Parent–offspring relationships in wintering barnacle geese

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Abstract. The relationship between parent geese, *Branta leucopsis*, and their offspring was monitored in order to discover some of the possible costs and benefits resulting from their association. Compared with birds without young the amount of time parents devoted to feeding was restricted in autumn and winter when they spent significantly more time being vigilant and aggressive. Family goslings fed without interruption for longer periods in autumn, were victims of attacks less often and grew fatter than unattached goslings. By the time the geese migrated to the breeding grounds in spring over 60% of goslings were unattached. The appearance of unattached young was related to the frequency of parental attacks on them and to inter-sibling aggression. However, the majority of parents were still associating with at least some of their brood after 9–10 months. Birds with more breeding experience associated with offspring for longer. Maintaining association with offspring did not reduce a parent's chances of surviving to, or breeding in, the following year. In fact, birds that remained with young for the longest period bred more successfully the next year than those with shorter periods of parental care. It is suggested that extended association with goslings may increase a parent's chances of breeding in the future due to the 'contributor' effect of the goslings that stayed in the family. Such goslings spend more time being vigilant and repelling neighbours which enables parents to increase their feeding time.

The benefit to parents from parental care is defined as the degree to which investment increases the survival of the offspring at hand and the cost as the degree to which the investment decreases the parent's ability to invest in future offspring (Parker 1985; Trivers 1985). In arctic nesting geese fat and nutrient reserves are thought to influence a female's reproductive success (Ryder 1970; Ankney & MacInnes 1978); heavy birds produce most offspring (Davies & Cooke 1983; Ebbinge, in press). During the early stages of reproduction, geese lose a substantial amount of weight (Owen 1980). This initial cost to breeding birds is apparent for at least 2 months after the nesting phase; it has been demonstrated, through brood size manipulations, that moulting date and weight are affected by the number of goslings in the brood in the summer (Lessells 1986). One further indication that parents suffer some cost in parental effort is the correlation between large brood sizes in the summer and delayed laying date the following season (Lessells 1986). In this paper, we attempt to assess any costs to *Branta leucopsis* parents and benefits to goslings while they associate as a family during the winter-

ing period. This is done by comparing the time budgets of family and non-family members as well as comparing the duration of parental care with parents' subsequent reproductive success and survival.

METHODS

The study was carried out on a migratory population of barnacle geese which breed in the Svalbard (Spitsbergen) archipelago and winter in the Solway Firth of northern Britain. Since 1973 more than 5000 birds have been marked with individually coded plastic rings; the codes can be read with a telescope at distances of up to 250 m. During the study, between 22 and 30% of the population (8400–10 500) had rings. There were over 15 000 sightings of ringed birds per annum. Determination of mates and the number of associated goslings were routine duties of ring readers (Owen 1982, 1984). Ringed birds' condition was also assessed according to the convexity of their abdomen using an index from 1 to 7. A weighted median abdominal profile was calculated for each successive 10-

day period through the season for each bird class (Owen 1981; Black & Owen 1987a). At least 40 individuals were assessed per point.

Behavioural observations were made on the Solway Firth during the wintering period (October–April 1982–1984), and in May 1986 in the Norwegian staging area. After determination of their pair and family status, focal birds were watched for as long as possible (usually 10 min) and their behaviour recorded on a cassette tape-recorder. The behaviour of up to three individuals (e.g. female, male and gosling of the same family) were recorded simultaneously. Time budgets were transferred onto a computer via an event recorder. A list of other behaviours and events not considered here can be found in Black (1987).

The time budgets of focal parent and non-parent paired adults (termed pairs) were compared in autumn (when goslings were 5 months old), winter and spring (when 10 months old). Data from 2 months were lumped according to seasonal changes: October + November = autumn, December + January = winter, and March + April = spring. February, a transition month, was excluded. Two sets of activities were chosen for comparison. The first included feeding and head-up vigilance. A barnacle goose devotes between 80% and 97% of its day to these two behaviours on the wintering grounds (Wells 1980; Black & Owen 1987a). Another measurable activity was the time spent in aggressive interactions. Threats and higher intensity attacks were lumped together (termed attacks), as aggression always resulted in the displacement of a subordinate (Black & Owen 1989). In goose flocks, an individual's time budget varies with its position in the flock (Inglis & Lazarus 1981). This was taken into account when comparing between classes by excluding data from positions that varied significantly from the edges of the flocks, where most samples were taken. Activity budgets were analysed in the form of percentage of total time devoted to each activity, its inter-bout interval and mean bout length.

The length of parent–offspring association was determined for pairs that had two or more sighting records with at least one gosling in attendance followed by two or more records with no goslings. The duration of gosling association was calculated from 1 July, the usual modal hatch date, and the mid-point between the last record with young and the first record without young. Birds included in the analysis were on average resighted 13·5 times
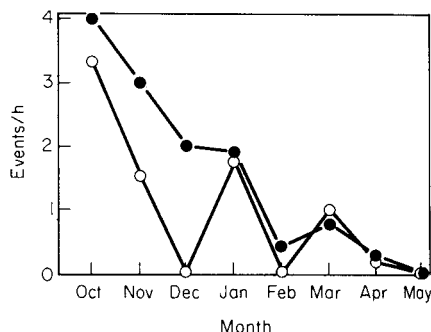

Figure 1. The frequency of food sharing by females (0, $N = 51$) and males (●, $N = 81$) through the study period.

