BRILL

SEX ROLES IN THE AMERICAN OYSTERCATCHER

by

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Introduction

Most species of birds are monogamous (WELTY, 1975; LACK, 1968). However, the quality and quantity of the contributions by each sex to parental care, often appear, or are assumed to be unequal (WILLSON & PIANKA, 1963; TRIVERS, 1972; ALEXANDER, 1974; ALCOCK, 1975; DAWKINS, 1976). TRIVERS' (1972) concluded that differential investment by each sex in their offspring was 'molded' from the initial differential gametic contribution of the sexes. The parent with the least invested in the offspring would be favoured by natural selection to desert (TRIVERS, 1972). This idea remains largely unchallenged today, in part because it predicts the structure of parental behaviour so well in terms of individual selection. GLADSTONE (1979) disagreed with the shape of Triver's cumulative investment curves when considering monogamous colonial species in which there was documented evidence for forced extra-pair copulations. In these species GLADSTONE concluded that the curves of both parents should be more or less equal because the pre-copulatory costs for males in territorial defence, nest building, and courtship displays should be as high as the costs for females of producing eggs. Males should be more likely to desert if cuckoldry is suspected because then their gametic contribution to the brood will be smaller than that of the females.

Although agreeing in principle with TRIVERS' conclusions, DAWKINS & CARLISLE (1976) emphasized the importance of future expectations rather

than past expenditure in determining the selective value of desertion by the parent with the least investment. This was expanded in mathematical terms by MAYNARD SMITH (1977), who devised a simple model to predict when it would pay for one or the other parent to desert. The deserter gains nothing by desertion unless it can find another mate, so that the degree of breeding synchrony and hence probability of finding an un-mated bird in a population must be accounted for in predicting any evolutionarily stable strategy (MAYNARD SMITH, 1977). Recently BURGER (1981) suggested that, in monogamous birds, the contribution of the male would be greater than that of the female because the male would expend a great deal of energy guarding the female to prevent cuckoldry. Several workers have found that during the pre-laying period males invest heavi-ly in territorial or mate defence (MONTEVECCHI & PORTER, 1980; MOCK, 1979; PIEROTTI, 1981).

Recent interpretations of sexual differences in parental behaviour are based on TRIVERS' premise that the relationship between the sexes during the breeding season involves an ongoing assessment by each member of the pair of their respective contributions (MOCK, 1979; GLADSTONE, 1979; MONTEVECCHI & PORTER, 1980; PIEROTTI, 1981), and that each sex attempts to maximize the care its mate provides while minimizing its own contribution. The inherent conflict between the sexes falls on a con-tinuum of intensity ranging from those species where offspring are easily raised by one parent (no cooperation) to species where biparental care is required to raise the young (high degree of apparent cooperation). TRIVERS (1972) termed the apparent cooperation as 'complementarity' of sex roles.

Natural selection should act to favour an efficient use of energy by the parents which results in the greatest genetic contribution to future generations (FISHER, 1958). The need for energetic efficiency will underlie the structure of the apparent cooperation between members of a pair. Unbalanced contributions by either sex to parenting should be in-terpreted as differences in levels of energetic efficiency in performing dif-ferent tasks. Conflict between the sexes would be predicted for cir-cumstances where energetic stresses affect the adults (e.g. food shortages).

The young of the American oystercatcher (*Haematopus palliatus*) require extensive parental care, and adults therefore should have sex roles based on apparent cooperation. To evaluate the hypothesis that sex roles in oystercatchers are complementary, I examine sex roles at each stage of the breeding season. The prediction is that apparent cooperation should be most developed during the period of breeding when total energy ex-

penditure is greatest, and least developed when energy expenditure is lowest. Cooperative behaviour is evaluated by examining the pattern of provisioning the young, by each sex, and by measuring the degree of joint participation in antipredator and territorial displays. Specific predictions for the cooperative versus competitive models are presented in the text. Finally, I compare cumulative energy expenditure curves for each sex over the breeding season. The prediction is that curves for each sex will be equal if neither sex can raise offspring alone.

Methods

Study area.

Oystercatchers were studied on Wallops and Assawoman islands, (37°50′N, 75°35′W), the dredge spoil areas west of these islands, and the salt marshes and dunes around the Chincoteague Channel, Chincoteague, Virginia (37°55′N, 75°23′W). Birds were observed for a period of 14 months over 3 breeding seasons (March-July 1981, April-July 1982, March-July 1983).

Habitats on Assawoman, northern Wallops Island and Chincoteague Point were characterized by sand dunes and pebbled beaches, with predominant vegetation of beachgrass (*Ammophila breviligulata*). The predominant vegetation of dredge spoils and salt marshes consisted of *Spartina alternifolia* and *Disticylus spichata*, and small stands of *Iva frutescens* and *Baccharis halimifolia*. Nest sites on the dredge spoils and in the salt marshes were surrounded by *S. alternifolia*, *Salicornia virginica*, and *Cakile endentula* in various stages of growth.

Estimation of time budgets.

Observations were made from blinds set on the study areas, from offshore boats or across channels from a distance of at least 30 m from the nests, using a 20 X Bushnell Space-master telescope. From each location I was able to observe from two to seven pairs simultaneously. Individuals were banded with aluminum bands and unique colour-band combinations.

Observational data were collected in 10-min continuous-observation focal-animal sampling sessions (ALTMANN, 1974) within 4 to 6 hour periods. During chick-rearing the sampling periods ranged from 0.85 h to 12 h of continuous observations.

Birds were chosen randomly for sampling during these periods. The periods were systematically chosen with respect to the time of the day. On each successive day sampling began 4 to 6 h later at a different phase of the tide. This resulted in all birds being observed at different times of the day and at different phases of the tide. Although this sampling scheme produced an unequal number of samples of each bird it had the advantage that each bird was sampled in each division of daylight hours and each stage of the tide (*i. e.*, ebb, low, flood, and high tide). The exact nature of the effect of the tide cycle on the behaviour of American oystercatchers is given elsewhere (NOL, 1984).

Data were collected in the pre-laying, laying, incubation and chick-rearing stages. For subsequent analyses the pre-laying and chick-rearing stages were divided into early and late periods (early pre-laying: before 31 march; late pre-laying: 31 March to egg-laying, and all pre-laying periods before renesting; early chick-rearing: before 1 June; late chick-rearing: 1 June and later). During the first three of these stages I collected data using an electronic event decoder (International Instruments Inc.). Pulses generated by the decoder were amplified and recorded on a Uher tape recorder. I coded 57 behavioural categories which I was able to record without removing my eye from the eyepiece of the

telescope. The event decoder provided a record of the time of occurrence for all behavioural categories. The resulting tapes were played back into a computer in the Department of Zoology, University of Toronto, and condensed and organized through a series of customized programmes.

