

PARENT AND GOSLING STRATEGIES IN WINTERING BARNACLE GEESE *BRANTA LEUCOPSIS*

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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 group or 'parasite' strategies, thus raising their foraging performance to a level similar to that of single non-family goslings.

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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 Nur 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 (Madsen 1981, Winkler & Walters 1983, Rowher 1985, Lessells 1986, Schindler & Lamprecht 1987, Sedinger & Raveling 1990, Forslund 1993, Williams *et al.* 1994, Loonen 1997), others have found no costs of increasing brood size (Lazarus & Inglis 1978, 1986, Scott 1980a, Rushforth *et al.* 1985, Rowher 1985, Lessells 1987, Rowher & Heusmann 1991). It is important to note, however, that all the above studies concentrated on the parent-gosling association before families left the breeding grounds. In geese, 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 (Lessells 1987). This study detected one long-term cost of large broods to parent Canada Geese *Branta canadensis* out of a suite of variables tested: they bred later in the following year.

Black & Owen (1989a) presented evidence that prolonged parental care is costly to Barnacle Geese *Branta leucopsis* (see Scott 1980a,b for similar findings in swans). During the non-breeding season, pairs with offspring were more vigilant, fed less and had more aggressive encounters with neighbours than those without young, and they had to share food with their goslings. Fighting with conspecifics is stressful and can be dangerous; injuries do occur (Scott 1980b, Black & Owen 1989b). Conversely, parent geese and swans enjoy the highest dominance status, and thus monopolize prime feeding areas (Scott 1980b, Black & Owen 1989b). Dominance in geese is related to the number of individuals in the unit,

where large families defeat small ones, families beat pairs and pairs beat singles (Boyd 1953, Raveling 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 intensifies (Black & Owen 1989a). Goslings have several alternative strategies available once they leave their parents: roaming singly, forming groups with other immatures, or following unrelated family units, 'parasitising' their vigilance and dominance 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 'parasitic' 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 grass pastures from October to May, over several seasons, at The Wildfowl & Wetlands Trust's Caerlaverock refuge in south-west Scotland. Around 25% of the population carried individual plastic leg rings which are readable at up to 250 m. The birds were sighted an average of eight times each year and the status of any associating birds recorded (see Owen *et al.* 1988). Unringed birds can be aged (adult 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

allocations are described in Black & Owen (1989a). Behaviour was classified as vigilant, grazing, walking, loafing, comfort 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 adults with and without families was also recorded. The space around each goose within foraging flocks is thought to indicate the birds' ability to feed without interruption, *ie* to minimise interference from conspecifics (Scott 1980a, Lessells 1987).

In a second phase of observations (1990-91), GMS watched goslings for a period between two and 15 minutes during which time their family status (size of family or type of non-family gosling) was established and behavioural data were collected using standardised procedures (as described below). 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 perimeter 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 50 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 geese, 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, *ie* a low density of good forage (Teunissen *et al.* 1985). While goslings were observed, the number and results of any aggressive encounters between the focal family and other geese 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 analyses since the interactions were used to define gosling status, so compromising the independence of the sample.

