Sex roles of the South Island pied oystercatcher, *Haematopus ostralegus finschi*

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Abstract We compared the behaviour, energy expenditure, and food intake of male and female South Island pied oystercatchers, *Haematopus ostralegus finschi*, breeding in pasture and crop paddocks in Canterbury. In this monogamous species, females spent more time inactive than males ($P=0.03$) and there was a trend for males to spend more time in territory defence than females ($P=0.08$). There were no significant differences in other behaviours and the sexes did not differ in their food intake rates. We used literature values for this species to estimate the energy expended in each activity and the energy expenditure rate over the breeding season. Despite the differences in the proportion of time spent in territory defence and inactivity by the sexes, males had a lower rate of energy expenditure than females over the breeding season ($P=0.07$). We suggest that behavioural differences are unlikely to compensate female South Island pied oystercatchers for their costs of gamete production and the difference in energy expenditure may reflect the uncertainty of paternity of males.

INTRODUCTION

Breeding will not always be a cooperative endeavour between the 2 sexes (Trivers 1972; Davies 1991; Westneat & Sargent 1996). Conflict may exist in the input each sex provides in to gamete production and parental care as each sex attempts to minimise its own investment while maximising their mate's investment in raising young (Westneat & Sargent 1996). Conflict between the sexes may also arise because males generally have less certainty of parentage than females (Westneat & Sargent 1996). Differences in the behaviours of the sexes during the breeding season have been proposed as a method of adjusting parental input into raising young (Gladstone 1979, Westneat & Sargent 1996).

An example of compensation of females by behavioural differences has been shown in American oystercatchers, *Haematopus palliatus*. Nol (1985) found that, resulting mainly from the costs of egg production, females expended about 16% more energy than males during the early part of the breeding season. Over the whole breeding season, however, females were partially compensated by male

behaviour which reduced the females' energy expenditure to about 5% greater than males.

We examined the compensation idea in South Island pied oystercatchers, *Haematopus ostralegus finschi*. This species nests in open breeding territories allowing relatively easy and complete observation of their behaviour. Oystercatchers generally pair with the same mate for several years and appear to have a high level of behavioural cooperation during the breeding season. They spend the non-breeding season on coastal estuaries and return to their breeding sites in pasture and riparian areas on the eastern side of the Southern Alps from early June (Pierce 1983) with females arriving slightly earlier than males (Sagar *et al.* 2000). Birds become territorial once at the breeding grounds and lay a clutch of 1-4 eggs, which is incubated for *c.* 4 weeks by both parents. Chicks fledge at 5-6 weeks of age and remain in their natal area for a further 2 weeks before dispersing to non-breeding areas on the coast (Baker 1969).

We studied food intake rates, behaviour, and estimated the energy expenditure of male and female South Island pied oystercatchers during the breeding season. We then assessed the energy expenditure of both sexes in relation to their estimated costs of gamete production.

METHODS

Study site

South Island pied oystercatchers breeding on farmland in the Mayfield area, Canterbury (43º49´S, Longitude 171º24´E, c. 85 km southwest of Christchurch), were monitored in 1997 and 1998. Birds were leg banded with unique colour band combinations. The sex of each bird was determined by discriminant analysis, which an earlier study (Baker 1974) had shown by dissection to be 96% accurate.

Food intake

Focal animal studies (Altman 1974) of 13 oystercatcher pairs were conducted early in the breeding season during feeding bouts between 27 July and 1 September 1997 (early observations). The time each bird took to complete 60 probes and the number of successful probes (60 probes)$^{-1}$ were recorded. A successful probe was recorded when either a prey item was seen to be eaten or if the bird tipped its head back several times to swallow a food item too small to be observed directly. The same birds were observed again, later in the breeding season between 8 and 24 October 1997 (late observations). Early and late observations of each pair were made at about the same time of day. Early observations were conducted during the pre-egg period. Late observations were conducted after the 1st clutch was laid but, because some pairs lost their 1st clutch, may have occurred during pre-egg, incubating, or chick-guarding phases.