(range 5–30 records). Parent–offspring associations were categorized as ending in autumn (92–154 days), winter (155–224 days) or later (spring and early summer).

Non-parametric two-tailed tests were employed (Siegel 1956) because of the extreme skewed distribution of the data. Because of the large number of significant results, marginally non-significant results and consistent trends in the data we were satisfied that our interpretation was not influenced by accepting spurious, chance statistical outcomes.

RESULTS

Food Sharing

Parents have a feeding behaviour that is strictly parental, termed here as 'food sharing'. Food sharing occurred when a parent allowed its gosling to feed on the same tussock of grass as itself. Normally if an unrelated goose tried to feed within two goose-lengths of another an attack would result. Food sharing was brief; after 1 or 2 s the parent invariably moved to feed in a new area.

The male shared food slightly more frequently than the female; males 1·82 times/h (44·4 h of observation) and females 1·2 times/h (42·5 h of observation), but this difference was not significant. Figure 1 shows that the frequency of food sharing declined from autumn to spring.

The Activities of Parents and Non-parents

Comparisons between the time budgets of parents and pairs revealed that parents' feeding time was restricted apparently because they devoted more time to vigilance and aggression, especially in

Table I. Comparison of parental males with non-parent paired males in autumn, winter and spring: potential parental effort behaviours (Mann–Whitney U-test)

Measure	Autumn			Winter			Spring		
	Parent	Non-parent		Parent	Non-parent		Parent	Non-parent	
Feeding									
% Time	66·8	85·1	***	77·5	89·6	*	78·4	86·0	NS
Mean bout length	17·7	21·1	*	18·4	25·6	**	22·6	21·1	NS
Inter-bout interval	24·9	24·4	NS	26·1	25·2	NS	27·9	23·9	NS
Vigilance									
% Time	21·3	7·6	***	15·0	6·1	**	12·0	6·5	*
Mean bout length	4·9	2·2	***	3·6	2·2	NS	3·4	2·2	**
Inter-bout interval	27·2	28·0	NS	25·3	33·6	*	26·6	28·0	NS
Aggressor									
% Time	0·6	0·0	*	0·7	0·0	NS	0·4	0·0	NS
Mean bout length	2·6	1·9	NS	2·2	2·7	NS	1·5	1·5	NS
Inter-attack interval	221·1	251·8	NS	172·5	251·8	NS	250·1	258·7	NS
Victim									
% Time	0·0	0·0	NS	0·0	0·0	NS	0·0	0·0	NS
Inter-attack interval	431·8	380·0	NS	489·0	294·2	NS	460·1	387·2	NS
Birds observed	39	54		30	19		41	41	
Total time (h)	6·3	6·5		4·3	2·3		6·8	6·2	

Data for male comparisons were from the side edge, inside edge, centre and mixed flock positions. Bouts and intervls are in seconds.
* P < 0·05; ** P < 0·01; *** P < 0·001.

autumn and winter (Table I). In spring, parental males still spent more time being vigilant but the difference in feeding measures disappeared. The behaviour of females was similar except that the disparity in time spent feeding disappeared in winter rather than spring, and disparity in vigilance measures dropped in spring (Table II). When data from all months were lumped together, male parents spent more of their time being vigilant and less time feeding than their mates (Mann–Whitney U-test, (males $N = 341$, females $N = 327$) $P < 0·001$ for both activities). In pairs without young there was no significant difference in the amount of time males and females were vigilant but females fed significantly more (Mann–Whitney U-test (males $N = 115$, females $N = 110$), % time, $z = 2·19$, $P < 0·05$).

Parental males were more frequently the aggressor in conflicts and were the victim less often than non-parental males in all months; but these differences were not quite significant except when all months were lumped together (Black & Owen 1989). Parental females were consistently and significantly more aggressive than non-parent females.

Goslings In and Outside the Family Unit

In autumn, family goslings grazed without interruption for longer periods and were victims significantly less frequently than unattached goslings (Table III). In spring, family goslings began to attack conspecifics to a greater extent than unattached young.

Figure 2 shows that males were the most active family member in conflict situations but their effort declined steadily from December. The goslings' aggressive effort increased from February to match the parents' in April and May.

Family Membership and Body Condition

There were no differences in the abdominal profile index between non-parent and parental females or males throughout the wintering period.