The 57 behavioural categories were reduced to 22 by (1) contextual criteria (e.g. standing or sitting with head back after a long period of standing quietly, with no in-truders nearby were condensed to the category resting), and (2) by running a transition matrix of the raw data through a multidimensional scaling programme (MDS) (SPENCE, 1978). Categories appearing in similar positions in a three-dimensional space were con-densed into one. For example, all preening activities had similar coordinates on all three axes of the MDS solution and thus I felt justified in considering any act of preening as simply preening. The matrix contained only those categories which I was not able to categorize by contextual criteria (e.g. shake head, scratch head, bob, etc.). The final categorization of behaviours is as follows: (1) Resting: Standing or sitting with head turned back and bill resting on back feathers. (2) Preening: Manipulating feathers with the bill. (3) Standing: Standing without head turned back. (4) Walking: Walking around without pecking at food items. (5) Searching for food and foraging: Walking while pecking and feeding. (6) Piping: The territorial display of the American oystercatcher (MILLER & BAKER, 1980), performed in flight or on the ground. (7) Sitting: Sitting without head back. (8) Bathing: Splashing water on feathers and preening while standing in water. (9) Brooding: Includes all nest directed activities: nest building, incubating or brooding chicks. (10) Feeding chicks: Presenting, and breaking up food for chicks. (11) Flying: Any flight except flights to and from feeding areas. (12) Crouching: Bending legs slightly to an almost sitting posture. (13) Piping displays: The frequency of piping. One piping display was considered terminated if there was a lapse of greater than 10 sec since the last act of piping. (14) Bobbing: Bobbing includes a summation of the frequency of each act of head up, look-up, bob, and single alarm notes. (15) Shaking: Shaking includes a summation of the frequency of each act of shake head, shake body, stretch leg, shake foot, scratch head, rub head, and yawn. (16) Chasing other species: Chasing or attacking any animal except conspecifics. Intruders or potential predators included willets (Catrotrophorus semipalmatus), fish crows (Corvus ossifragus), Northern harriers (Circus cyaneus), and laughing gulls (Larus atricilla). I considered chasing other species as anti-predator behaviour. (17) Chasing other oystercatchers. (18) Being chased by oystercatchers. (Total number of chases equals the sum of the number of (16), (17), and (18) above.) (19) Drinking: Drinking. (20) Off ter-ritory. The bird was seen to fly toward a feeding area, and while there was assumed to be feeding. Off territory is analysed as a separate variable from searching for food, the latter being foraging time only around the nesting territory. Off territory is assumed to equal feeding in all stages but chick-rearing. During chick-rearing I was always able to see birds leaving and returning with food and have therefore categorized these trips separately: (21) Foraging trips (a): The number of foraging trips while feeding chicks. (22) Foraging trips (b): The total amount of time spent away from the territory on a foraging trip during the chick-rearing period.

Estimation of energy budgets.

Basal metabolic rates (BMR) were calculated separately for males and females using the equation of ASCHOFF & POHL (1970) for non-passerines. Daily energy expenditure (DEE) of each sex was calculated by summing the product of the amount of time spent in each ac-tivity by the energetic cost of that activity in kj. I then took the mean of the DEE for all in-dividuals for each sex sampled on each day. The following caloric values were assigned to each activity: Resting = $1.24 \times$ BMR (ASCHOFF & POHL, 1970); Preening = $2.5 \times$ BMR; Standing = $1.5 \times$ BMR; Walking = $2.8 \times$ BMR (MAXSON & ORING, 1980); Searching for food = $3 \times$ BMR (ORIANS, 1961; CUSTER & PITELKA, 1972); Piping = $9.3 \times$ BMR (similar to fighting in *Actitis macrularia*, but less vigorous, MAXSON & ORING, 1980); Sitting =

1.24 × BMR (Aschoff & Pohl, 1970); Bathing = 2.5 × BMR (similar to preening); Incubation and brooding = 1.14 × BMR (females), 1.16 × BMR (males) (Ricklefs, 1974); Feeding chicks = 3 × BMR (similar to feeding); Flight = 15.6 × BMR (females), 14.9 × BMR (males) (King, 1974, cost of flight for females was multiplied by 1.06 to account for the 6% larger wing loading of female oystercatchers (2.41 g/cm, 2.28 g/cm, t = 3.48, n = 30 for each sex, $P < 0.001$). Crouching = 2.5 × BMR (similar to preening); Bobbing = 2 × BMR (between the values for preening and standing); Shaking = 2.5 × BMR (similar to preening); Chases = 5 × BMR (Orians, 1961; King, 1974); Foraging trips = 3 × BMR (Orians, 1961; Custer & Pitelka, 1972). The cost of egg-laying was taken as 8.9 kj/g egg wet weight (Ricklefs, 1974).

Cumulative mean daily energy expenditure curves were constructed separately for each sex by plotting cumulative DEE for 37 successive days in the pre-laying period, 10 days in the laying period, 26 successive days in the incubation period, and 53 successive days in the chick-rearing period. The number of days correspond to the approximate length of each stage. I often had data for many more days in each stage, so I arbitrarily chose the days that corresponded to the average dates of those stages for the population. This resulted in the inclusion of those days for which I had sampled the largest number of individuals, and therefore had the most accurate estimate of DEE.

In addition to the continuous-observation sampling I also observed 28 pairs of oystercatchers during the pre-laying period for lengthy periods (4.5 to 10 h) and recorded behaviour and location (on or off territory) every 10 minutes in a scan sampling scheme (Altmann, 1974). These scan samples were done to measure the degree of concordance between the behaviour of a bird and that of its mate. If the birds were off the territory, they were usually seen previously flying to their feeding territories. I considered that mates were behaving similarly if both members of the pair were sitting, standing, or preening, or both members were out of view, presumably both on the feeding territories. The pairs were considered to be behaving differently if one member was out of view and the other was in view, or they were both observed simultaneously performing different activities.

Statistical methods.

Time-budget data were tested for normality using the Kolmogorov D statistic (Sokal & Rohlf, 1981). If the data were found to be skewed, arcsin (for percentage data), and squareroot transformations (for frequency data) were applied (Sokal & Rohlf, 1981). For data that were still skewed after the transformations I used the Kruskal-Wallis distribution-free test to test for positive effects of either sex within each stage of the breeding season, or stage of the breeding season within each sex. Otherwise, I used parametric tests on the transformed data.

Data on the number and duration of foraging trips were normally distributed so standard parametric tests were used on untransformed data. Data on anti-predator behaviour were skewed, with a preponderance of zeros, so Spearman's rank correlation coefficients were used to test for relationships between members of a pair. Standard canonical discriminant analysis on transformed time budget data was used to describe sex roles (Pimental & Frey, 1978). Briefly, this analysis examines all behavioural variables simultaneously and calculates which variable or combination of variables best describes differences between the sexes or stages of the breeding season (see Cooley & Lohnes, 1971).

Additional analyses included the use of Pearson's correlation coefficient to test for correlations between morphological characters within a pair (*i.e.* assortative mating). A three-way contingency table was constructed to observe the pattern of provisioning the young by each sex and by different pairs. The table was analyzed using a log-linear model (Fienberg, 1970). This analysis calculates the frequencies of events that would be expected under all possible conditions of interaction using the classifying variables. In all analyses P-values < 0.05 were taken to be significant.

Results

A. Sampling effort.

A total of 1254 bird-hours of continuous observations were made during the pre-laying, laying, incubation and chick-rearing stages of the breeding season on from 18 to 42 individuals (Table 1). For the most part different individuals were sampled every year. In the following analyses individuals are used as sampling units. I omitted from the total sample all individuals for which I had fewer than 10 samples of 10-min observations.

B. Nesting and feeding areas.

Oystercatchers defend a territory that usually contains suitable nesting habitat. Nesting territories only rarely contain extensive areas with abundant suitable food. Most birds fly from 100 to 1000 m to traditional feeding areas where they may or may not defend the area around them against other oystercatchers. Aggressive interactions on the feeding areas were usually brief compared to those on the nesting areas. In the following time budgets feeding time is defined as all time off the nesting territory although it is possible that birds did not always feed while off the territory. It was never possible for me to follow individual birds to the feeding areas when they left the nesting territories. However, observations on the feeding areas suggest that birds spent most of their time there feeding.

C. Time of day differences.

I tested whether time of day had a significant effect on the time budgets of breeding oystercatchers. Females stood for slightly less time in the morning than in the afternoon or evening during pre-laying ($P<0.06$; Kruskal-Wallis test). They fed more during the afternoon during incubation ($P<0.04$), but showed no diel pattern in their behaviour during the chick-rearing stage. During incubation, males also fed more frequently in the afternoon ($P<0.04$). In the chick-rearing stage males brooded the chicks less during the afternoon than the morning or evening ($P<0.05$). There were no other differences in behaviour by time of day for either sex.