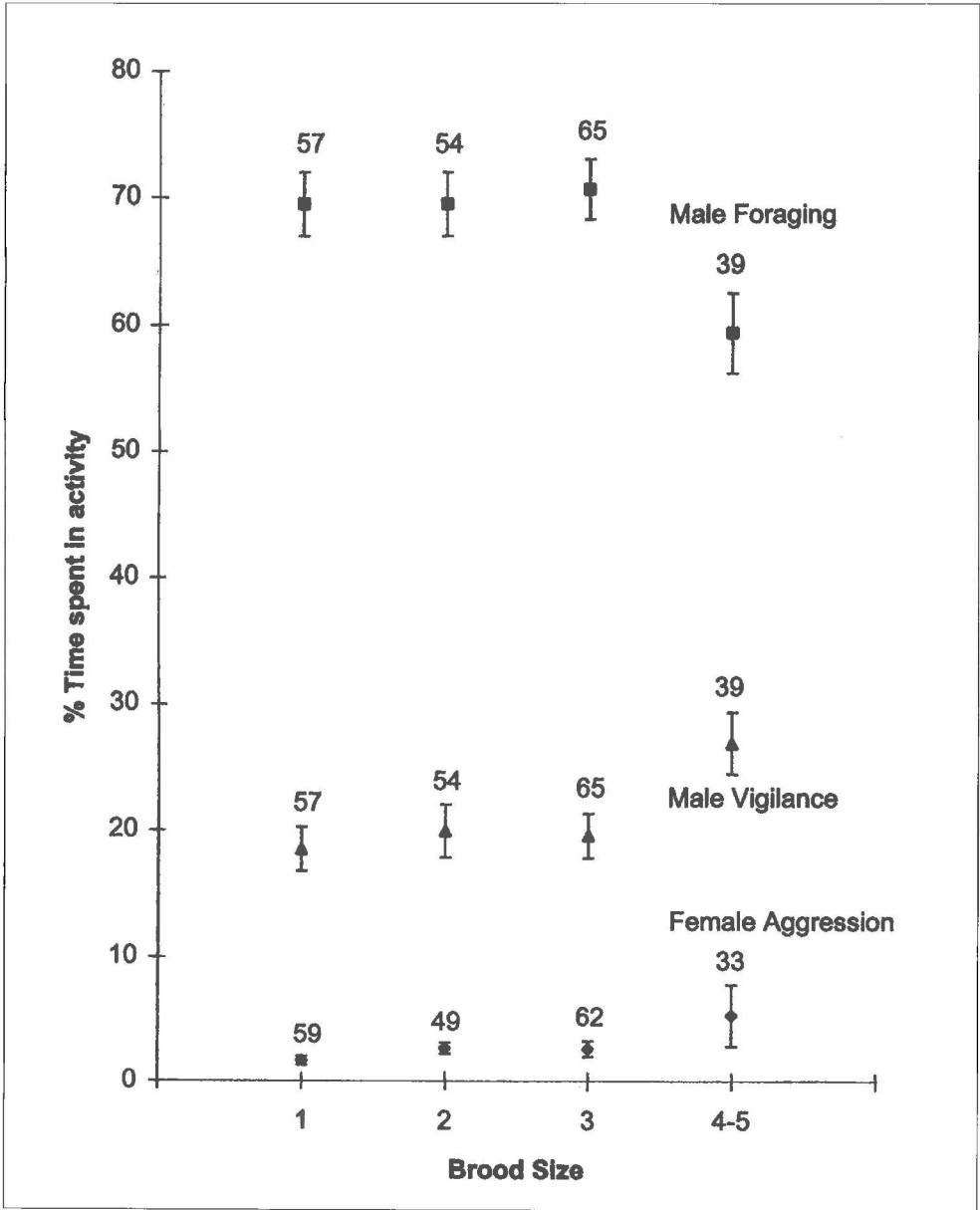


Figure 1. Activity budgets of parents attending broods of different sizes. Bars show \pm one standard error. Male parents of large families fed significantly less ($H = 9.88$, 3 d.f., $p = 0.020$), and spent significantly longer being vigilant ($H = 9.14$, 3 d.f., $p = 0.028$) than those with fewer young. Female parents with large families spent more time taking part in aggressive encounters than did the other classes ($H = 8.06$, 3 d.f., $p = 0.045$). Other activities did not vary among brood sizes for males (walking $H = 2.20$, $p = 0.532$; loafing $H = 1.55$, $p = 0.671$; comfort $H = 2.67$, $p = 0.446$; aggression $H = 1.49$, $p = 0.684$; all d.f.=3), or females (vigilance $H = 2.43$, $p = 0.488$; walking $H = 0.92$, $p = 0.822$; loafing $H = 5.26$, $p = 0.155$; grazing $H = 2.50$, $p = 0.476$; comfort $H = 1.82$, $p = 0.611$; all d.f.=3).

The data for each measure of the behaviour of adults and goslings described above were averaged by season (autumn = 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 vigilant 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 fewer young (**Figure 1**). The other activities of female parents showed little brood-size-related variation. A corresponding trend for parents to be involved in more aggressive encounters as family size increases was shown by Black & Owen (1989b).

Nearest neighbour distances

Parents maintained greater distances from other flock members than did non-parents (means (SEs) in goose lengths: parents 3.48 (0.19), non-parents 2.45 (0.24); Wilcoxon test: $W = 23685.0$, $p = 0.0008$). Similarly, goslings in families had larger nearest neighbour distances than did non-family goslings (means (SEs): 6.16 (0.28) versus 3.43 (0.20) goose lengths, $H = 72.42$, 1 d.f., $p < 0.001$). Neighbour distances differed for goslings in different sized families (**Figure 2**), there being 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., $p = 0.002$): 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%) versus 7.70% (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 $H = 2.80$, $p = 0.095$; social $H = 0.07$, $p = 0.793$; 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; time for 50 pecks for non-family goslings (mean (SE)) 22.40s (0.54s) and for family goslings 24.70s (0.46s), $H = 8.17$, $p = 0.04$; time for 10 steps (mean ((SE)) for non-family goslings 18.79s (0.70s) and for family goslings 23.82s (0.59s), $H = 29.22$, $p < 0.001$; 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) and 17 (4-5); time for 50 pecks: $H = 1.53$, $p = 0.675$; time for 10 steps: $H = 3.41$, $p = 0.333$; each 3 d.f.), or between the three strategies adopted by non-family goslings ($n = 107$ (single goslings), 87 (grouped goslings) and 10 (parasitic goslings); time for 50 pecks: $H = 1.68$, $p = 0.431$; time for 10 steps: $H = 4.44$, $p = 0.109$; each 2 d.f.).