The number of unattached young was small until spring, when their profiles were compared with those of family juveniles. Figure 3 shows that family gosling profiles were consistently larger than those of unattached young. This difference was tested by categorizing the number above, below

Table II. Comparison of parental females with non-parent paired females in autumn, winter and spring: potential parental effort behaviours (Mann–Whitney U-test)

Measure	Autumn			Winter			Spring		
	Parent	Non-parent		Parent	Non-parent		Parent	Non-parent	
Feeding									
% Time	73·2	90·9	***	85·4	89·6	NS	84·7	91·1	NS
Mean bout length	26·9	31·5	NS	21·6	28·3	NS	27·1	30·8	NS
Inter-bout interval	36·9	33·8	NS	26·5	33·8	NS	31·8	33·6	NS
Vigilance									
% Time	13·4	4·3	***	9·5	4·6	**	7·4	4·3	NS
Mean bout length	5·1	1·9	***	3·1	1·9	NS	2·6	1·9	NS
Inter-bout interval	40·5	42·6	NS	28·8	37·1	*	33·6	40·5	NS
Aggressor									
% Time	0·3	0·0	***	0·2	0·0	NS	0·3	0·0	**
Mean bout length	2·4	1·3	***	13·5	13·7	NS	2·1	1·0	**
Inter-attack interval	262·0	371·6	**	210·8	339·0	NS	263·6	371·6	*
Victim									
% Time	0·0	0·0	NS	0·0	0·0	NS	0·0	0·0	NS
Inter-attack interval	452·4	367·1	*	371·3	339·0	NS	421·0	378·8	NS
Sample size	65	59		37	20		43	44	
Total time (h)	11·5	8·8		5·1	2·6		7·0	6·5	

Data for comparisons were from the side edge, centre, inside edge, leading edge and mixed flock positions. Bouts and intervals are in seconds.
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

and at the median value ($N = 170$). The test was highly significant ($x^2 = 40.6$, $df = 2$, $P < 0.001$) in favour of larger profiles for family goslings.

Possible Conflict Between Parents and Offspring

When a goose is attacked by a higher-ranking mate or kin, it submits by lowering its head and gives a characteristic vocalization (Radesater 1974). This behaviour (referred to as a 'greeting') is part of the Triumph Ceremony which when fully developed contains repetitive calls and exaggerated head and neck movements (Black & Owen 1987a). The behaviour is thought to appease a more aggressive bird, thus facilitating continued association (Fischer 1965).

Parents were seen attacking their young throughout the study period. However, attacks were usually of low intensity and infrequent until February, when goslings were 8 months of age. It appeared that performance of greeting displays by goslings appeased these attacks (Fig. 4). In May,

however, goslings showed fewer greeting responses and at the same time parental attacks increased threefold. Figure 5 shows that the proportion of unattached goslings increased until May, when over 60% of the young were separated (all were split up by mid-June).

Separation takes place by reduction in the number of brood members rather than the breakup of whole families. Mean brood size when the geese arrived in Scotland, October 1984, excluding unattached goslings, was 2·46 ($SE = 0.05$, $N = 314$ families). In March and April, brood size was 2·1 ($SE = 0.05$, $N = 338$). On arrival at the Norwegian staging islands, it had declined to 1·44 ($SE = 0.07$, $N = 48$), and to 1·08 ($SE = 0.06$, $N = 25$) in the week prior to departure to the breeding grounds. Some of the reduction was due to gosling mortality (5% during winter, Owen 1982), but was mostly due to separation.

If families break up gradually, it would be expected that pairs with large initial broods would be associated with at least part of their brood for longer than those with small broods. Figure 6

Table III. Comparison of family goslings with separated goslings in autumn, winter and spring: potential benefits from parental association to goslings (Mann–Whitney U-test)

Measure	Autumn			Winter			Spring		
	Family	Separated		Family	Separated		Family	Separated	
Feeding									
% Time	87·3	79·6	NS	91·3	81·5	NS	84·4	86·2	NS
Mean bout length	48·6	18·1	*	38·2	24·6	NS	36·1	49·3	NS
Inter-bout interval	54·6	36·9	NS	44·3	24·7	NS	40·3	51·3	NS
Vigilance									
% Time	3·1	4·8	NS	2·3	8·6	NS	5·8	3·2	NS
Mean bout length	3·0	2·5	NS	1·7	3·2	NS	3·3	2·7	NS
Inter-bout interval	63·9	44·5	NS	57·2	51·3	NS	49·0	51·3	NS
Aggressor									
% Time	0·0	0·0	NS	0·0	0·0	NS	0·2	0·0	*
Mean bout length	2·6	1·3	NS	1·9	0·7	NS	2·1	1·0	*
Inter-attack interval	362·6	223·0	NS	315·4	338·7	NS	233·5	254·8	NS
Victim									
% Time	0·0	0·2	***	0·0	0·3	**	0·0	0·0	NS
Inter-attack interval	428·8	204·6	***	353·7	146·9	*	405·4	221·5	**
Sample size	41	22		36	6		41	15	
Total time (h)	6·7	2·7		4·7	1·1		7·0	1·5	

Data for gosling comparisons were from the side edge, centre, inside edge and mixed flock positions. Bouts and intervals are in seconds.
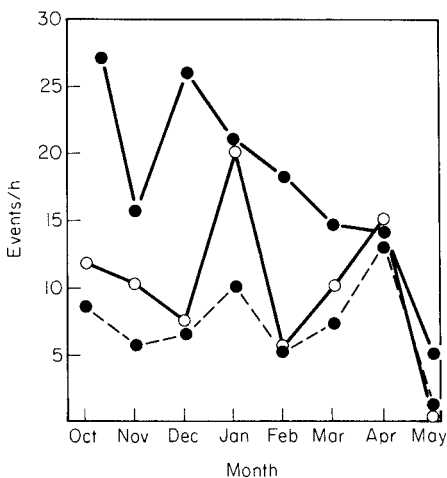* P < 0·05; ** P < 0·01; *** P < 0·001.