D. Sex differences and stage of breeding.

The proportion of time spent by either sex in each activity and the frequencies of activities were compared within each stage of breeding. Dur-

TABLE 1. Sampling effort expressed as number of focal-animal samples and total number of hours observed by sex and stage of breeding cycle

	Sex	Number of birds	Number of 10-min samples	Mean time (h)	Total number of hours	Range of number of hours/bird
Prelaying	F	26	402	2.5	67	0.75-5.2
	M	27	384	2.2	64	0.70-5.8
Laying	F	19	384	3.5	64	0.76-7.5
	M	16	312	3.1	52	0.80-9.1
Incubating	F	26	456	2.8	76	0.72-6.4
	M	24	390	2.5	65	0.73-5.3
Chick-rearing	F	19	$-^1)$	22.1	421	0.85-105.3
	M	23	$-^1)$	19.3	445	0.85-104.7

$^1)$ During chick-rearing sampling periods were continuous and varied from 0.85 h to 12 h.

TABLE 2. Proportion of time spent and frequency of activities by male and female American oystercatchers during the pre-laying stage

Activity$^1)$	Females	Mean$^2)^3)$ rank	Males	Mean$^2)^3)$ rank
Resting	18.8	27.5	18.6	26.5
Preening	7.0	23.6	7.3	30.3
Standing	17.4	28.0	16.7	26.0
Walking	4.9	26.3	4.6	27.7
Searching for food	10.9	29.5	9.4	24.6
Piping	0.7	29.6	0.5	24.5
Sitting	7.0	28.0	6.9	26.1
Bathing	0.2	25.9	0.2	28.1
Nest-building	1.4	26.7	1.4	27.3
Flying	1.3	28.9	0.9	25.2
Crouching	0.1	27.2	0.1	26.9
Piping frequency	0.07	28.0	0.07	26.0
Bobbing	0.2	29.0	0.2	25.1
Shaking	0.15	25.5	0.17	28.5
Chase others	0.003	24.9	0.009	29.0
Chase oystercatchers	0.002	25.3	0.005	28.7
Chased by oystercatchers	0.0007	26.5	0.002	27.5
Drinking	0.0008	27.5	0.00	26.5
Chases (total)	0.005	24.6	0.016	29.3
Off territory (foraging)	30.4	26.5	33.4	27.5

$^1)$ Numbers represent percentages when data based on porportions, and number of acts/100 sec, when data are based on frequencies.
$^2)$ Rank is Wilcoxon's rank sum.
$^3)$ No significant differences between males and females for any activity.

ing pre-laying the behaviour of males and females was similar for all activities (Table 2). Individuals showed a high degree of concordance between their own behaviour and that of their mates. In 3326 of 3603 scans (92%) both members of a pair were behaving similarly, and 277 (8%) each member of the pair was behaving differently.

I analysed whether this similarity of behaviour between the sexes occurred both early and late in the pre-laying period, because the later period should contain the actual period of follicle formation (RICKLEFS, 1974). A rough estimate of the length of this period for renesting American oystercatchers was about 10 days (n = 8). During the early pre-laying period females spent slightly more time searching for food and piping than did males ($P < 0.09$). Late in pre-laying there were no differences between the behaviour of males and females. Significant differences between early and late pre-laying were found in seven activities of females and five activities of males (Fig. 1).
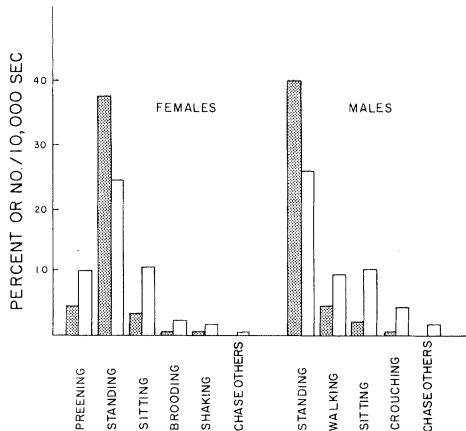
Fig. 1. Time spent in different activities by males and females early (stippled bars) and late (open bars) in the pre-laying stage.

During the laying period males stood more than females, tended to crouch less, and chased other oystercatchers more (Table 3). During incubation, the number of differences in the time-budgets between the sexes increased. Males rested more, preened more, sat more, flew slightly more, incubated less, performed more comfort movements, and chased oystercatchers more than females (Table 4).

During the chick-rearing period the behaviour of the sexes was again similar (Table 5). Males performed all activities except chasing at about

TABLE 3. Proportion of time spent and frequency of activities by male and female American oystercatchers during the laying stage

Activity[1])	Females (n = 19)	Mean[2]) rank	Males (n = 16)	Mean[2]) rank	Significance
Resting	13.6	17.7	13.6	18.3	n.s.[3])
Preening	7.1	16.6	9.7	19.7	n.s.
Standing	15.9	14.9	24.4	21.7	$P < 0.0527$
Walking	5.2	15.7	7.7	20.7	n.s.
Searching for food	18.8	16.8	22.2	19.4	n.s.
Piping	0.9	17.3	1.0	18.8	n.s.
Sitting	5.2	19.1	2.4	16.7	n.s.
Bathing	0.2	17.2	0.3	18.9	n.s.
Incubating/brooding	38.8	20.5	26.3	15.0	n.s.
Flying	0.7	16.4	1.0	19.9	n.s.
Crouching	0.8	20.3	0.07	15.3	$p < 0.089$
No. of piping	0.04	16.8	0.05	19.4	n.s.
Bobbing	0.07	20.0	0.08	15.6	n.s.
Shaking	0.05	16.5	0.08	19.8	n.s.
Chase others	0.004	16.2	0.015	20.1	n.s.
Chase oystercatchers	0	15	0.016	21.6	$P < 0.0044$
Chased by oystercatchers	0	17.5	0.0012	18.6	n.s.
Drinking	0	18.4	0	17.5	n.s.
Total no. of chase	0.004	15.1	0.033	21.5	$P < 0.038$

[1]) Numbers represent percentages when data based on proportions, and number of acts/100 sec, when data are based on frequencies.
[2]) Rank is Wilcoxon's rank sum. [3]) n.s. means not significant.

the same frequency or duration as females. Males chased and were chased by other oystercatchers and were involved in more chases overall than were females.

E. Feeding trips.

I observed foraging trips of 19 pairs, but for the following analyses I use only data from ten pairs for which I have greater than 10 foraging trips during the chick-rearing period. Foraging trips are assumed to be the most costly of activities for American oystercatchers because of the distances flown to feeding areas and because these trips are frequent during the chick-rearing stage.

The pattern and frequency of foraging trips might be expected to differ if the pair is engaged in a conflict over raising the young, or if the relationship within the pair is based on apparent cooperation. For example, if, after each foraging trip to provision the young, the male hesitates

TABLE 4. Proportion of time spent and frequency of activities by male and female American oystercatchers during the incubation stage[1])

Activity	Females (n = 26)	Mean rank	Males (n = 24)	Mean rank	Significance
Resting	5.5	20.7	8.9	30.7	$P < 0.016$
Preening	7.2	20.7	13.4	30.7	$P < 0.016$
Standing	14.4	22.8	15.8	28.5	n.s.
Walking	5.3	24.5	5.7	26.6	n.s.
Searching for food	9.2	23.7	12.4	27.4	n.s.
Piping	0.8	24.8	0.9	26.3	n.s.
Sitting	1.5	21.9	4.4	29.4	$P < 0.058$
Bathing	0.1	22.7	0.3	28.5	$P < 0.072$
Incubating/brooding	56.9	31.3	38.7	19.2	$P < 0.0036$
Flying	1.0	23.5	1.1	27.6	n.s.
Crouching	0.2	23.9	0.2	27.3	n.s.
No. of piping	0.16	24.3	0.07	26.8	n.s.
Bobbing	0.06	24.8	0.17	26.3	n.s.
Shaking	0.20	21.1	0.32	30.3	$P < 0.028$
Chase others	0.01	27.0	0.01	23.8	n.s.
Chase oystercatchers	0.004	20.4	0.02	31.0	$P < 0.003$
Chased by oystercatchers	0.0002	23.9	0.0045	27.2	n.s.
Drinking	0.034	25.8	0.028	25.2	n.s.
Total no. of chases	0.0165	22.8	0.027	28.5	n.s.