Behaviour

The behaviour of South Island pied oystercatchers was recorded every 2 weeks in 1996 and 1997 from mid-June, when the 1st oystercatchers returned to the breeding grounds, until mid-December when the last birds left. Pairs observed in 1996 were not restudied in 1997. Data gathered in 1996 were not significantly different from data gathered in 1997 data so the 2 data sets were combined.

Logistical constraints prevented completely randomising the order of visits to each breeding territory: 3-6 oystercatcher territories in the same area were assigned to 1 of 9 groups that were in turn assigned to 3 districts. The order of visiting districts was randomised and, once at each district, the order of visiting each group was randomised. Observations were carried out from c. 0730 h until 1700 h at the start of the breeding season, and progressively extended from approximately 0700 h until 2000 h as daylight hours increased.

South Island pied oystercatcher pairs were observed from a car. Use of traditional, non-mobile hides would have limited the study to fewer pairs as the oystercatchers were spread over 15 km and at best only 2 or 3 territories were visible from any single location. A car offered the additional advantage that it did not require any set up time and South Island pied oystercatchers were accustomed to farm vehicles. Cars have been used as hides in other oystercatcher studies (for example Vines 1979).

Behavioural categories were derived from Marchant & Higgins (1993) and are self explanatory except for "territory defence" which was defined as birds running towards an intruder with tails depressed and fanned, wings raised, necks extended forwards and bills directed downwards, with or without piping or object tossing. "Inactive" was sitting on the ground or standing.

Pairs were given 10 minutes to adjust to the presence of the observer as the birds took 5-6 min to resume behaviours they had been performing before the interruption. Behaviour was then recorded on the minute for 10 min – instantaneous sampling (Altman 1974). A 10 min observation period of each pair was chosen as it allowed sufficient time to observe the entire study population over 2 consecutive days. If a pair could not be located immediately, their territory was searched for 10 minutes. If they could not be seen after 10 min no data were recorded for that pair. The sex of each bird was unknown to the observer so that observer blinding was maintained. If individuals of a pair could not be distinguished during an observation point that sample point was excluded from the analysis. Thus we compared the proportion of the total observations each bird spent in each behaviour.

The behaviour of males and females was compared within the pair in a pair-wise manner using the Wilcoxon signed rank test as the data were not normally distributed. The number of pairs analysed varied as pairs with tied values were excluded from the analysis by the Statistix (Analytical Software 1985) software package. The data were analysed for the whole of the breeding season and also analysed separately during the pre-egg laying and post-egg laying phases of the breeding season. The post-egg laying phase of the breeding season combined data from pairs incubating eggs and guarding chicks as there were too few pairs with chicks to draw meaningful conclusions. Post-egg data also included pairs that lost their eggs or chicks but did not relay.

Energy expenditure

Day-time basal metabolic rates (BMR) of male and female pied oystercatchers were calculated using the equation, Day time BMR (Watts) = 4.41 x mass (kg)$^{0.729}$ for non-passerine birds adapted from Aschoff & Pohl (1970). We estimated the energy expenditure rate of males and females during the pre-egg phase, the post-egg phase and the whole of the breeding season. Mean weights were calculated from weights recorded from

Table 1 Energy costs of each activity used to calculate South Island pied oystercatcher (*Haematopus ostralegus finschi*) energy expenditure over the breeding season. BMR, basal metabolic rate. References: 1, Aschoff & Pohl (1970); 2, King (1974); 3, Ricklefs (1974); 4, Maxson & Oring (1980); 5, Custer & Pitelka (1972) in Nol (1985); 6, Kersten (1996).