Figure 2. Frequency of aggressive conflicts with neighbours by family members through the study period (parent females, ○ N = 404; parent males, ● N = 679; family juveniles, ●– – –● N = 290).
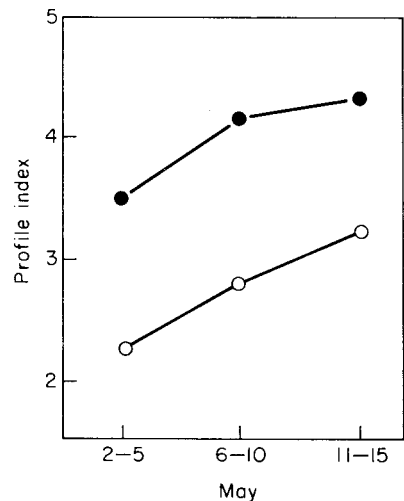

Figure 3. Comparison of abdominal profiles for family and unattached goslings during 3 weeks on the Norwegian staging islands. Mean sample sizes are 23·7 (SD = 6·8) for family juveniles (●) and 33·0 (SD = 12·1) for unattached juveniles (○). Points are weighted medians (Owen 1981).
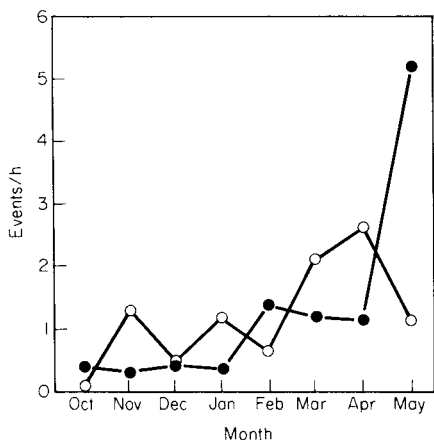
Figure 4. The frequency of parental threats and attacks at their own offspring (female $N=27$; male $N=99$, ●) and the frequency of goslings' greeting displays ($N=96$, ○).

shows that parent–offspring association increased with brood size (Spearman rank correlation, season mean duration, $r_s = 1.0$, $N=5$, $P < 0.01$).

Parenthood and Future Breeding

Because the geese are prone to disastrous breeding in some years (Owen 1984), comparisons were limited to the years of moderate breeding: 1982 (21% of birds more than 3 years old bred, $N=680$
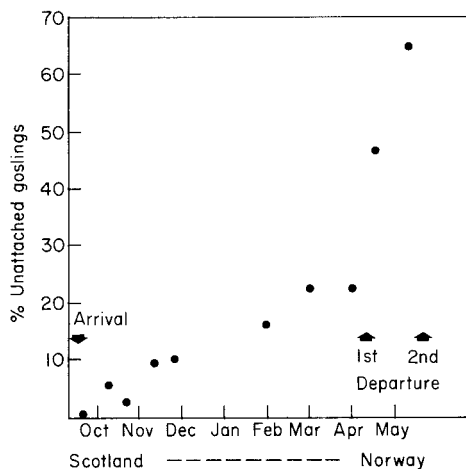

Figure 5. The percentage of unattached goslings from counts made through the study period in relation to the timing of migration from Scotland and Norway ($N=2418$ goslings).

females), 1983 (14%, $N=662$) and 1984 (36%, $N=554$). The duration of parental care in this comparison was not controlled for; the definition of reproductive success used here is association with young at least to autumn in Scotland. Since survival after this stage is high (Owen 1982), this is close to real reproductive success (i.e. contributing to the next breeding generation). Age-related reproductive success was also controlled for by excluding birds of less than 4 years old (Owen 1984).

The hypothesis that the amount of parental effort affects future reproduction (Trivers 1974) was tested: do birds that bred in the first year have lower reproductive success the next year than birds that did not breed the first year? Clearly, the 2×2 contingency chi-squared tests reveal that breeding successfully in 2 successive years is independent; thus it appears that hatching and rearing young (till autumn) does not lessen a bird's chances of producing young in the future (Table IV).

Family Duration and Future Reproductive Success

Of the calculated parent–offspring associations, 16% ended in autumn, 22% in winter and 62% in spring ($N=433$). To establish whether the duration of parent–offspring association influenced a bird's ability to produce offspring in the future we checked each bird's reproductive success in the next year and categorized positive and negative success according to the previous year's parent–offspring association. If there is a cost to parental effort during the duration of parent–offspring association, and if these costs affect the future success, then birds that invest in their young for the shortest time will be more likely to bring young back the next year. Females that associated with their young through to spring returned more often the next year with offspring than parents that split with their young earlier ($\chi^2 = 10.4$, $df=1$, $P < 0.01$, Table V). The trend was the same for males but was not quite significant ($\chi^2 = 3.65$, $df=1$, $P < 0.1$).