[1]) Superscripts same as in Table 3.

before leaving for the next trip in anticipation that the female will take the initiative and leave, and if the female, after returning employs the same strategy, then the system should fixate at alternation of foraging trips (*i.e.* tit for tat, AXELROD & HAMILTON, 1981). This result should occur only if there is a cost associated with leaving the young unattended. The cost provides the incentive for a 'returner' to return before the 'leaver' leaves due to its own food stress.

On the other hand if energetic considerations determine the parents' pattern of foraging for the young then the number of trips by males and females should be adjusted so as to minimize overall energy expenditure by each member of the pair and to maximize the amount of food brought back to the chicks. In the following analyses I assume that males and females forage with equal intensity. I compare the length of the foraging trips, the number of trips per time spent feeding the young, and the length of time since the last foraging trip by the returner and the leaver.

The length of time between the return of a male from a foraging trip and the leaving of a female (M-F) is shorter than the opposite pattern of a

TABLE 5. Proportion of time spent and frequency of activities by male and female American oystercatchers during the chick-rearing stage[1])

Activity	Females (n = 19)	Mean rank	Males (n = 23)	Mean rank	Significance
Resting	2.8	22.4	2.8	20.8	n.s.
Preening	3.9	23.4	2.7	20.0	n.s.
Standing	37.4	23.2	31.4	20.1	n.s.
Walking	5.3	20.7	5.9	22.2	n.s.
Searching for food	24.7	21.9	23.2	21.2	n.s.
Piping	2.2	19.5	2.6	23.1	n.s.
Sitting	4.7	22.5	6.9	20.7	n.s.
Bathing	0.05	22.3	0.3	21.7	n.s.
Brooding	7.9	24.1	3.1	19.4	n.s.
Flying	0.65	20.8	0.8	22.0	n.s.
Crouching	0.45	22.9	0.23	20.4	n.s.
No. of piping	0.064	20.1	0.081	22.7	n.s.
Bobbing	0.029	19.9	0.044	22.8	n.s.
Shaking	0.029	22.6	0.025	20.6	n.s.
Chase others	0.0097	20.9	0.010	22.0	n.s.
Chase oystercatchers	0.0068	18.2	0.018	24.2	$P < 0.084$
Chased by oystercatchers	0.0057	18.2	0.014	24.2	$P < 0.079$
Drinking	0.0043	22.1	0.0037	21.0	n.s.
Total no. of chases	0.022	17.8	0.042	24.5	$P < 0.054$
Feeding chicks	7.8	20.7	7.9	22.2	n.s.

[1]) Superscripts same as in Table 3.

TABLE 6. Lengths of foraging trips, rate of foraging trips and lag intervals between trips for male and female American oystercatchers

Variable	Males (n = 548)	Females (n = 363)	Significance[1])
Trip length (min)	10.2	9.1	$P < 0.068$
Trip rate (# trips/100 min feeding time)	2.4	1.9	$P < 0.054$
Lag since last trip by same sex (min)	15.4[2])	12.0[3])	$P < 0.039$
Lag since last trip by mate (min)	13.4[2])	9.6[3])	$P < 0.001$
Lag since last trip (min)	14.3	10.9	$P < 0.078$

[1]) Significance tested with Wilcoxon two-sample test.
[2])[3]) Significant differences between values indicated by different superscripts.

returning female followed by a leaving male (F-M) (Table 6). The time between two successive trips by the male (M-M) is about one-third longer than the time between two successive trips by the female (F-F) (Table 6). The time between successive trips is more variable for females than for males (S.D.; F-F trips, 1.88, M-F trips, 2.02; M-M trips, 1.81,

TABLE 7. Number of foraging trips during the chick-rearing stage, preceded by same sex, or opposite sex in 10 pairs of oystercatchers

Pair	Trip preceded by:	Trip followed by:	
		male	female
A4	Male	9	8
	Female	9	13
I1	Male	20	3
	Female	4	4
I4	Male	12	13
	Female	12	8
20	Male	58	33
	Female	32	34
N2	Male	14	8
	Female	7	5
PD	Male	20	13
	Female	13	18
PE	Male	37	31
	Female	32	21
PF	Male	48	22
	Female	16	13
PG	Male	33	17
	Female	16	18
18	Male	23	11
	Female	12	7
Total	Male	274	159
	Female	153	141

$\chi^2 = 9.44$; $P < 0.005$.

F-M trips, 1.82). Regardless of which member of the pair took the previous trip the male waits longer before leaving on his trip than does the female. For females, the length of the wait also is not dependent on who took the previous trip. These results suggest that it is internal motivation rather than past events which trigger when a bird will leave on a foraging trip. Overall, males make about 25% more foraging trips per unit time than do females (Table 6). Males also make slightly longer foraging trips than do females (Table 6).

I then analysed the distribution of feeding trips within an observation period (Table 7). M-M trips predominated and F-F trips were higher than the number expected by chance (log-linear model, FIENBERG, 1970), and this pattern was more or less consistent among pairs. This result suggests that trips by males and by females were clumped in time. I then plotted the rate of trips by each sex as a function of the time of day. Females made proportionally more trips later in the day than did males.

Males appeared to spread the timing of their trips evenly throughout the
day, with the exception of early in the day when both males and females
made the greatest number of trips (Fig. 2). Within all pairs observed,
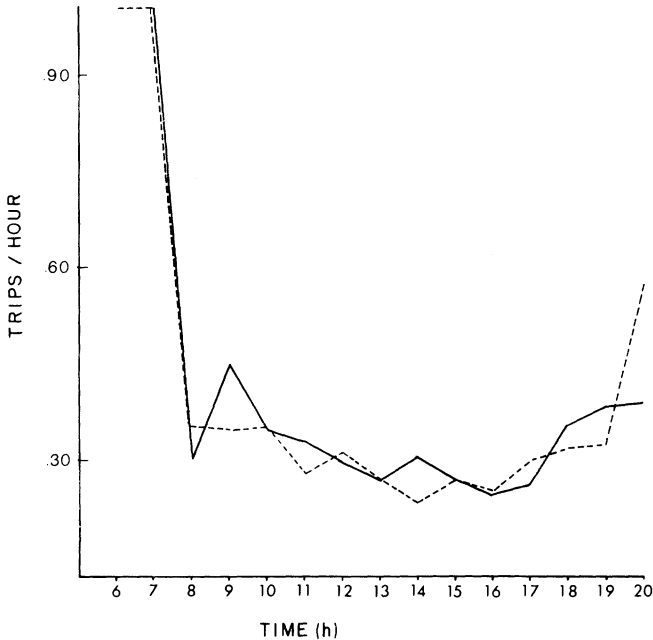males made more foraging trips than females.

Fig. 2. Average hourly rates of foraging by males (solid lines) and females (broken lines)
to provision the young. Time is based on a 24 h clock.

F. Anti-predator and territorial behaviour.

Anti-predator behaviour - 'cooperative' model.

