*Ensis directus*); (2) the edges of channels where stout razor clams (*Tagelus plebeius*) burrowed in the mud; and (3) small salt pannes (<1 ha); these harbored horse mussels (*Modiolus demissus*), at the base of *Spartina alterniflora* clumps. A full description of the study area is given in Nol (1985).

Nesting territories were searched before and during laying to locate and mark eggs. Eggs were weighed and measured. Volumes were calculated using the equation: volume (cc) = 0.48 (length × breadth²) - 1.318 (Nol et al. 1984). During the study period most first clutches in this study area contained three eggs (Nol et al. 1984). Nest losses were high, and in the 3 years virtually all birds lost at least one of their first clutches to predators or high tides. Females then laid replacement clutches varying in size from one to three eggs (mode = 2, Nol et al. 1984). Therefore, I compared the number of eggs in the replacement clutch among pairs. I also examined average egg mass, laying dates, and the interval between loss of the first clutch and laying of a replacement clutch (the interclutch interval). Visits to the nest were restricted to the laying period, until the chicks had hatched, to avoid attracting predators to the nest. I captured and measured as many known-aged chicks as possible, ranging in age from 1 to 36 days. As an estimate of fitness for a pair I calculated the num-

ber of young raised to fledging age (ca. 40 days) on that territory over the 3 years of the study. For most analyses, I used only those territories where the pair bond had remained intact over the study period. No pairs moved to new territories; hence, the effect of pair and territory are always confounded. Annual fledging success was also determined for some pairs from 1978 to 1980 and in 1984. These data are used in calculating variability in reproductive success.

Four measures of food supply were used: (1) size of the nearby feeding area, (2) the density of food in the nearby feeding area, (3) the time required to fly from the nesting area to the center of the regular distant feeding area, and (4) the profitability of food on the distant feeding area. Profitability (gram wet weight/minute of handling time, MacArthur and Pianka 1966), rather than density was recorded for the distant feeding areas. The capture rate on the distant feeding areas was similar both early and late in the season (Nol 1984) and this, coupled with the large size of these areas (>3 ha) led me to assume that the prey could not be depleted and that only the former measure would influence the time budget of a pair.

I determined (1) above using my pace (0.83 m/pace) and a compass. Density of food, (2) above, was measured using 15–35 randomly-selected 1-m² quadrats in the nearby feeding area. In each quadrat all bivalves were counted visually, or, for the submerged species, by assessing the number of siphon holes. Estimates based on the number of siphon holes were checked on three to five quadrats per territory, by digging for the clams. These two estimates did not vary by more than 10%. The total number of quadrats in the nearby feeding area varied depending on the variance of food in the territory: the larger the variance the greater the number of quadrats used. I observed birds, using binoculars, flying from nesting to distant feeding areas. The flight times between these areas, (3) above, were mean values for at least 10 flights. Oystercatchers were only seen at distant feeding areas when they were actually feeding, so I presume that all flights to these areas resulted in feeding bouts and not in resting. I recorded the capture rate in each of the three major feeding habitats, on an event recorder. Wet and dry weights were obtained for specimens from each of the three habitats. The product of capture rate and wet weight of prey in that habitat was used to indicate the profita-

TABLE 1. Statistical descriptions of variables representing food availability and reproductive performance of American Oystercatchers near Chincoteague, Virginia.

Variable	Number of pairs	Mean	Median	SD	Range	CV (%)
Size of nearby feeding area (m ²) ¹	41	2,244	199	5,230	0–21,675	233
Density of food on nearby feeding area (no./m ²) ¹	41	4.5	1.05	7.46	0–25.8	166
Flight time to distant feeding area (sec)	41	46.7	42.6	21.78	19.2–111.6	47
Food profitability at distant feeding area (g wet weight/min)	41	2.4	2.4	0.78	1.2–4.2	33
Initial clutch size	41	2.8	3	0.31	2–3	11
Average replacement clutch size	30	2.4	2.4	0.54	1–3	22
Average egg volume (cm ³)	41	42.2	42.4	1.9	38.0–45.6	5
Clutch-initiation dates (days from 1 April)	41	20.9	20.1	5.86	11.7–35	28
Interclutch interval (days)	33	14.0	13	4.05	9–26	29
Annual fledging success (young/year)	44 ²	0.24	0	0.39	0–1.25	150
Three-year fledging success (young)	41	0.90	0	1.51	0–5	178

¹ Includes territories with no nearby feeding area.