Behaviour	Multiple of BMR		Energy cost (W)	
	Male	Female	Males (W)	Females (W)
Territory defence	2.00^2	2.00^2	5.46	5.74
Incubating	1.29^3	1.27^3	3.52	3.65
Inactive	1.8^6	1.8^6	4.91	5.17
Probing	3.00^5	3.00^5	8.19	8.61
Preening	2.50^1	2.50^1	6.83	7.17
Walking	2.80^4	2.80^4	7.64	8.04
Flying	14.23^2	14.28^2	38.85	40.99
Day time BMR			2.73	2.87

Table 2 Male and female foraging success rates and time taken – $\bar{x}$ (SE $_{\bar{x}}$) – for South Island pied oystercatchers (*Haematopus ostralegus finschi*) to perform 60 probes during the breeding season between 27 July and 1 September (early) and 8 and 24 October (late) in the breeding season.

	Number of successful probes (60 probes)$^{-1}$		Time taken to complete 60 probes (s)	
	Early	Late	Early	Late
Males	4.4 (0.7)	3.9 (0.7)	221 (22)	332 (37)
Females	5.5 (0.9)	5.2 (0.8)	240 (33)	312 (46)

the Mayfield population. Female South Island pied oystercatchers (554 g, 95% C.I. 548.4-561.2) on average weighed seven per cent more than males (519 g, 95% C.I. 511.1-527.1).

The energetic cost of each behaviour was calculated from literature values (Table 1). The different energy costs for males and females of incubation and flight reflect differences in the weight of the sexes. For example, the cost of raising the temperature of eggs from the ambient temperature to 35°C is slightly more expensive for males because of their smaller body mass. Video recording of nests showed eggs were often left unattended for considerable periods (J. Banks unpub. data).

The energy cost of each activity was then multiplied by the proportion of the observation periods spent in each activity by members of a pair. The category "Other" was excluded from the analysis as it was a minor proportion of the observations and impossible to assign an energy cost.

The minimum cost of producing eggs was calculated using Ricklefs's (1974) formula. Eggs of precocial land birds contain 6.91 kJ.g^{-1} fresh weight. The mean weight of South Island pied oystercatcher eggs was 44.2 g, and in 1996 and 1997 the mean clutch size, including replacement clutches, was 3.11, giving a mean minimum energy value for an average clutch of 950 kJ.

RESULTS

Food intake

There was no significant difference in the food intake rate of males and females (Table 2). Males and females had similar numbers of successful probes (60 probes)$^{-1}$ early (paired t test, $n=16$, $t=1.60$, $P=0.13$), and late (paired t test, $n=13$, $t=1.76$, $P=0.10$) in the breeding season. Both members of the pair

took similar lengths of time to complete 60 probes early (paired t test, $n=16$, $t=0.95$, $P=0.36$) and late (paired t test, $n=13$, $t=0.16$, $P=0.88$) in the breeding season.

Behaviour

During the pre-egg phase, females spent a significantly greater proportion of the observations inactive than males (Wilcoxon signed rank test, $Z=2.056$, $P=0.04$) and males showed a trend to spend a greater proportion of the observations in territory defence than females (Wilcoxon signed rank test, $Z=1.675$, $P=0.09$) (Table 3). In the post-egg phase, females spent more of their time inactive, although not significantly so (Wilcoxon signed rank test, $Z=1.581$, $P=0.11$), and males spent a significantly greater proportion of the observations in territory defence than females (Wilcoxon signed rank test, $Z=2.052$, $P=0.04$) (Table 3).

Over the entire breeding season, males showed a strong tendency to spend a greater proportion of time in territory defence than females (Wilcoxon signed rank test, $Z=1.751$, $P=0.08$) while females spent a significantly greater proportion of time inactive (Wilcoxon signed rank test, $Z=2.212$, $P=0.03$). Males and females had no significant differences in the other behavioural categories (Table 4).

Within sex comparisons between the pre-egg and post-egg stages of the breeding season showed that females spent less time during the post egg period in territory defence (Wilcoxon signed rank test, $Z=1.887$, $P=0.06$), and in probing (Wilcoxon signed rank test, $Z=2.528$, $P=0.01$) than in the pre-egg period. Females showed no other significant differences between pre-egg and post-egg periods of the breeding season (Fig. 1).