If both members of a pair have an equivalent 'interest' in preventing nest
predation and if participation by both members is more likely to cause
predators to find the nest (as in incubation), then one would expect the
member of the pair that contributes less to incubation to chase more and
there should be no correlation between the occurrence of chasing by one
member of the pair and the occurrence of chasing by its mate. During
chick-rearing there should be no difference in the number of chases of
potential predators between the sexes, and a positive correlation between
the occurrence of chasing by one member of the pair, and chasing by its
mate (Table 8).

Anti-predator behaviour - 'uncooperative' model.

By contrast, if members of the pair have different interests, then during incubation and early in chick-rearing before chicks are fully mobile there should be a correlation between the occurrence of chasing by one bird and the occurrence of chasing by its mate. This should be true if the risk of predation of the eggs or brood is higher when there is no attempt to chase off predators, than when the predators are being chased off and the eggs or brood are uncovered. During chick-rearing when there is little brooding, but a high risk of predation (after the chicks are mobile) the correlation by occurrences of chasing between mates should be high,

TABLE 8. Predictions for degree of joint participation between members of a pair, in territorial and anti-predator behaviour, under two models

| Stage | Behaviour | Degree of joint participation under model: | |
		Cooperative	Uncooperative
Incubation	anti-predator	low	high
	territorial	high	low
Chick-rearing	anti-predator	high	high
	territorial	high	low

because regardless of their motivation, each bird will benefit from adequate protection of young from predators. As the chicks get older and the risk declines, then there should be less correlation between members of the pair, and a large variance in chasing behaviour as one or the other member tries to minimize their respective contributions.

Territorial behaviour - 'cooperative' model.

During incubation, if both members of a pair have an equal interest in preventing intrusions by conspecifics on their territory and if the occurrence of territorial acts does not affect the probability of loss of young to predators then there should be a correlation between the occurrence of territorial acts by one member of the pair and the occurrence of these acts by its mate. During chick-rearing, if parental contributions are equal, then territorial acts should be equal and the occurrences correlated. If, however, the chick-rearing contributions are unequal, the parent that has 'more time' should contribute more to territorial activities than its mate.

TABLE 9. Spearman rank correlation coefficients within pairs of the American oystercatcher on the incidence of territorial and anti-predator behaviour during incubation, and early and late chick-rearing stages

Activity		Incubation (n = 133)	Early chick-rearing (n = 117)	Late chick-rearing (n = 85)
Bobbing	r	0.35	0.55	0.75
	P	0.001	0.0001	0.0001
Piping (sec)	r	0.21	0.70	0.81
	P	0.014	0.0001	0.0001
Number of	r	0.18	0.60	0.73
piping displays	P	0.036	0.0001	0.0001
Chasing non-	r	-0.09	0.38	0.46
conspecifics	P	n.s.[1])	0.0001	0.0001
Chasing	r	0.04	0.41	0.31
conspecifics	P	n.s.	0.0001	0.0043
Chased by	r	0.00	0.40	0.22
conspecifics	P	n.s.	0.0001	0.0441
All chases	r	0.10	0.27	0.27
	P	n.s.	0.0037	0.0134

[1]) n.s. means not significant.

Territorial behaviour - 'uncooperative' model.

If members of the pair have unequal interests during incubation there should be a strong correlation in the frequency of their territorial behaviour, if the function of the territory is to protect a nest site, because this behaviour is clearly in the interests of both members of the pair. During chick-rearing, if the function of territorial behaviour becomes less important there should be little correlation in behaviour of members of a pair. Each sex should avoid territorial behaviour if the mate is there to do it, and on average each sex should engage in it equally, but not simultaneously.

Correlations to measure the joint participation in the same activities by mates were computed pairwise for the three categories of chasing behaviour, piping, the number of piping displays and bobbing in the incubation and chick-rearing stages. Spearman's rank correlation coefficients between the frequency of acts given by males and females during a single sampling session are given in Table 9. Correlations between members of the pair were significant and high for all acts when the pair had chicks. During incubation, correlations were significant only for piping, number of piping displays and bobbing. Each member of the pair

appeared to act independently when chasing conspecifics or potential predators. These results support the pattern of correlations predicted by the cooperative models (Table 8).

G. Effect of stage of breeding.

For females, the time spent in every activity except the amount of time spent walking changed over the course of the breeding season (Fig. 3). For males, walking, the number of piping displays, and the number of
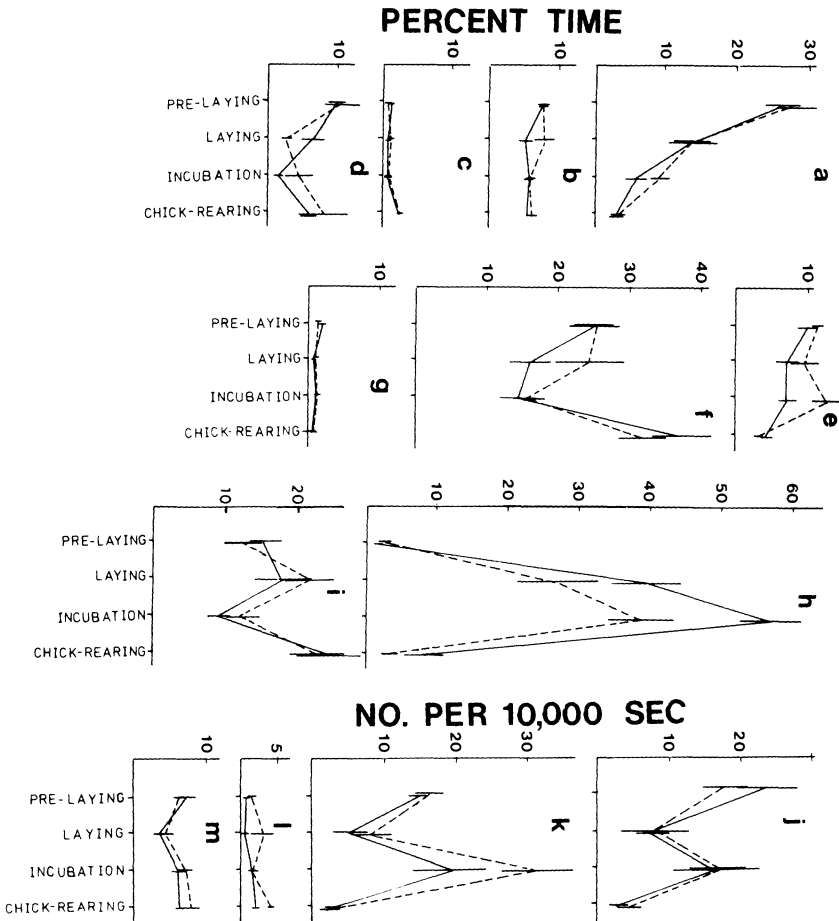

Fig. 3. Time spent and frequency of activities in four stages of the breeding season by male (dashed lines) and female American oystercatchers (solid lines). Activities are coded as follows: resting (a), walking (b), piping (c), sitting (d), preening (e), standing (f), flying (g), brooding (h), searching for food (i), bobbing (j), shaking (k), chases (l), and piping frequency (m).

chases directed at other species all stayed constant and occurred random-
ly over the four stages of the breeding cycle. This latter fact lends some
credence to the assumption that the number of potential predators in the
study area remained roughly constant over the breeding cycle.

H. Sex roles and behavioural repertoire.

To discuss sex roles strictly in relation to time spent in one activity
without regard to preceding, concurrent or following activities over-
simplifies the definition of a sex 'role'. A sex role should be viewed as a
complex interaction of various components of the full behavioural reper-
toire of an individual. For example high negative correlations were found
between incubating and sitting because the activities are mutually ex-
clusive. Hence it is misleading to look at each component of the time
budget in isolation. Therefore I have chosen to describe the sex roles
through multivariate analysis, which considers all variables simul-
taneously (COOLEY & LOHNES, 1971).