Duration of Parent–Offspring Association

The likelihood of a change in parent–offspring association from one year to the next was tested in 52 individuals by cataloguing their durations in 2 consecutive years (Table VI). When a change did occur, the parent–offspring association increased 14 out of 16 times (binomial test, $P=0.004$). Only 6% of the birds that kept their young till spring in
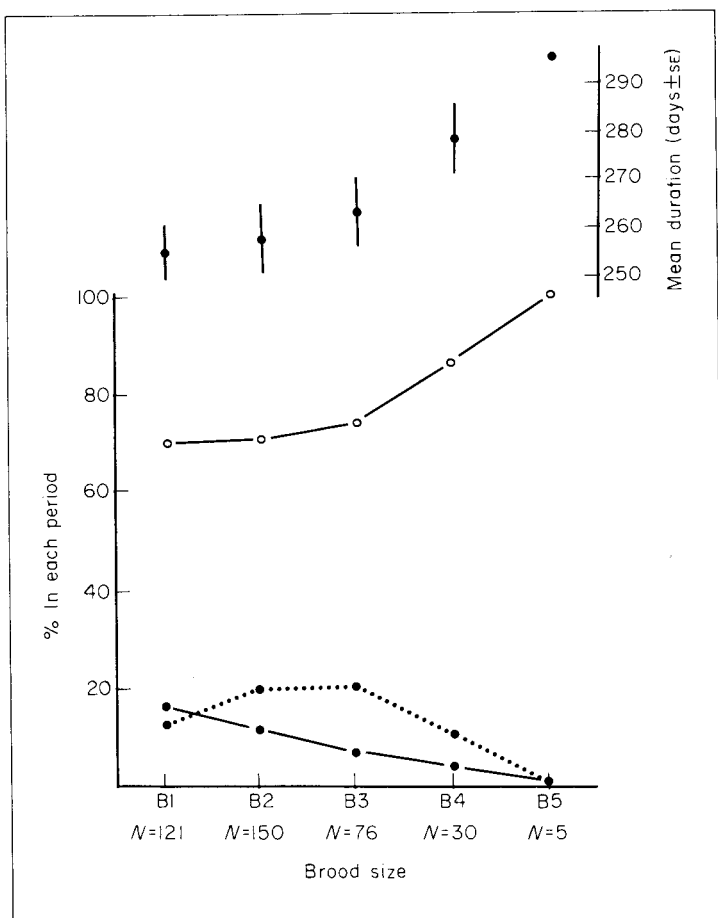
Figure 6. The percentage of different parent–offspring durations that ended in autumn (●———●), winter (●. . .●) and spring (○) for families of different sizes. Initial brood size was determined at the beginning of the study period; including data from all years. At the top of the figure is the seasonal mean duration for each brood class (*N* = total number of broods).

the first year had shorter parent–offspring associations the next year.

Effect of breeding experience

To detect whether the duration of parent–offspring association was related to previous breeding experience we calculated the proportion of associations that lasted until autumn, winter and spring for birds who previously brought young back for 1 or more years.

The duration of association for both females (*N* = 254) and males (*N* = 259) increased with breeding experience (Table VII). The frequency of spring durations was correlated with the number of years a bird brought young to Scotland (females $r_s = 1·0$, $P < 0·01$). The trend for males was in the

same direction but was not significant. However, this result must be thought of as preliminary until the sample of birds that bred in 4 or more years increases.

Effect of Parental Effort on Survival

If associating with young is costly to parents then survival, as future reproductive success, should be affected. This was investigated by determining an individual's reproductive success in one year and seeing if it was more or less likely to return the next year. Data included birds of more than 3 years. The rate of mortality for this sample of birds was the same for all ages except those ringed before 1973 (Owen 1982). These were excluded. Table VIII lists

Table IV. The relationship between breeding in one year and breeding in the next

	Females > 3 years				Males > 3 years			
	1982–1983 comparison		1983–1984 comparison		1982–1983 comparison		1983–1984 comparison	
	%	(N)	%	(N)	%	(N)	%	(N)
First/second								
+/+	3·2%	(17)	3·2%	(20)	2·4%	(13)	4·1%	(27)
+/0	18·3%	(98)	10·0	(62)	20·4%	(110)	9·0%	(59)
0/+	10·3%	(55)	26·9%	(166)	10·8%	(58)	24·7%	(161)
0/0	68·3%	(366)	59·8%	(369)	66·4%	(357)	62·1%	(405)
Total		(536)		(617)		(538)		(652)
% Bred next year								
Breeders	15%		24%		11%		31%	
Non-breeders	13%		31%		14%		28%	
χ^2	0·23		1·49		0·96		0·32	
P	NS		NS		NS		NS	

+: at least one gosling, 0: no goslings.

Table V. Parent–offspring association and success in bringing back young to the wintering grounds in the following year

Timing of family duration (days)	Female success		Male success	
	+ to +	+ to 0	+ to +	+ to 0
Autumn (92–154)	0	9	0	9
Winter (155–224)	0	19	4	22
Later (>224)	35	88	37	101

+: at least one gosling: 0: no goslings.
Data includes durations from 1982 to 1984.