² Includes some pairs monitored since 1978.

bility of food on the distant feeding areas. The correlation between wet and dry weight for all food items was >0.95, (4) above. The energy content of the three food species is assumed to be similar (Cummins and Wuycheck 1971), and an average profitability for each of the three areas was used in the analyses.

Spearman's rank correlations were used to examine univariate relationships between pairs of variables. Multiple regression was used to compute first, the relationship between the measures of food supply and clutch size, and second, the relationship between these four measures with fledging success over the 3 years. Canonical correlation analysis was used to relate the measures of food supply and laying date, clutch size, and average egg size. Highly variable results were normalized using a log-transformation before applying the latter two statistical tests.

RESULTS

Measures of the food supply and reproductive performance were obtained from 41 territories. Flight times from nesting to distant feeding areas ranged from 19 sec to 2 min (Table 1). Some neighboring pairs used feeding areas at similar distances from their nesting areas. Elsewhere, neighboring pairs used distant feeding areas at very different distances from their nests. In general, food supply varied more among territories than did reproductive variables (Table 1). Of the measures of reproductive performance, both mean annual fledging success and fledging success over the 3 years were highly variable (Table 1).

Pairs with larger nearby feeding areas laid earlier, had larger eggs, and higher fledging success in the 3 years, than those with smaller, or no nearby feeding areas (Table 2). Pairs with high densities of food on the nearby feeding area flew shorter distances to their distant feeding areas, where the prey was more profitable. These last results reflect the spatial pattern of nests, as pairs nesting well into the salt marsh usually had prey on their territory and flew only short distances to other, similar patches of profitable prey (usually *Modiolis demissus*). Among the measures of reproductive performance only laying dates were negatively correlated with fledging success; earlier laying females had greater fledging success over the 3 years of the study (Table 2).

REPLACEMENT CLUTCH SIZE

None of the four measures of food supply accounted for a significant proportion of variation in replacement clutch size (multiple regression full model: $r^2 = 0.08$, $P > 0.05$). Females that travelled long distances to distant feeding areas were just as likely to lay a three-egg replacement clutch as those that travelled shorter distances.

CLUTCH INITIATION DATES, CLUTCH AND EGG SIZE AND INTERCLUTCH INTERVALS

The measures of food supply were compared with replacement clutch size, average egg size, laying dates, and interclutch intervals, using canonical correlation analysis. The correlation between these two first canonical variates was positive but not significant (canonical $r^2 = 0.64$, $F_{1,16} = 1.13$,

TABLE 2. Spearman's rank correlations between variables representing food availability and reproductive performance.

Variable ¹	Correlation with:				
	(2)	(3)	(4)	(5)	(6)
(1) Size of nearby feeding area	-0.14	0.48**	0.07	-0.06	0.30*
(2) Flight time to distant feeding area	1	-0.36*	0.05	-0.15	-0.34*
(3) Density of food at nearby feeding area		1	0.37*	0.06	0.06
(4) Food profitability at distant feeding area			1	-0.22	-0.16
(5) Replacement clutch size				1	0.07
(6) Average egg volume					1
(7) Clutch-initiation dates					
(8) Interclutch interval					
(9) Mean annual fledging success					
(10) 3-year fledging success					

¹ Sample sizes for variables are given in Table 1.

* denotes $P < 0.05$.

** denotes $P < 0.01$.

$P < 0.37$). In general the match between food supply and reproductive performance was weak.

FOOD SUPPLY AND FLEDGING SUCCESS

Food supply variables were compared with fledging success for the 3 years. Food supply weakly predicted fledging success on a particular territory and for a particular pair ($r^2 = 0.51$, $F_{4,22} = 5.74$, $P < 0.003$). However, the size of the nearby feeding area had the highest contribution to the regression, and was the only variable with a significant partial regression coefficient with fledging success ($t = 3.37$, $n = 27$, $P < 0.003$). Thus, pairs with larger nearby feeding areas raised more young over the 3 years of the study. The results for annual fledging success were similar. Only the size of the nearby feeding area significantly contributed to variation in annual fledging success ($t = 2.87$, $n = 27$, $P < 0.009$).