TABLE 10. Mahalanobis distances between centroids of sex and stage of
breeding groups, and associated probabilities for equality[1])

	Pσ	P♀	Lσ	L♀	Iσ	I♀	Cσ	C♀
Pσ	0	—	—	—	—	—	—	—
P♀	0.94	0	—	—	—	—	—	—
Lσ	1.79***	2.09***	0	—	—	—	—	—
L♀	2.45***	2.52***	1.45	0	—	—	—	—
Iσ	2.84***	3.01***	1.92	1.82	0	—	—	—
I♀	3.63***	3.80***	2.56***	1.84	1.81***	0	—	—
Cσ	3.76***	3.82***	3.86***	4.32***	4.64***	5.05***	0	—
C♀	3.38***	3.34***	3.25***	3.52***	4.12***	4.32**	1.51	0

[1]) Stages of the breeding season are indicated as prelaying (P), laying (L), incubation (I)
and chick-rearing (C). *** = $P < 0.0001$, ** = $P < 0.001$, * = $P < 0.01$.

Examination of the Mahalanobis' distances among groups illustrates
that differences between the sexes at any stage were less than those within
each sex from one breeding stage to the next (Table 10). All distances ex-
cept that between pre-laying males and pre-laying females were signif-
icantly different than zero. The distance a female 'travels' in multivariate
space from the pre-laying to the laying stage (2.52 units) is not much
greater than the distance travelled by the male (1.79 units). Intuitively it
would seem that females are making a bigger transition because of the

demands of egg-laying. Males, however, begin assisting in incubation as soon as the females start to incubate (after the laying of the second egg), and males then consistently perform the same proportion of incubation throughout this breeding stage. Hence the males' place in discriminant space is also affected by the onset of laying (Fig. 4). The largest change in position occurs between incubating and chick-rearing birds of either sex. This is because the proportion of time in nearly all activities for each sex changes considerably (Tables 4 and 5). The positions of each group plotted in discriminant space (Fig. 4) also illustrate that distances among stages are always greater than the distances between the sexes at any one stage.
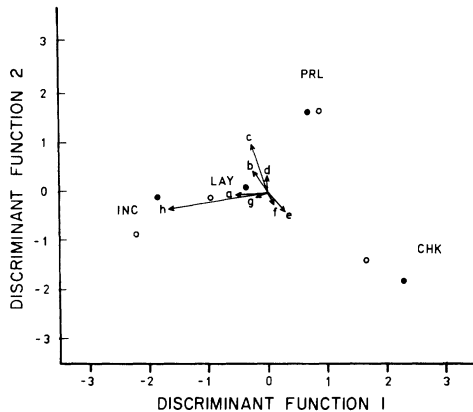

Fig. 4. Plot of group centroids of male (solid circles) and female (open circles) American oystercatchers showing sex roles during pre-laying (PRL), laying (LAY), incubation (INC) and chick-rearing (CHK). Vectors indicate the relative importance of individual variables to the sex roles. Variables are identified as follows: shaking (a), preening (b), resting (c), bobbing (d), piping (e), chased by oystercatchers (f), standing (g), incubating/brooding (h).

When group centroids and the variable vectors are plotted on the first two canonical axes, it is possible to determine which variable contributes most to the position of the group in discriminant space. The vectors orient in one of three directions (Fig. 4). The vectors for incubation, comfort movements and standing all orient toward incubating birds. Resting, preening and bobbing and the vectors representing piping and being chased by other oystercatchers separate chick-rearing birds from those incubating or pre-laying. Only preening, resting and piping make substantial contributions to group separations.

TABLE 11. Costs (in kj/14 hr) of activities by male and female American oystercatchers, used in constructing energy expenditure curves

Cost (kj/14 hr)	Males	Females
Resting	146.7 (1.24)	160.1 (1.24)
Preening	295.9 (2.5)	323.1 (2.5)
Standing	177.7 (1.5)	193.9 (1.5)
Walking	331.1 (2.8)	361.6 (2.8)
Searching for food	354.9 (3.0)	387.5 (3.0)
Piping	1100.2 (9.3)	1201.3 (9.3)
Sitting	146.7 (1.24)	160.1 (1.24)
Bathing	295.9 (2.5)	323.1 (2.5)
Incubating/brooding	137.1 (1.16)	148.1 (1.14)
Flying[1])	1758.9 (14.9)	2012.3 (15.6)
Crouching	295.9 (2.5)	323.1 (2.5)
Bobbing	236.6 (2.0)	258.3 (2.0)
Shaking	295.9 (2.5)	323.1 (2.5)
Chasing	1758.9 (14.9)	2012.3 (15.6)
Drinking	295.9 (2.5)	323.1 (2.5)
Out of view/Foraging trips	354.9 (3.0)	387.5 (3.0)
BMR	118.3	129.2

The multiple of the basal metabolic rate (BMR) is in parentheses.
[1]) The amount of time spent flying includes the length of time to fly to and from foraging areas. $\bar{x} = 35.3 \pm 14.8$ sec. $N = 14$ territories.

I. Sexual dimorphism.

Female American oystercatchers on average weigh about 19% more than males (NOL et al., 1984). In all other mensural characters, females are significantly larger (unpublished data). American oystercatchers do not seem to mate assortatively with respect to size. Of 13 Pearson correlations computed on characters of mated birds, none were significantly correlated between members of a pair. The plots of the values of each character by pair were examined. It was clear that each sex was as likely to be mated with a bird with a large measure of a particular character, as a small. Only for the character bill length did all 15 females have larger bills than their mates.

Differences in morphology between males and females may account for differences in the time budgets between the sexes. The energetic costs of most activities are measured as a multiple of the basal metabolic rate (BMR) expressed as kj per unit time. Since BMR is derived from weight, then the BMR of females will be greater than that of males, and hence for most activities the cost in kj per unit time will be greater for females. The cost expressed as a multiple of the BMR will usually be similar for each

sex. However the costs of incubation and flying (and all activities involving flying) depend on a multiple of BMR but are mediated by a range of other variables which effect the efficiency of performing those activities. The energetic cost of incubation is a negative power of body weight and includes the cost of raising the temperature of the clutch from ambient (taken here as 20°C) to 35°C. Consequently it is slightly more expensive for a male to incubate a clutch of 150 g (three eggs, NOL et al., 1984) than it is for a female. Conversely, the cost of flight depends on relative wing loadings (g/cm²). The lower the wing loading, the more efficient is flight. Males have a significantly lower wing loading than do females (see Methods). This difference in efficiency (6%) is multiplied by the cost of flying at a certain body weight, to get the relative costs of flying by males and females. The relative costs of various activities (Table 11) were compared with the amount of time spent in these activities (Tables 2-5). During incubation males incubate 18% less than females. The cost of incubation for males is 2% more than the cost for females. Males make 26% more foraging trips to provision the young than do females (Table 6), and the cost of flight for males is 15% less than for females. Therefore only part of the difference in sex roles can be accounted for by differences in the costs of these activities for each sex.

J. Energy expenditure over breeding cycle.

Parental investment was measured using energy expenditure as an index. I have converted the time budget data to costs in terms of kj per day, and accumulated the daily energy expenditure over the breeding season (Fig. 5). In so doing I have attempted to duplicate TRIVERS' original cumulative investment curves for monogamous species (TRIVERS, 1972, p. 145). Two assumptions underlie these curves: the first is that cumulative energy expenditure is a measure of parental investment, and second, every act a bird does during the breeding season is related to fledging offspring. Presumably these assumptions are appropriate for all birds that spend time on a nest territory, rather than time simply feeding or resting (as in non-breeding birds).

