PARENT AND GOSLING STRATEGIES IN WINTERING BARNACLE GEESE Branta leucopsis

GAVIN M. SIRIWARDENA and JEFFREY M. BLACK

1 Present address: British Trust for Ornithology, The Nunnery, Nunnery Place, Thetford, Norfolk IP24 3PU, UK.
2 Present address: Department of Wildlife, Humboldt State University, Arcata, California, 95521-8299, USA.

Barnacle goose parents caring for four or more goslings devoted less time to foraging than did those with fewer offspring and more time was spent being vigilant. Goslings gained substantial benefits from being in the family unit, including better foraging opportunities and higher dominance status. Apart from greater distances from their neighbours, goslings did not benefit from being in larger sized families. Time budgets and foraging performance did not differ between the three parentless gosling types. It is possible that only weaker goslings adopted the order or 'parasite' strategies thus rendering their foraging performance to a level similar to that of single non-family goslings.

Keywords: Aggressive Interactions, Foraging, Parent-offspring Conflict, Precedent Birds, Time Budgets.

Many studies of altricial birds have found that the costs involved with parental care increase with brood size and that this affects subsequent breeding success (reviewed by May 1988). This suggests a trade-off between production in each breeding episode and individual lifetime reproductive success, as predicted by Williams (1966). However, the situation is less clear in birds with precocial young. Whereas several studies have demonstrated some brood-size-related behavioural and/or fitness costs (McLean 1981; Woolf & Walters 1983, Rowles 1985, Lestas 1986, Schneider & Leprechts 1987, Sedgman & Raveling 1990, Fordham 1993, Williams et al. 1994, Lestas 1997), others have found no costs of increasing brood size (Kuenen & Ingle 1978, 1986, Scott 1988a, Mushforth et al. 1988, Rowett 1985, Lestas 1987, Rowett & Heamsran 1991). It is important to note, however, that all of the above studies concentrated on the parent–growing association before families left the breeding grounds. In goslings, family units can persist for several years (Warren et al. 1993), and the costs of parental care may well be compounded over the full duration of the parent–offspring association. Of those studies which have considered costs on the wintering grounds, indirectly by measuring the consequences of brood size in the following breeding season, only one has manipulated brood size to control for the effects of parental quality (Lestas 1987). This study detected one long-term cost of large broods to parent Canada–Greenland Brants: cannibalism of a suite of variables selected by their parents in the following year.

Black & Owen (1989a) presented evidence that prolonged parental care is costly to Barnacle Goeese Branta leucopsis (see Scott 1989ab). However, in barnacle goslings, there is no evidence for a long-term cost of brood size on the wintering grounds. During the non-breeding season, pairs with offspring were less vigilant, fed less and had more aggressive encounters with neighbours than those without young, and they had less access to the feeding grounds. However, the costs of rearing are not the same as those in goslings, which are relatively immobile and cannot move away from sites. In barnacle goslings, the costs of rearing are related to the number of individuals in the unit, and the costs of rearing are higher in larger broods.
where large families deter small ones, families beat pairs and pairs beat singles (Boyd 1973, Rawling 1970).

Barnacle Goose goslings fledge after eight weeks and become increasingly mobile, periodically moving in and out of the vicinity of their parents. Some goslings lose contact with their parents by their fourth month, but most remain in family groups for nine to 11 months, when parental aggression towards them wanes (Black & Owen 1989a). Goslings have several alternative strategies available once they have their parents; roaming singly, forming groups with other immatures, or following unrelated family units, 'parasitising' their vigilance and defence status (Black & Owen 1984). The costs and benefits of these alternative strategies may strongly affect the preferred duration of a gosling's association with its natal family unit.

We present data on behavioural indicators of the costs and benefits of different family sizes to both Barnacle Goose parents and goslings, collected in winter when the birds were foraging in large flocks. We consider a range of family sizes, as well as single goslings (outside family units), groups of parentless goslings, and goslings which are 'parasitised' on families. The results are discussed with a view to identifying optimal brood sizes for both parents and goslings.

Method

We observed Barnacle Geese on grassy vales near from October to May, over several seasons, at The Wildfowl & Wetlands Trust's Cley Marsh, north of Norwich, in east coast England. Around 35% of the population carried individual plastic leg rings which were readable at up to 250 m. The birds were sighted an average of eight times each year and the status of any associated birds recorded (see Owen et al. 1988). Unpaired birds can be aged (three or first winter) from plumage differences (Owen 1980).

Time budget data for parents and goslings from different family sizes (one, two, three, four to five, and single goslings with no accompanying parents) were collected by JMB in 1982-84. The methods for the time budget

alterations are described in Black & Owen (1989b). Behaviour was classified as righting, grazing, walking, feeding, courtship activity, and aggression, and the percentage time engaged in each activity was calculated. These data were analysed for variation with respect to brood size and between family and single goslings. The distance, in goose-lengths (c. 45 cm), to the nearest non-family neighbour for each with and without families was also recorded. The area around each goose within foraging flocks is thought to indicate the birds' ability to feed without interference from competitors (Scott 1980a, Lepsis 1987).