Table VI. Distribution of parent–offspring association periods in 2 consecutive years

Duration in the second year	Duration in the first year		
	Autumn	Winter	Spring
Autumn	1	0	0
Winter	1	2	2
Spring	5	8	33

Table VII. Variation in parent–offspring duration with previously successful breeding years (age/experience)

No. of previously successful years	Parent–offspring association period			Percentage in spring
	Autumn	Winter	Spring	
Females				
1	24	22	98	68%
2	9	10	47	71%
3	5	2	24	77%
4	0	1	10	91%
5	0	0	2	100%
Males				
1	17	19	97	73%
2	10	13	60	72%
3	2	5	20	74%
4	0	0	11	100%
5	0	0	5	100%

the results. There were no significant differences in the mortality rates of either sex. More than 95% of individuals were resighted annually which meant that the chance of mistakenly assuming a bird to be dead was only 0·14% (Owen 1982).

DISCUSSION

In geese, young birds are thought to learn the

Table VIII. The relationship between breeding in one year and surviving in the next

	Females > 3 years				Males > 3 years			
	1982–1983 comparison		1983–1984 comparison		1982–1983 comparison		1983–1984 comparison	
	%	(N)	%	(N)	%	(N)	%	(N)
Breeding and survival status (bred/alive)								
+/+	17·8%	(140)	9·5%	(71)	18·1%	(139)	10·5%	(80)
+/0	1·8%	(14)	2·1%	(16)	2·2%	(17)	2·2%	(17)
0/+	73·5%	(578)	74·8%	(561)	72·7%	(557)	74·1%	(566)
0/0	6·9%	(54)	13·6%	(102)	6·9%	(53)	13·2%	(101)
Total		(786)		(750)		(766)		(764)
% Mortality								
Breeders	9%		18%		11%		18%	
Non-breeders	9%		15%		9%		15%	
χ^2	0·05		0·52		0·73		0·37	
P	NS		NS		NS		NS	

On the left of the /; +: bred and 0: did not breed.
On the right of the /; +: alive the next year and 0: dead the next year.

migratory route and wintering area from their parents (Owen 1980). Once they arrive, the parents can either associate with their young for as long as possible or expel them some time after arrival. Which strategy they choose will depend on the relative costs and benefits to parents and offspring and the effect that parental effort has on future events.

Goslings belonging to the highest-ranking social class, the family, eat better foods, suffer fewer displacements, feed without interruption for longer bouts and gain more weight than unattached goslings (Black & Owen 1984, 1989, this study). Offspring may also benefit from learning important social skills from parents (Trivers 1985) such as when to compete and when to retreat in conflicts. Goslings reared by aggressive parents dominate those reared by less aggressive birds after both have fledged and are no longer part of the family (Black & Owen 1987b). Survival to fledging age is also highest for goslings belonging to the most aggressive parents (Black & Owen 1987b). Another important skill concerns the selection of the most profitable foods. This would be especially desirable for geese, which have an inefficient digestive system, and whose main foods are relatively low in nutritional content (Owen 1980). Initially, goslings feed on different foods than adults, then switch to the same types after a month (Madsen & Fox 1981).

Since parents devote less time to food sharing each month over the wintering period it might be assumed that goslings are gradually learning appropriate feeding skills. It would therefore appear that the first option, keeping offspring in the family, would ensure parents that their offspring had better chances of survival.

However, maintaining association would be adaptive only if continued association with offspring did not excessively decrease the parents' future reproductive success. For their offspring to enjoy benefits from parental care, parents devote substantial effort to parental duties which appears to impinge on their overall time budget. Such duties include food sharing, chasing neighbours away and being vigilant. Besides scanning for potential food competitors and predators parents probably also devote a proportion of their time to monitoring goslings' proximity (Black 1987). At least five other goose studies (four during the post-hatch period and one during the winter) and another on wintering swans contribute to documenting parental effort costs, assuming Trivers' (1974) definitions: differences in parent/non-parent time budgets, changes in time budgets with brood size, and a decrease in parental duties with increasing offspring age (Lazarus & Inglis 1978; Scott 1980; Madsen 1981; Lessells 1987; Schindler & Lamprecht 1987; Black & Owen 1989). The second

option, expelling goslings soon, would therefore mean parents could save further parental effort for future broods.

Despite the measurable parental effort costs inferred from differing parent/non-parent time budgets in this study, parent birds appear to be able to replenish fat reserves that were lost initially during the nesting phase and continue to compensate for any losses due to continued association. Furthermore, birds that breed one year do not suffer in their ability to breed the next year nor is there any difference in mortality after successful breeding. In fact, those birds that keep at least one of their young into spring are significantly more likely to return the next year with another brood.

Why, then, do not all parents keep some offspring for as long as possible? The benefits to parents from parental care diminish faster than the benefits to offspring since the parental benefit is one-half that for each offspring (Lazarus & Inglis 1986). Thus, conflict will arise near the time when parents decide that young are capable of coping on their own and when additional parental effort may decrease the parents' ability to produce more young.