   In examining the curves it is clear that large differences do not occur between the sexes at any stage of the breeding cycle. As was reported above, the sexes expended about equal amounts of energy towards their future offspring during pre-laying. Just prior to the estimated time of follicle formation the rate at which females expended energy appeared to go up relative to males, and by the end of the laying period females had
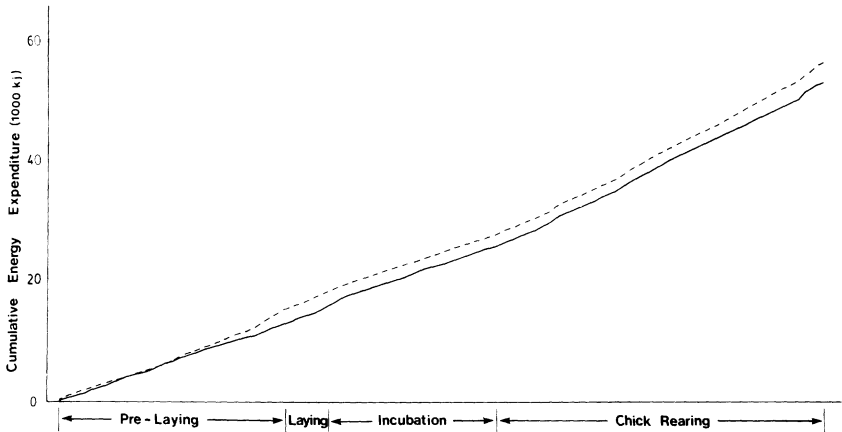
Fig. 5. Cumulative daily energy expenditure (kj) for male (solid line) and female American oystercatchers (dashed line) over the breeding season.

expended about 16% (17,985 vs 15,569 kj) more energy than males, mostly due to the costs of egg-laying. This 16% difference in 'invest-ment' is maintained until the start of incubation when males raise slightly their rate of energy expenditure and by the end of incubation the dif-ference between males and females has narrowed to about 5%. Both sexes increase their rate of energy expenditure equally during the chick-rearing period over that during incubation, except during the last 10 days when chicks are very near to fledging (about 43 days). At this time the rate of energy expenditure of the female increases relative to that of the
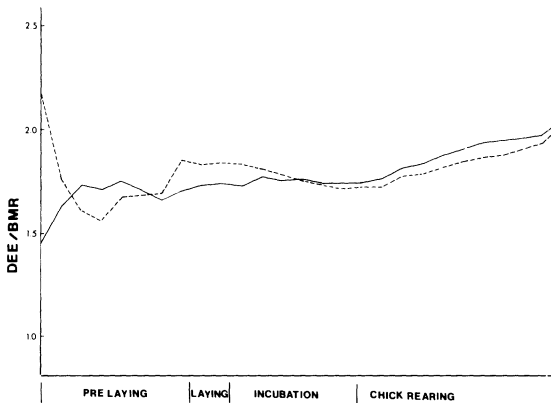

Fig. 6. Daily energy expenditure (kj) as a proportion of basal metabolic rate for male (solid line) and female (dashed line) American oystercatchers over the breeding season.

male and the final total energy expenditure of the female is slightly higher than that of the male (54,647 kcal *vs* 51,410 kcal). With respect to the percentage of cumulative daily BMR (Fig. 6), males in the pre-laying stage expended a larger multiple of their BMR than did females. The situation is reversed during laying and through the first 15 days of incubation, but thereafter both sexes expend about equal and steadily increasing multiples of their daily BMR's through to the period when chicks are present. At fledging, both parents are expending an average of two times their cumulative daily BMR to feed the chicks.

Discussion

It is clear from the results of this study that the interaction between the sexes was not adversarial. Complementarity between mates, through coordinated provisioning of young, and territorial and anti-predator defense, was well-developed. Complementarity was particularly well-developed during chick-rearing, when energy expenditure by each sex was highest.

I did not specifically test whether oystercatchers could raise young alone, but I suggest that it is very unlikely. This is because of both the spatial relationship between nesting and feeding areas, and the high predation rates in this species (NOL, 1984). To feed chicks, one parent must be off the territory for about ten minutes for each food item. The other parent is then required to tend the young. Predation and starvation are the two major causes of chick loss, and in general, reproductive success is low (*i.e.*, 5-10% of population fledge young in any one year, NOL, 1984). Given these ecological restrictions, one parent successfully raising young to independence is unlikely.

A basic condition for the evolution of cooperative rather than adversarial interactions between parents is that the young cannot be raised successfully by one parent alone. The probability of finding another mate after deserting should only be an important factor (vis. MAYNARD SMITH, 1977) in influencing a birds 'decision' to desert if there is a sufficient probability that the deserted mate can raise the offspring by itself. Otherwise the former decision becomes irrelevant.

Complementarity of parental abilities (TRIVERS, 1972) should evolve when bi-parental care is necessary to successfully rear young. The sex with the choice of mate should choose a mate that not only provides genes that promote the survival of the offspring (MAYNARD SMITH, 1956), but also provides parental care so the offspring are raised efficiently.

Complementary *vs* similarity.

Pre-incubation.

Behaviour patterns were extremely similar, but not complementary dur-
ing pre-laying, and this was presumably because males gaurd females to
protect the male's paternity. Increased chasing of conspecifics by males
during laying suggests that cuckoldry may occur. Although I never
observed cuckoldry, the following observation was made in 1979 by A. J.
BAKER. Both members of one pair returned on schedule but only the
female of a neighbouring pair returned. For 10 days the male of the first
pair copulated both with its mate and with the lone female. The mate of
the lone female then returned and the first male discontinued the extra-
pair copulations. During the period when cuckoldry is likely to occur
(during the late pre-laying and early laying periods) mates stay very close
to each other and are usually in the same place. This also implies mate
guarding. Are there males in the population who could possibly be a
threat to paternity? During the pre-laying period in one year of the study
(1982) seven mated males were removed from a stretch of beach adjacent
to the main study area. In June of that year six of the females were still
unmated, which suggests that there were few excess males in the popula-
tion, or if there were they chose not to pair with these unmated females.
In July of each year it was common to observe single birds land on the
territories of pairs of oystercatchers and engage in prolonged piping
displays with the residents. These single birds, if males, were more likely
scouting for a place in the subsequent years' breeding population than at-
tempting to cuckold existing territory holders. Cuckoldry may be rare,
but the costs of being cuckolded (particularly considering the high cost of
parental care) so great as to warrant the intensive precautions seen here.
Mate guarding by the female to reaffirm the pair bond is probably im-
plicated in the observation that after a piping bout in the air during the
pre-laying stage, the pair almost always copulated, with the female ap-
parently initiating the copulation (pers. obs.).

Incubation.

During incubation, sex roles and energy expenditure by each sex diverge
from that observed during pre-laying and laying. At least a part of the
difference in roles is accounted for by differences in the relative efficien-
cies with which each sex performs different tasks. Males spend more time
watching for predators, and females spend more time incubating, and it
costs females less per unit time to incubate, hence, the roles of each sex

are complementary. Selection should favour some form of bi-parental in-
cubation if high losses of eggs due to predation or exposure occur when
the nest is unattended. As well, selection should act against birds which
are overly exploitive of their partners during incubation if their partners
are in correspondingly poorer condition for chick-rearing, because of the
exploitation (NIEBUHR, 1983). Only rarely did I see conflict at the nest
over changeovers. Perhaps, as hypothesized for herring gulls (*Larus argen-
tatus*), the bird incubating may try to accommodate to the schedule of its
mate (NIEBUHR, 1983) if this accommodation increases the probability of
its mate surviving to the next breeding season (COULSON, 1966; MILLS,
1973).

Chick-rearing.