Males also spent a significantly less time probing in the post-egg stage of the breeding season (Wilcoxon signed rank test, $Z=2.097$, $P=0.04$). There were no other significant differences between the pre-egg and post-egg periods in the males' behaviour (Fig. 1).
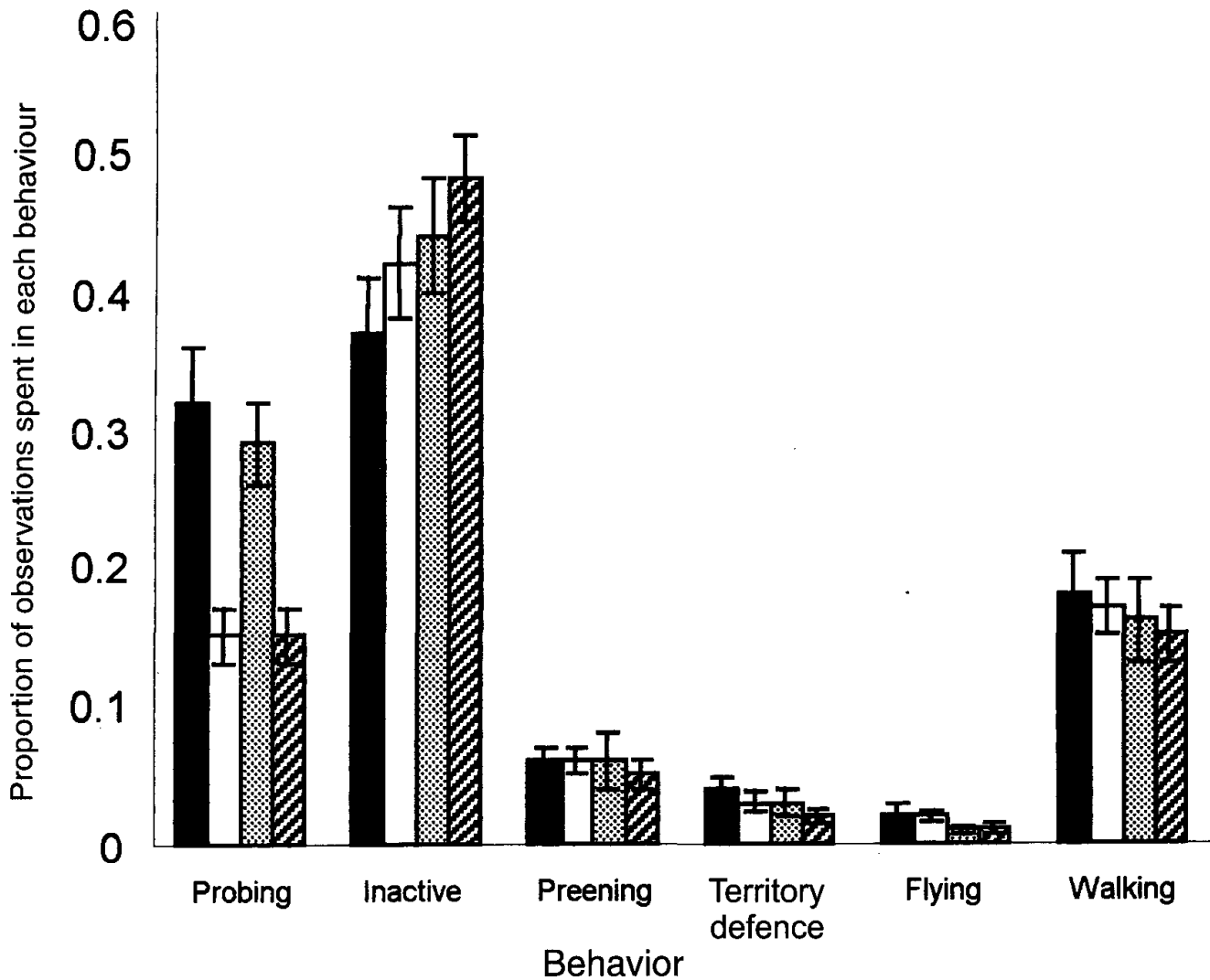
Fig. 1 Comparisons of male and female pre-egg and post-egg behaviours (±SE $_{\bar{x}}$) in the South Island pied oystercatcher (*Haematopus ostralegus finschi*). Filled column, male pre-egg; open, male post-egg; stippled, female pre-egg; mid-fill, female post-egg.