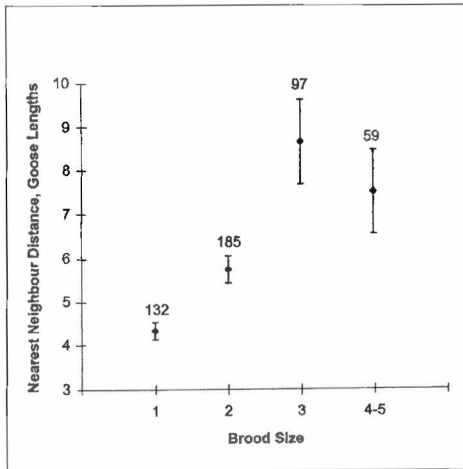


Figure 2. Distances to the nearest non-family neighbours of goslings in different brood sizes. Bars show \pm one standard error. Neighbour distances varied for goslings in different sized families ($H = 36.52$, 3 d.f., $p < 0.001$).

Aggressive encounters

Family goslings both won in more and lost in fewer interactions than would be expected by chance, compared to non-family young (see **Table 1**). The frequencies 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 parasitic goslings could not be included in this analysis they experienced a higher rate of losing encounters during observation periods (0.33 per min) than did the other single gosling types (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 behavioural 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 data sets 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 greater costs accrue to parents with large broods, i.e. increased vigilance and reduced feeding for males, and increased aggressiveness for females. If this limitation on 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 longer-term benefits (Black *et al.* 1992). This is due to the help that goslings give in fighting with and scanning for competitors/predators, and to the enhanced 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 fattening 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 walking between areas of suitable foraging, superior peck and step 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).

Gosling type	Duration observed, min	Winning encounters	Losing encounters
Family	2045	53 (45.3)	14 (46.1)
Non-family	707	8 (15.7)	65 (15.9)
χ^2 (1 d.f.), p		5.09, <0.025	87.16, <0.0005

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).

Brood size	Duration observed, min	Winning encounters	Losing encounters
1	721	26 (18.8)	5 (5.0)
2	746	16 (19.4)	7 (5.1)
3	414	9 (10.8)	3 (2.9)
4-5	154	2 (4.0)	0 (1.1)
χ^2 (3 d.f.)		4.65, N.S.	1.26, N.S.

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).

Gosling type	Duration observed, min	Winning encounters	Losing encounters
Single	554	6 (6.2)	43 (39.5)
Grouped	161	2 (1.7)	8 (11.5)
χ^2 (1 d.f.)		0.03, N.S.	1.38, N.S.

best. Goslings are also thought to learn useful social and foraging skills from parents during the prolonged parent-offspring association (Black & Owen 1987, Marshall & Black 1992).

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 live on the periphery 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 parasitic goslings probably paid a cost in terms of physical attacks from the 'host' family members (see also Black & Owen 1984). Parasite 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 (1989a) showed that the fatness 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 with fewer than four offspring (although, this is dependent on the fitness trade-off described above). In spring, when goslings are about six months of age, parental attacks on offspring substantially increase (Black & Owen 1989a). We suspect that goslings depart the family at the 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 1989a).

Future research must assess whether the

brood-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 brood sizes. So far, none 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 1986, survival and subsequent clutch size in Canada Geese; Rohwer & Heusmann 1991, survival in Wood Ducks *Aix sponsa*; Williams *et al.* 1994, mass and time of moult in Lesser Snow Geese *Chen caerulescens caerulescens*; Loonen 1997, mass and time of moult in Barnacle Geese). Indeed, Loonen (1997) found that the post-moult body mass of females was higher for those which had cared for larger broods. It is still possible, however, that fitness costs in many of the studies so far conducted have been obscured by the confounding effects of parental quality: more cross-fostering experiments of the kind widely used for altricial species (see review by Partridge 1990), but conducted only once with geese (Lessells 1986), are needed to resolve this.

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