In a second phase of observations (1990-91), GNS-wounded goslings for a period between two and 12 minutes during which they received no family status (type of family or type of non-family gosling) was established and behavioural data were collected using standardised procedures (as described above). Goslings without parents were classified as single (not moving with any other birds), grouped (moving with a group of goslings with no attendant adults) or parasitic (moving on the periphery of a family unit but subject to occasional attacks from its family members and often with visible plumage differences from the other goslings; see Black & Owen 1984). The distance (in goose-lengths) from the gosling's nearest non-family neighbour, the time taken for 30 pecks (sharp upward neck movements to break grass blades) to be made, and the time taken for 10 steps (during active foraging) were recorded. In general, a faster rate of pecking is associated with shorter, lower quality grazing, and a faster rate of stepping, with a high search time for suitable grass blades, or a low density of good forage (Teunissen et al. 1985). While goslings were observed, the number and results of any aggressive encounters between the local family and other goslings were recorded. The data collected for the above measures were analysed with respect to family status (as described above). Note, however, that aggressive interaction data for parasitic goslings could not be included in statistical analysis since the interactions were used to define gosling status, so compromising the independence of the sample.
Figure 1. Activity budgets of parents attending broods of different sizes. Bars show ± one standard error. Male parents of larger families fed significantly less (F = 9.88, 3 d.f., p = 0.029), and spent significantly longer being vigilant (F = 9.14, 3 d.f., p = 0.029), than those with fewer young. Female parents with large families spent more time taking part in aggressive encounters than did those with smaller classes (F = 8.06, 3 d.f., p = 0.045). Other activities did not vary among brood sizes for males (walking H = 2.20, p = 0.532; loafing H = 1.55, p = 0.673; comfort H = 2.67, p = 0.466; aggression H = 1.49, p = 0.684, all d.f. = 3), or females (vigilance H = 2.43, p = 0.489; walking H = 0.92, p = 0.632; loafing H = 3.26, p = 0.155; grazing H = 2.30, p = 0.476; comfort H = 1.42, p = 0.613; all d.f. = 3).
The data for each measure of the behaviour of adults and goslings described above were averaged by season (summer = October and November; winter = December to 15 February and spring = 16 February to May), where multiple observations of each family occurred, to preserve the independence of observations. The data were analysed using Kruskal-Wallis non-parametric one way analyses of variance, as indicated in the text by H values, unless otherwise indicated. Checks were made for effects of season on each variable by analysing the data for each season alone as well as pooled together.

Results

Parent time budgets

Male parents of large families (broods of four or five) fed significantly less and spent significantly longer being vigile than males with fewer young (Figure 1). Other activities showed little variation with respect to brood size.

Female parents with large families (broods of four or five) spent more time taking part in aggressive encounters than females with few young (Figure 1). The other activities of female parents showed little broad-size-related variation. A corresponding trend for parents to be involved in more aggressive encounters as family size increases was shown by Duck & Owen (1989).

Nearest neighbour distances

Parents maintained greater distances from other flock members than did non-parents (mean SEs in goose lengths: parents 2.48 (0.19), non-parents 2.45 (0.24). Wilcoxon test: W = 136.85, p = 0.0038). Similarly, goslings in families had larger nearest neighbour distances than did non-family goslings (means (SEs): 6.14 (0.18) versus 3.45 (0.20) goose lengths, H = 72.82, 1 d.f., p < 0.001). Neighbour distances differed for goslings in different sized families (Figure 2), with those of larger distances to the neighbours of larger families, especially those with three or more goslings. The non-family strategy adopted by parentless goslings also gave rise to significant variation (H = 12.34, 2 d.f., p = 0.003); parasitic goslings had the largest nearest-neighbour distances (mean (SE): 4.22 (1.43) goose lengths), singles were intermediate (mean (SE): 3.70 (0.24)) and grouped orphans had the smallest (mean (SE): 2.28 (0.18)).

Gosling time budgets

Family and non-family goslings differed in their allocation of time to walking behaviour (mean (SE): 4.26 (1.31) percent of 7.05 (0.67); H = 12.70, d.f. = 1, p < 0.001), but not in terms of the other behaviours described (vigilance H = 0.07, p = 0.786; loafing H = 2.66, p = 0.103; grazing H = 0.01, p = 0.915; comfort H = 2.80, p = 0.099; vocal H = 0.07, p = 0.793; all d.f. = 1). There were no significant differences between the time budget allocations of goslings from the different family sizes (vigilance H = 4.64, p = 0.201; walking H = 1.33, p = 0.721; loafing H = 5.28, p = 0.153; grazing H = 5.85, p = 0.120; comfort H = 3.62, p = 0.306; aggression H = 3.91, p = 0.272, all d.f. = 3).