Table 3 Proportions of time $-\bar{x}$ (SE$_{\bar{x}}$) – that South Island pied oystercatchers (*Haematopus ostralegus finschi*) spent on different behaviours at the pre- and post-egg phases of the breeding season and the differences between the sexes. Defence, territory defence; n, number of pairs; P, probability level for difference between sexes. Number of pairs varies because some behaviours were not carried out by some pairs during the observation points.

| | Pre-egg | | | | Post-egg | | | |
	Male	Female	n	P	Male	Female	n	P
Probing	0.319 (0.035)	0.289 (0.031)	34	0.66	0.154 (0.021)	0.150 (0.018)	37	0.85
Inactive	0.373 (0.042)	0.440 (0.041)	35	0.04	0.416 (0.037)	0.484 (0.033)	38	0.11
Incubating					0.152 (0.037)	0.129 (0.035)	29	0.88
Preening	0.064 (0.013)	0.064 (0.016)	19	0.29	0.057 (0.014)	0.053 (0.012)	31	0.86
Defence	0.032 (0.009)	0.032 (0.009)	15	0.09	0.030 (0.008)	0.027 (0.005)	19	0.04
Flying	0.017 (0.009)	0.011 (0.003)	7	0.21	0.016 (0.004)	0.015 (0.004)	18	0.79
Walking	0.180 (0.029)	0.162 (0.031)	26	0.53	0.174 (0.023)	0.148 (0.017)	37	0.16
Other	0.005 (0.003)	0.001 (0.001)	3	0.11	0.001 (0.001)	0.005 (0.017)	7	0.128

Energy expenditure

Mean energy expenditure rate of females during the pre-egg phase was significantly higher (7.16 W, SE_x=0.177) than males (7.15 W, SE_x=0.320) (Wilcoxon signed rank test, Z=2.037, P=0.04).Post-egg energy expenditure rate of males 6.36 W (SE_x=0.173) was not significantly different from females 6.53 W (SE_x=0.196) (Wilcoxon signed rank test, Z=0.798, P=0.43).

Males showed a tendency to expend energy at a lower rate (6.62 W, SE_x=0.14) than females (6.88 W, SE_x=0.16) over the whole breeding season (Wilcoxon signed rank test, Z=1.780, P=0.07).

DISCUSSION

Our results go some way to understanding the sex roles of South Island pied oystercatcher during the breeding season. Our results agree with Baker's (1969) observation that male South Island pied oystercatchers breeding on riverbeds spent more time than females in territory defence. Baker (1969), however, reported that females incubated the eggs for 3-4 h periods while males incubated for c.1 h periods whereas we found males spent a greater proportion of the observation points incubating than females, although the difference was not significant. This difference between our results and Baker's may be due to the different habitats of the study populations (pasture nesting compared to riverbed nesting pairs).

During the pre-egg phase of the breeding season females spent significantly more time than males in the energetically "cheap" inactive behavioural category while males spent more time in the energetically expensive activity of territory defence. Despite these differences females still expended more energy than males during the pre-egg phase. The higher energy expenditure rate by females continued during the post egg phase and over the whole breeding season females had a higher rate of energy expenditure than males. Females did not compensate for their higher rates of energy expenditure by obtaining food more efficiently than males during the breeding season as both sexes were equally successful at catching prey and caught prey at a similar rate throughout the breeding season.