GROWTH RATES, BROOD SIZE AND NUMBER OF PROVISIONING TRIPS

If food supply influences reproductive success, then we can predict a positive relationship between the number of young oystercatchers that parents are feeding and the number of trips to provision them, assuming that profitability of provisioned prey is similar among broods of different sizes. No such relationship was found. Average rates of provisioning young from hatching to fledging were similar in broods of different sizes: one-chick broods, 2.0 trips/hr \pm 0.22, $n = 6$ pairs; two-chick broods, 1.83 trips/hr \pm 0.135, $n = 9$; three-chick broods, 1.64 trips/hr \pm 0.243, $n = 7$; $F_{2,20} = 0.69$, ns. Rejection of food by chicks, even in broods of three was often seen. Growth rates of chicks in different-sized

broods were also relatively uniform: $K = 0.14$ in broods of one, two, and three chicks; adjusted asymptotes (Ricklefs 1967) were 400 g ($n = 14$ weights from eight chicks), 400 g ($n = 36$ weights from 17 chicks), and 385 g ($n = 70$ weights from 24 chicks), respectively.

VARIABILITY IN REPRODUCTIVE SUCCESS

Annual reproductive success at this study site was extremely variable, both among and within pairs. The production of fledged young by the population varied from lows of zero (1984, 11 nests monitored) and three young produced (1979, 21 nests monitored) to highs of 17 (1982) and 20 (1983) young (41 nests monitored in each of latter years). Annual reproductive success for individuals that hatched at least one egg (25 of 45 nests), ranged from zero in 6 years (seven pairs) to young in 2 of 3 years (one pair). The mean percentage success for those birds that hatched at least one egg was 24.6% (SD = 30.5) or one successful nesting attempt every 4 years. These birds often lay two replacement clutches (Nol et al. 1984) so this represents an average of one success for every eight to 12 nesting attempts. Mean percentage success was 14.0% (one in 14 to 21 nesting attempts, SD = 19.7) when the 20 pairs that failed to hatch even one chick are included (total number of nest years observed = 174, $\bar{x} = 4$ years per nest).

Nest losses for those pairs that experienced reproductive failure year after year were primarily from high waters during spring tides (Table 3). Predation and high tides accounted for losses of chicks in nests where eggs hatched but no young were fledged (Table 3).

TABLE 2. Extended.

	Correlation with:			
	(7)	(8)	(9)	(10)
	-0.53**	-0.23	0.50**	0.49**
	0.21	0.14	-0.07	-0.05
	-0.33*	-0.02	-0.09	-0.11
	-0.11	-0.18	-0.22	-0.16
	-0.07	-0.10	0.00	-0.19
	-0.18	0.12	0.16	0.23
	1	0.14	-0.39*	-0.39*
		1	-0.09	-0.02
			1	0.89**
				1

DISCUSSION

FOOD SUPPLY AND CLUTCH SIZE

In this population, clutch size was not enhanced by having better access to food. However, pairs that had territories closer to food resources did lay earlier and produced larger eggs. This result suggests that the measures of food supply used here reflected what was available to the birds. The lack of influence on clutch size can mean that either the range of food was not great enough to result in a correlation during the study period (other factors accounting for the differences among individuals, Arcese and Smith 1988), or that the relatively small size of oystercatcher eggs can be formed from reserves and clutch size is not influenced by the food supply.

The first possibility can be addressed by examining populations with more variable food supplies. In three comparative studies of the European Oystercatcher breeding in contrasting habitats, there was no relationship between food supply and clutch size, despite large differences in the nature and possibly the energy content or nutritional quality of food (e.g., earthworms vs. mussels) among territories (Heppleston 1972, Briggs 1984, Safriel 1985). This suggests that clutch size is not affected by food availability over a wide range of prey densities. Each oystercatcher egg constitutes only 6–7% of the fe-

male's body weight (Nol et al. 1984) and egg formation may not be energetically stressful.