Gosling foraging performance

Rates of both pecking and stepping were faster for non-family goslings than for those in families (n = 125 and 244, respectively times for 50 pecks for non-family goslings (mean (SE): 22.40 (0.54)) and for family goslings 24.70 (0.46); H = 8.17, p = 0.04; time for 10 steps (mean (SE)): for non-family goslings 10.79 (0.70) and for family goslings 23.82 (0.59); H = 26.22, p < 0.001; each 3 d.f.).

There were, however, no significant differences between family goslings from different brood sizes (n = 107 (brood size 1), 87 (2), 33 (3) mm (4); time for 50 pecks H = 1.53, p = 0.675; time for 10 steps H = 3.41, p = 0.33; each 3 d.f.). Of between the three strategies adopted by non-family goslings (n = 107 (single goslings), 87 (grouped goslings) and 30 (parasitic goslings) time for 50 pecks: H = 1.66, p = 0.431; time for 10 steps: H = 4.44, p = 0.199, each 2 d.f.).
Figure 2. Distances to the nearest non-family neighbours of goslings in different brood sizes. Bars show ±1 standard error. Neighbour distances varied for goslings in different sized families ($F = 34.32$, d.f. $p < 0.001$).

Aggressive encounters

Family goslings with wool are more and less in fewer interactions than would be expected by chance, compared to non-family young (see Table 1). The frequency of winning and losing did not, however, differ among family goslings from different brood sizes (Table 2) or between single and grouped goslings (Table 3). Although aggressive goslings could not be included in this analysis they experienced a higher rate of losing interactions if the other single gosling were (single goslings: 0.08 per min; grouped goslings: 0.05 per min). This reflected attacks on parasites from their 'adoptive' parents.

Effects of season

We repeated the analyses for each behaviour parameter with respect to brood size and gosling class for each part of the winter season: autumn, mid-winter, and spring. The trends in the smaller classes were similar to those which gave rise to significant results for the pooled data set.

Discussion

Elsewhere, we have shown that parent Barnacle Geese experience costs in terms of their activity budget throughout the 11 months of their association with goslings (Black & Owen 1989a,b, Black et al. 1992). These costs are particularly obvious for male parents that feed less, spending time instead in increased vigilance and aggression. In this study we have shown that, contrary to our hypothesis, large broods increased vigilance and reduced feeding for males, and increased aggressiveness for females. If this lowering of the activity budget led to reduced future fitness, we would anticipate that parents that care for more than three goslings would suffer, whereas those with fewer offspring would not.

There is some evidence, however, to suggest that the investment in goslings may actually lead to long-term benefits (Black et al. 1992). This is due to the help that goslings give in fighting with and scaring off competitors and predators, and to the increased feeding opportunities that are achieved at the edges of the flocks where families are usually found (Black & Owen 1989a). Parents with larger broods are more likely to retain their offspring into the spring 'settling period' when this extra help is particularly useful (Black & Owen 1989a).

Goslings in larger families had larger distances between themselves and potential competitors, but there were no other clear benefits to being a part of a particular size of family, and such distances could simply be an artefact of the greater space occupied by larger families. Although competition between family members is likely to have been less severe than that with unrelated individuals, some interference between family members foraging in close proximity does occur.

There were numerous benefits to family goslings versus non-family goslings. These included more space in foraging flocks, less time spent feeding, greater vigilance, superior peck and stop rates and a higher dominance status. If these benefits are reflected positively in future fitness we would predict that the goslings that remain with their parents for the longest periods will perform the
Table 1. Frequencies of winning and losing aggressive encounters for family and non-family goslings. Relative proportions derived from the duration each class was observed were used to calculate the expected values (in parentheses).

<table>
<thead>
<tr>
<th>Gosling type</th>
<th>Duration observed, min</th>
<th>Winning encounters</th>
<th>Losing encounters</th>
</tr>
</thead>
<tbody>
<tr>
<td>Family</td>
<td>2045</td>
<td>53 (45.3)</td>
<td>14 (14.1)</td>
</tr>
<tr>
<td>Non-family</td>
<td>707</td>
<td>8 (11.5)</td>
<td>65 (15.9)</td>
</tr>
<tr>
<td>$\chi^2 (1 df)$</td>
<td>$&lt;0.025$</td>
<td>87.16, &lt;0.0005</td>
<td></td>
</tr>
</tbody>
</table>

Table 2. Frequencies of winning and losing aggressive encounters for family goslings from different brood sizes. Relative proportions derived from the duration each class was observed were used to calculate the expected values (in parentheses).