We did not make any observations of behaviour at night as the sexes are indistinguishable without observing the bands and we did not have access to night vision equipment that allowed us to identify individual birds. It may be that the sexes showed differences in behaviour or food intake rates at night. We think this possibility unlikely as Hulscher (1976) found no difference in the amount of food ingested by male and female European oystercatchers feeding on estuarine mud flats during the day and the night. This aspect of oystercatcher behaviour requires more study.

Table 4 Mean proportion $-\bar{x}$ (SE_x) – of observation points for the entire breeding season during which South Island pied oystercatchers (*Haematopus ostralegus finschi*) were observed performing specified behaviours and the differences in proportions between the sexes. Defence, territory defence; n, number of pairs for entire breeding season; P, probability level for difference between sexes.

Behaviour	Male	Female	n	P
Probing	0.236 (0.027)	0.230 (0.006)	47	0.46
Inactive	0.416 (0.028)	0.465 (0.028)	47	0.03
Incubating	0.079 (0.021)	0.062 (0.017)	30	0.69
Preening	0.061 (0.010)	0.056 (0.010)	44	0.89
Defence	0.032(0.006)	0.027 (0.006)	33	0.08
Flying	0.014 (0.003)	0.014 (0.003)	26	0.73
Walking	0.159 (0.017)	0.143 (0.013)	44	0.27
Other	0.003 (0.001)	0.003 (0.002)	9	0.68

A difficulty with estimating the energy expenditure rate of South Island pied oystercatchers is assessing the appropriateness of the allometric equation used to derive the birds' BMR and the multiples used to estimate energy expenditure of the sexes. Literature reports using alternative methods of calculating the BMR support our calculations. For example, Kersten et al. (1998) measured the oxygen consumption of a captive European oystercatcher, *Haematopus ostralegus ostralegus*, the sister subspecies of the South Island pied oystercatcher, and calculated its BMR as 2.91 W. Our values for the BMR of 2.73 W for male South Island pied oystercatchers and 2.87 W for females using the allometric equation of Aschoff & Pohl (1970) agree very closely with this value. Likewise, both male and female South Island pied oystercatchers had a daily energy expenditure of 2.3 BMR, which again approximates the energy expenditure estimated from other studies. Kersten (1996) found European oystercatchers expended energy at 2.1 BMR during incubation, increasing to 2.7 BMR during chick rearing.

Gladstone (1979) suggested that differences in the behavioural repertoires of males and females may allow females to recoup some of their higher costs of gamete production. Males and female oystercatchers are likely to have large differences in the energy used to produce gametes. Female oystercatchers invested a minimum of 950 kJ in their gametes. Chicken eggs increase in weight exponentially in the 9 days before ovulation from almost 0 to 16 grams (Etches 1996). If oystercatcher eggs mature at a similar rate this would represent an 18% increase in daily energy expenditure over the maturation period. In comparison, if male oystercatchers produce sperm at a rate similar to domestic chickens, the males' cost of gamete production is 5.02 kJ day^{-1} (Ricklefs 1974) and male oystercatchers may lower their investment in gametes still further as male chickens reabsorb sperm

if it is not ejaculated (Etches 1996). Female oystercatchers do not appear to fully compensate by behavioural differences for their higher energy expenditure in producing gametes, as although both sexes reduced their energy expenditure in the post egg stage, males reduced their expenditure by a greater amount than females. It may be that males' lower input into raising young reflects their uncertainty of paternity as genetic analysis of the parentage of European oystercatcher chicks found a 5% rate of extra-pair fertilisations (Heg 1993).

Male and female South Island pied oystercatchers differed in their behavioural repertoires. Females spent more of their time inactive and males spent more time in the energetically expensive territory defence, but once the total energy expenditure rate of each sex was calculated, there was no significant difference in the energy expenditure of males and females. It seems unlikely that females use behavioural differences to compensate fully for the energy used to produce gametes.

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