Complementarity should be most evident during energetically costly
periods in the breeding cycle. While raising young, the activities of
members of a pair were highly complementary. Males, which can fly at
less energetic cost, took more trips to provision young, whereas females
spent more time standing near the brood. Both sexes, at the end of the
chick-rearing period, had expended about equal amounts of energy, and
there was no evidence to suggest that either parent was defaulting in its
obligations to parental care. Foraging trips by each sex, were sometimes
so frequent, that in all pairs observed, the young rejected food presented
by the parents.

   Oystercatcher chicks, on hearing the alarm notes of their parents, flee
to the nearest cover and crouch (LIND, 1965), unless they are less than
one week of age when they simply crouch in place. The most effective
anti-predator behaviour for maintaining the safety of the brood early in
chick-rearing, would be for one parent to stay near the brood if the
predator strays too close, or otherwise participate in the anti-predator
chases by the mate. Later in chick-rearing, the most effective behaviour
would be for both parents to chase off or distract the potential predator.
Standing near the site where the chicks last were might increase the prob-
ability of discovery of the chicks by the predator. Hence, from the early to
late periods of chick-rearing, the coordination of anti-predator
behaviours between mates increased. The coordination of territorial
defence between mates also increased, possibly reflecting the need for
larger or more exclusive feeding areas with larger chicks.

   Sex roles in American oystercatchers diverge during late chick-rearing
when males perform more piping bouts with intruding oystercatchers
than do females. Females spend more time than males near the chicks.

Females are still involved with territorial behaviour at this time but participate for shorter periods. Presumably the function of the territory is still important to both sexes, but because the chicks are grown, the number of foraging trips decreases and the threat of predation is less. Therefore there is less need for both adults to spend all their time caring for the chicks. After the chicks fledged, the male territory owner was often seen on the territory defending it vigorously from conspecifics, while the chicks and female were away on the foraging areas. The female and chicks would usually return in the evenings. Defending the territory may have an important function in securing the territory for the next breeding season. It is late in the season when the threat from single 'floaters' appearing on the territory becomes most intense and it may be that this division of parental effort is again strictly following functional needs.

The chick-rearing period (especially near the end), is the time when deserters in the pair bond are most likely to be observed. This is because the mate that continues with the parental duties has so much to lose if it does not continue (TRIVERS, 1972), and the defaulter would likely get away with minimal fitness cost, and would gain if it decreased its own probability of mortality. Defaulting by one parent at the end of this period is common in several monogamous shorebirds that do not have extensive parental care (e.g., lapwing (Vanellus vanellus), green sandpiper (Tringa ochrops), common sandpiper (Actitis hypoleucos), (BANNERMAN, 1961); stilt sandpiper (Micropalama himantopus) (JEHL, 1973); greenshank (Tringa nebularia) (NETHERSOLE—THOMPSON, 1951); ruddy turnstone (Arenaria interpres) (NETTLESHIP, 1973); dunlin (Calidris alpina) (SOIKKELI, 1967); killdeer (Charadrius vociferus) (LENINGTON & MACE, 1975)). This phenomenon has been linked to food stress and declining weight of the deserter (usually female, HOLMES, 1966; ASHKENAZIE & SAFRIEL, 1979). Desertion by one mate is less common in short-distance migrants than in long (LENINGTON, 1980) and this is probably because the post-breeding energetic demands are less. American oystercatchers migrate only short distances, and not until several months after the end of the breeding season. On the basis of LENINGTON's (1980) observation, desertion by one sex, in this species should be (and is) rare.

Parental investment.

Cumulative energy expenditure (CEE) curves matched the generalized curves of GLADSTONE (1979) for colonial birds where extra-pair copulations have been observed. They indicate that CEE is equal in the sexes.

The only way 'parental investment' could be drastically different from what is depicted in the curves is if there was differential mortality between the sexes on the wintering grounds, in which case, the sex with a higher rate of mortality would be investing a larger proportion of his or her residual reproductive value (WILLIAMS, 1966) to this year's reproductive effort (assuming mates are of the same age, and begin breeding at the same age). If the rate of annual return to the nest site is assumed to be a measure of the survival rate and not a measure of the dispersal rate, then it appears that both sexes of the American oystercatcher have nearly identical mortality rates (= 1 - survival rate) (males, 30 birds, 84.4% mean annual return; females, 30 birds, 84.6% mean annual return; rates averaged over 5 years).

Second condition of complementarity.

Complementarity of mates should be enhanced when the probability of maintaining the same pair bond in future breeding attempts is high (TRIVERS, 1972; NIEBUHR, 1983), or the probability of finding a new mate of comparable or better quality is low. Cooperative behaviour should be found most often in long-lived species with stable pair bonds. Earlier, however, I stated that the one pre-condition for the evolution of cooperative behaviour was a difference between the probability of raising chicks alone, and the probability of raising chicks with a mate. Complementarity, and the need for extensive bi-parental care probably evolved together, along with stable pair bonds and longevity. Extensive parental care by the male may have originated in response to increasing reproductive synchrony on the part of the female (KNOWLTON, 1979). Once extensive male parental care was in place, it became difficult for males to obtain new mates from one season to the next, and it 'paid' both parents to act cooperatively.

   Finally, a mechanism is likely to have evolved whereby a parent can assess the incompetence of its mate, and either divorce the mate early in the breeding cycle, or raise chicks with an incompetent mate. M. D. CADMAN (pers. comm.) has observed one divorce in oystercatchers after loss of the first clutch of eggs to predators, and the altercation between the mates appeared to be initiated by the male. Incompetence was observed in one parent that 'presented' food repeatedly to a newly hatched chick from over 100 m away, out of view of the chick. Unfortunately this pair was unmarked and the fate of the pair bond is unknown. Presumably if one of the parents is incompetent then the other will seek a new mate at the beginning of the next breeding season.

Summary

American oystercatchers have extensive parental care. As a result sex roles are similar and highly complementary. During the pre-laying period the roles of males and females, except during copulation, are indistinguishable. During the laying period the roles diverge slightly with males spending more time chasing conspecifics. Presumably the similarity during pre-laying, and the differences during laying, function to prevent the male from being cuckolded. Males begin assisting in incubation as soon as the females begin incubating and then consistently perform the same proportion of incubation throughout this breeding stage. During incubation, females incubate more often than males, and consequently rest less, preen less and fly less than males. During chick-rearing males are involved in more chases than females and take more foraging trips to provision young but wait longer between successive trips. The pattern of foraging by each sex is complementary. Breeding season energy expenditure is approximately equal in both sexes. There is no evidence for conflict between the sexes over the contributions to parental care. Where sex roles diverge the differences in behaviour can be partly explained by the relative energetic efficiencies of each sex performing different tasks.

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Résumé

Les soins parentaux sont très développés chez l'huitrie americain; le rôle des sexes est
complémentaire. Avant la ponte, le rôle du mâle et de la femelle sont identiques. Durant
la ponte, leur comportement est légèrement différent; les mâles passent plus de temps à
chasser des congenères, probablement pour éviter d'être cocufiés. Les mâles aident à
l'incubation dès que les femelles commencent à incuber; la proportion du temps qu'ils
passent à incuber reste constante. Les femelles incubent plus souvent que les mâles; elles
se reposent, se toilettent et volent moins qu'eux. Pendant l'élevage des jeunes, les mâles
sont impliqués dans un plus grand nombre de poursuites que les femelles; ils font plus de
voyages pour nourrir les jeunes, mais ils attendent plus longtemps entre chaque voyage.
La dépense énergétique totale durant la saison de reproduction est à peu près la même
pour les deux sexes. Il n'y a pas d'indication de conflit entre mâle et femelle pour la répar-
tition des soins parentaux. Quand le comportement des deux sexes diffère, cela s'explique
en partie par l'efficité énergétique différente de chaque sexe exécuter les différentes
tâches.