For the population as a whole a measurable conflict between parents and offspring appears after the coldest mid-winter months when parents begin threatening and biting their young with increasing frequency. Although goslings may be trying to thwart these attacks by performing greeting postures and vocalizations, more and more unattached goslings appear in the flocks.

There are two types of offspring as identified in theoretical models for life-long monogamous species. If juveniles take more parental effort than parents are selected to give, they become 'conflictors', causing a decline in parents' fecundity, and 'non-conflictors' if they do not (Parker & MacNair 1978; Parker 1985). A third possibility is for an offspring to increase a parent's reproductive potential. Such offspring have been labelled 'helpers' when it refers to older offspring assisting in the care of subsequent siblings (Emlen 1984; Woolfenden & Fitzpatrick 1984). In species like geese in which siblings rarely overlap it may also be possible for offspring to increase their parents' future reproductive success by lessening the parental burden in other ways besides duties associated with younger siblings; such offspring could be termed 'contributors'. For geese it seems that those goslings that stay in the family are in agreement with their

parents over the amount of parental effort that is given and taken: a compromise scenario (MacNair & Parker 1979). The goslings that are expelled, on the other hand, would presumably have become conflictors due to feeding competition within the family which results when goslings become more proficient feeders.

We hypothesize that one of the reasons that parents retaining broods do not suffer in terms of replenishing and building essential fat reserves is because of the behavioural contributions of the goslings that stay in the family. We suggest that, rather than deceiving a parent about their need for more investment (Trivers 1974), goslings that stay in the family assist parents. The status of goslings that stay or leave is unknown at this point. However, since a dominance rank order develops within broods relative to a gosling's sex, age, size and experience in encounters (Black & Owen 1987b), high-ranking siblings may influence the order in which brood members leave. Both parents and dominant siblings attack smaller goslings to the point at which it is more profitable for subordinate siblings to leave the family (see Pierotti & Murphy 1987). In late spring smaller goslings spend more time at greater distances from the parents (Black 1987).

Two of the ways in which goslings may help their parents are: decreasing the parents' vigilance burden by increasing their own, and by lessening the parents' burden in conflicts with neighbours by initiating and winning more conflicts (see Brown 1982). In the present study, family goslings increased their aggressive effort through the wintering period and, by spring, parents spent as much time feeding as non-parents. However, we can only speculate about the cause and effect of this relationship. If parents do have more time for feeding in spring because of their offsprings' behaviour, then compared with birds that expel offspring earlier they should acquire more fat reserves not only because of the time budget effect but also because family units spend more time feeding in areas with more plant biomass (Black & Owen 1989).

Given that fat reserves are important for future breeding attempts, retaining at least some of the brood appears to be the most profitable option for barnacle geese. The concept of contributor offspring that help parents may explain why the parents in this study that kept their young longest bred better the next year and why Lessells (1986) found that in Canada geese, *Branta canadensis*,

males that suffered the stresses of reproduction but subsequently lost their brood did not breed as well in the following year.

Table VII provides preliminary evidence that parent–offspring associations are shorter for birds with less experience. We also know that parents' aggressive effort increases with breeding experience (Black & Owen 1989). In another study, we speculated that the presence of pairs with less mutual experience was the reason for the correlation between pairing too close to the breeding season and low reproductive success (Owen et al. 1987). If this is the case, a pair/parental quality effect related to accumulated experience may explain why some goslings leave the family early and why some parents have longer associations with offspring. On the other hand, if bird quality, rather than the contributor-offspring effect, was responsible for the relationship between the duration of parent–offspring association and reproductive success, the next year we would expect to find significant variation in individual reproductive rates. Table IV shows that the probability that the same birds breed or fail to breed 2 years in a row is similar to that expected by chance. Owen (1984) also showed that the frequency distribution of the number of years that individuals breed successfully in the population was not significantly different from that expected from a random (Poisson) distribution. It seems, therefore, that bird quality may not be completely responsible for differences in future reproduction.

ACKNOWLEDGMENTS

REFERENCES

Ankney, C. D. & MacInnes, C. D. 1978. Nutrient reserves and reproductive performance of female lesser snow geese. *Auk*, **95**, 459–471.

Black, J. M. 1987. The pair-bond, agonistic behaviour and parent–offspring relationships in barnacle geese. Ph.D. thesis, University of Wales, Cardiff.

Black, J. M. & Owen, M. 1984. The importance of the family unit to barnacle goose offspring: a progress report. *Skrifter*, **181**, 79–85.

Black, J. M. & Owen, M. 1987a. Variation in pair-bond and agonistic behaviors in barnacle geese on the wintering grounds. In: *Waterfowl in Winter* (Ed. by M. Weller), pp. 39–57. Minneapolis: University of Minnesota Press.

Black, J. M. & Owen, M. 1987b. Determinant factors of social rank in goose flocks: acquisition of social rank in young geese. *Behaviour*, **102**, 129–146.

Black, J. M. & Owen, M. 1988. Agonistic behaviour in barnacle goose flocks: assessment, investment and reproductive success. *Anim. Behav.*, **37**, 199–209.

Brown, J. L. 1982. Optimal group size in territorial animals. *J. theor. Biol.*, **95**, 793–810.