Replacement clutch size was consistent in this study (two or three eggs) over the 3 years of intensive observation, but since American Oystercatchers can breed for at least 10 years in this study area (pers. observ.), the possibility of an age effect cannot be discounted. Some support for this comes from changes in the population distribution of clutch sizes over time. Greater numbers of two-egg first clutches were found in early years of the study (Nol et al. 1984) and recently, in nests of unmarked, possibly younger birds (pers. observ.), whereas most first clutches contained three eggs in the intervening years (1981–1985, Nol et al. 1984 and pers. observ.). In kittiwakes, clutch size increased over the first 3 years of breeding, and then remained stable for the next 10 years (Coulson and Thomas 1985). If the changes I observed do relate to changes in age distribution, then the age distribution of the breeding population is not stable (Lotka 1922), although that of the entire population may be. This is not unusual in natural populations (Travis and Heinrich 1986). Annual rates of disappearance are variable (averaging 15% but ranging from 10% to 50%; Nol 1985, unpubl. data). These fluctuations result in a variable number of openings for young, first-time breeders, and hence an unstable breeding-age distribution.

FOOD SUPPLY AND FLEDGING SUCCESS

Individuals that raised large numbers of young over the 3 years of the study had large nearby feeding areas. Why was the size of the feeding area rather than the prey density important to reproductive success? The answer may lie in the structure of the foraging habitats and not in the quantity or profitability of food available to successful pairs. Dense prey areas consisted mostly of mussels and these areas were usually small and enclosed by dense stands of marsh grasses. In these areas visibility was poor and vigilance for predators was probably difficult. By contrast, the large feeding areas were open mud flats con-

TABLE 3. Sources of complete nest or chick loss for different categories of reproductive failure.

Category	Number of pairs	Mean number of years observed	Sources of failure		
			High tides	Predation	Unknown
Failed to hatch eggs in any year	20	3.1	18	2	0
Hatched eggs but fledged no young	7	5.6	3	2	2

taining razor clams. In these areas, vigilance was enhanced both by the lack of vegetation and because other oystercatchers usually also fed there that were also watching for predators. Of the seven nests where predation on chicks was known to occur, six were from territories with small (or no) nearby feeding areas, and one had a large feeding area ($P < 0.05$, binomial test).

Lower profitability or density of food was not correlated with lower reproductive success, probably because starvation was not a common cause of chick loss. If starvation were a consistent cause of reproductive failure, then a relationship between either brood size and the rate of provisioning young, or brood size and the growth rates of those young would be expected. Neither relationship was found, not even weakly. Almost all partial losses of broods occurred early in the chick-rearing phase, and were thought to be due to predation or flooding but not starvation. This is not to say that American Oystercatcher chicks never die from starvation, but during this study, starvation was never observed. This is unlike American Black Oystercatchers (*H. bachmani*), and possibly European Oystercatchers (Safriel 1981), where, after the establishment of a sibling hierarchy (Groves 1984), a subordinate chick often dies due to competition for food (Groves 1984).

Better territories for the American Oystercatcher appear to be those where parents can spend more time watching over the brood rather than those containing more food, given some minimum, but adequate level of food in the environment. This result is much like that found for the European Oystercatcher where losses of chicks were due to predation and not starvation (Harris 1967, Heppleston 1972). Birds that flew to distant areas had young that grew as fast as birds flying to closer feeding areas (Heppleston 1972), but had much lower fledging success. This was attributed to the lack of vigilance of the parents and resulting predation (Heppleston 1972, Safriel 1985).

Of general interest in these data was the highly variable reproductive success, both for a particular pair and for the population, and the large proportion of pairs that failed to fledge even one chick over a number of years. As reproductive success of nidifugous birds is sometimes evaluated on the basis of hatching success alone, because the young are so difficult to follow, these measures can generally be assumed to be greatly

overestimated. In oystercatchers, unlike other nidifugous birds that do not feed their chicks, the presence of chicks can usually be ascertained with some certainty through observations of the parents.

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