<table>
<thead>
<tr>
<th>Brood size</th>
<th>Duration observed, min</th>
<th>Winning encounters</th>
<th>Losing encounters</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>721</td>
<td>25 (18.8)</td>
<td>5 (5.0)</td>
</tr>
<tr>
<td>2</td>
<td>746</td>
<td>16 (19.9)</td>
<td>12 (15.9)</td>
</tr>
<tr>
<td>3</td>
<td>414</td>
<td>10 (21.2)</td>
<td>3 (2.9)</td>
</tr>
<tr>
<td>4</td>
<td>154</td>
<td>5 (4.0)</td>
<td>0 (1.1)</td>
</tr>
<tr>
<td>$\chi^2 (3 df)$</td>
<td>4.65, N.S.</td>
<td>1.26, N.S.</td>
<td></td>
</tr>
</tbody>
</table>

Table 3. Frequencies of winning and losing aggressive encounters for non-family goslings adopting different strategies. Relative proportions derived from the duration each class was observed were used to calculate the expected values (in parentheses).

<table>
<thead>
<tr>
<th>Gosling type</th>
<th>Duration observed, min</th>
<th>Winning encounters</th>
<th>Losing encounters</th>
</tr>
</thead>
<tbody>
<tr>
<td>Single</td>
<td>354</td>
<td>16 (22)</td>
<td>43 (395)</td>
</tr>
<tr>
<td>Grouped</td>
<td>161</td>
<td>2 (1.7)</td>
<td>8 (115)</td>
</tr>
<tr>
<td>$\chi^2 (1 df)$</td>
<td>0.01, N.S.</td>
<td>1.39, N.S.</td>
<td></td>
</tr>
</tbody>
</table>
best. Goslings are also thought to learn useful social and foraging skills from parents during the prolonged parent-offspring association (Black & Owen 1983). Marshall & Black (1981).

Once outside the family unit, non-family goslings do not seem to be able to improve on their status or foraging performance by joining groups of other single goslings or by attempting to join the goslings of unrelated families. For the most part, the non-family gosling classes did not differ in their activity budgets, feeding performance, or dominance status. The strategy adopted by non-family goslings had little effect on their fate in aggressive interactions, but parity goslings probably paid a cent in terms of physical attacks from the host family members (see also Black & Owen 1985). Parity goslings did, however, have more space in foraging flocks because of the dominance status of their ‘family’ unit. It is possible that only weaker parentless goslings adopted the group or parasite strategies, thus raising their foraging performance to a level similar to that of the single non-family goslings.

Black & Owen (1985) showed that the fitness profiles of non-family goslings do not develop as much as family-goslings prior to spring migration. This is consistent with our findings of reduced foraging performance and lower dominance status in non-family goslings. Goslings should therefore attempt to remain within the family unit for as long as possible. Parents, on the other hand, might attempt to reduce their family to a size where costs are minimal, which seems to be below ten or more offspring (although this is dependent on the fitness trade-off described above). In spring, when goslings are at least eight months of age, parental attacks on offspring substantially decrease (Black & Owen 1983). We suspect that goslings depart the family at this point when it becomes more profitable to fend for themselves. It is possible that this point occurs sooner in families with young, inexperienced parents that are less able to provide adequate feeding opportunities. There is some indication that the smallest goslings, which are the lowest ranking within the family, are the first to depart (Black & Owen 1985).

Future research must assess whether the broad-size related differences in behaviour found here actually translate into differences in future survival, mate finding ability and reproductive success for goslings from, and parents with, different sized goslings. For instance, of the studies that have looked for fitness consequences of pre-fledging brood size in parents, have found a substantial cost to large families (Lessells 1976, survival and subsequent clutch size in Carusara Geese: Poole 1984; Lessells & Haversham 1974, survival in Wood Ducks: Allen et al. 1974; and time of moult in Lesser Snow Geese: Chen coeolists communis; Lessells 1977, mass and time of moult in Barnacle Geese). Indeed, Lynch (1977) found that the proportion of body mass of families was higher for clutches which had scored for larger goslings. It is still possible, however, that fitness costs in many of these studies may be due to the confounding effects of parental quality more so than the actual size of the group. F oversees the kind widely used for domestic species (see review by Parrish 1978), but conducted only once with goslings (Lessells 1976), are needed to resolve this.

We would like to thank Jack H. Heintz, Alie Beck, Paul Samways and the staff of WWF for their help with various parts of this study. We are also grateful to Sharmila Choudhury, Margaret Lamont and Mary Ann Owen for their comments on earlier drafts.

References


Williams G.C. 1966. Natural selection, the
costs of reproduction and a refinement of
Fitness consequences of parental behaviour
in relation to offspring number in a precocial
species: the Lesser Snow Goose. Auk
111:563-572.
Winkler, D.W. & Walters, J.R. 1983. The
determination of clutch size in precocial
birds. In: Johnson, R.E. (Ed.). Current