Davies, C. J. & Cooke, F. 1983. Annual nesting productivity in snow geese: prairie droughts and arctic springs. *J. Wildl. Mgmt*, **47**, 291–296.

Ebbinge, B. S. In press. Do lemmings really rule the Arctic: a plea for a multifactorial explanation for variation in breeding performance in brent geese *Branta bernicla bernicla*. *Ibis*.

Emlen, S. T. 1984. Cooperative breeding in birds and mammals. In: *Behavioural Ecology*. 2nd edn (Ed. by J. R. Krebs & N. B. Davies), pp. 305–339. Oxford: Blackwell Scientific Publications.

Fischer, H. 1965. Das Triumphgeschrei der Graugans. *Z. Tierpsychol.*, **22**, 247–304.

Inglis, I. R. & Lazarus, J. 1981. Vigilance and flock size: brent geese. The edge effect. *Z. Tierpsychol.*, **57**, 193–200.

Lazarus, J. & Inglis, I. R. 1978. The breeding behaviour of the pink-footed goose: parental care and vigilant behaviour during the fledging period. *Behaviour*, **65**, 62–88.

Lazarus, J. & Inglis, I. R. 1986. Shared and unshared parental investment, parent–offspring conflict and brood size. *Anim. Behav.*, **34**, 1791–1804.

Lessells, C. M. 1986. Brood size in Canada geese: a manipulation experiment. *J. Anim. Ecol.* **55**, 669–689.

Lessells, C. M. 1987. Parental investment, brood size and time budgets: behaviour of lesser snow geese *Anser c. caerulescens*. *Ardea*, **75**, 189–204.

Macnair, M. R. & Parker, G. A. 1979. Models of parent–offspring conflict. III. Intrabrood conflict. *Anim. Behav.*, **27**, 1202–1209.

Madsen, J. 1981. Post hatching behaviour of families and non-breeding Greenland white-fronted geese. In: *Greenland White-fronted Goose Study: Report of the 1979 GWGS Expedition to Eqalungmiut Numat, West Greenland* (Ed by A. D. Fox & D. A. Stroud), pp. 116–122. Aberystwyth: National Library of Wales.

Madsen, J. & Fox, A. D. 1981. The summer diet of the Greenland white-fronted goose. In: *Greenland White-fronted Goose Study: Report of the 1979 GWGS expedition to Eqalungmiut Numat, West Greenland* (Ed. by A. D. Fox & D. A. Stroud), pp. 108–115. Aberystwyth: National Library of Wales.

Owen, M. 1980. *The Wild Geese of the World. Their Life History and Ecology*. London: Batsford.

Owen, M. 1981. Abdominal profile: a condition index for wild geese in the field. *J. Wildl. Mgmt,* **39,** 271–279.

Owen, M. 1982. Population dynamics of Svalbard barnacle geese, 1970–1980. The rate, pattern and causes of mortality as determined by individual marking. *Aquila,* **89,** 229–247.

Owen, M. 1984. Dynamics and age structure of an increasing goose population: the Svalbard barnacle goose *Branta leucopsis. Skrifter,* **181,** 37–47.

Owen, M., Black, J. M. & Liber, H. 1987. Pair-bond duration and timing of its formation in barnacle geese, *Branta leucopsis.* In: *Waterfowl in Winter* (Ed. by M. Weller), pp. 23–38. Minneapolis: University of Minnesota Press.

Parker, G. A. 1985. Models of parent–offspring conflict. V. Effects of the behaviour of the two parents. *Anim. Behav.,* **33,** 519–533.

Parker, G. A. & Macnair, M. R. 1978. Models of parent–offspring conflict. I. Monogamy. *Anim. Behav.,* **27,** 1210–1235.

Pierotti, R. & Murphy, E. C. 1987. Intergenerational conflict in gulls. *Anim. Behav.,* **35,** 435–444.

Radesater, T. 1974. On the ontogeny of orienting movements in the triumph ceremony in two species of geese (*Anser anser* L. and *Branta canadensis* L.). *Behaviour,* **50,** 1–15.

Ryder, J. P. 1970. A possible factor in the evolution of clutch size in Ross' geese. *Wilson Bull.,* **82,** 5–13.

Schindler, M. & Lamprecht, J. 1987. Increase of parental effort with brood size in a nidifugous bird. *Auk,* **104,** 688–693.

Scott, D. K. 1980. Functional aspects of prolonged parental care in Bewick's swans. *Anim. Behav.,* **28,** 938–952.

Siegel, S. 1956. *Nonparametric Statistics for the Behavioral Sciences.* Tokyo: McGraw-Hill.

Trivers, R. L. 1974. Parent–offspring conflict. *Am. Zool.,* **14,** 249–265.

Trivers, R. L. 1985. *Social Evolution.* Menlo Park, California: Benjamin/Cummings.

Wells, R. 1980. The ecology, behaviour and energetics of barnacle geese (*Branta leucopsis*) wintering in South West Scotland. Ph.D. thesis, University of Bristol.

Woolfenden, G. E. & Fitzpatrick, J. W. 1984. *The Florida Scrub Jay.* Princeton: Princeton University Press.