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FACTORS AFFECTING THE SURVIVAL OF BARNACLE GEESE ON MIGRATION FROM THE BREEDING GROUNDS

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SUMMARY

(1) The survival of 1594 adult, 153 yearling and 439 young barnacle geese *Branta leucopsis* between the breeding area in Svalbard and the wintering area in Scotland was determined by individual marking in 1986. Annual resighting rates of birds alive and ringed is in excess of 95% annually, so the non-sighting of a bird in 2 consecutive years is a good indication of its death (ring loss is negligible over the first 3 years).

(2) Birds were caught in seven different parts of the breeding area; there were highly significant differences in body mass and moult stage of adults, and in the age and body mass of goslings, between areas.

(3) On arrival in Scotland, after an early onset of winter in Svalbard in 1986, paired adult geese were in poor body condition; the poorest of the 8 years for which data are available.

(4) Of the 1747 full-grown geese (adults and yearlings) marked in summer 1986, 1668 (95.5%) were seen in the wintering area, either in the following winter or in 1987–88 (a minimum survival rate), compared with 65.1% of birds ringed as goslings. Losses in other years were much lower.

(5) Gosling survival was related to their age and body mass (corrected to the median catching date). Only three of fifteen young (20%) weighing under 600 g on 1 August were seen in Scotland, compared with more than 70% of those over 700 g. The effect of age was not as great. The effect of body mass was significant within each of the three most common age-groups, so body mass affected survival independently of age.

(6) There were indications that breeding and brood rearing affected female body mass and probably survival; those females returning to Scotland with broods were heavier than those that had nested (brood patch present) but had no young in winter. There were several possible explanations for this.

(7) This population has recently shown a density-dependent decline in recruitment. This study showed that, despite the fact that density-related factors had acted earlier in the breeding cycle, competition between families on the rearing areas still resulted in a reduction in recruitment through mortality of young on migration; the density effect was magnified by an early onset of winter in 1986.

(8) Post-fledging mortality has been studied in few migratory species, and whether or not substantial migration loss has been demonstrated depends on the situation and species. Losses on autumn migration probably represent a substantial proportion of first-year mortality in those species that undertake long migrations without the opportunity of feeding in transit.

INTRODUCTION

Arctic animals have a limited period in which to breed, which makes the timing of their reproduction crucial to its success. In many migratory birds, including geese, fat and protein reserves for breeding are carried to the nesting areas (Ryder 1970; Pienkowski & Evans 1985), and if these are not used up quickly for breeding they become depleted because of the animals' requirements for maintenance energy. Late nesting also jeopardizes the chances of the young to mature sufficiently before autumn migration (Barry 1962; Perrins 1966).

Populations of migratory birds are usually studied either on the breeding grounds or in winter. The losses between egg-laying and fledging, and mortality after arrival on the wintering area can be quantified, but it is rarely possible to estimate the losses incurred on the journey between the nesting and wintering areas. Yet many species undertake hazardous long-distance migrations over the sea with the potential for considerable mortality in transit. The effect of density-dependent factors that act on migratory bird populations is poorly understood (O'Connor 1985), except perhaps in seabirds (Birkhead & Furness 1985).

Most wild geese are legal quarry for hunters and the majority of their deaths are due to shooting. There have been very few studies of natural sources of mortality; indeed the losses from natural causes seem to be very small for most geese (Owen 1980). Because of the relatively high hunting pressure, goose populations are often not exposed to density-related factors which would act on a naturally regulated population.

In one population of barnacle geese, *Branta leucopsis* (Bechstein) which is protected throughout its life cycle, natural mortality accounts for half the deaths. The autumn migration, which is in excess of 3000 km, mostly over the sea, is one of the most demanding and hazardous stages in the life cycle (Owen & Gullestad 1984). The stresses of breeding, particularly in females, which are emaciated after incubation, may be manifested in deaths on autumn migration (Owen 1982). The population has shown density-dependent decline in breeding success since the early 1970s; this may partly be brought about by competition between families for food during the rearing period (Owen 1984). There is some direct evidence that such competition exists, from studies on the breeding grounds (Prop, van Eerden & Drent 1984). Inter-family competition could result in some of the young failing to gain sufficient body reserves to complete the autumn migration and dying on the journey (Owen 1984).

This paper describes a study in 1986 to test the hypothesis that mortality on migration, particularly in juveniles and breeding females, is an important factor limiting the growth of this population of barnacle geese.

STUDY POPULATION, BACKGROUND AND METHODS

The research is part of a long-term study into the ecology and dynamics of the closed population of barnacle geese that winters on the Solway Firth in northern Britain and breeds in the Svalbard archipelago, chiefly on the main island, Spitsbergen (77°79'N, 12°15'E). The breeding and wintering areas and the normal autumn migration routes are shown in Fig. 1.

The population is one of three groups of barnacle geese in the North Atlantic, but there is little or no interchange between them (see below). The Svalbard stock is the smallest; numbers declined to a low of only 300 birds in 1948, but the population has since been protected from shooting and many of its haunts have become reserves. Numbers rose to

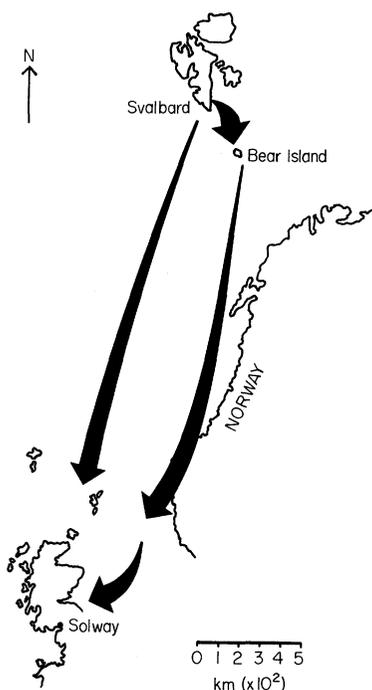


FIG. 1. The breeding, wintering and autumn staging area of the Svalbard barnacle goose, and the normal migration routes followed on the southwards migration.

3–4000 in the 1960s and the total has fluctuated around 10 000 birds in the 1980s. As numbers have increased, the relative breeding success (% young in the autumn flock) has declined. Fig. 2 shows the growth of the population since 1970, when the winter refuge increased in size. This caused a reduction in mortality from around 25% annually to about 11% (Owen 1982) and led to a period of exponential growth. The subsequent decline in relative breeding success is apparently density-related; in the 1980s the population grew more slowly, even though the annual mortality remained constant, at 10–12%.

Since 1973, a proportion of the geese has been marked with plastic rings with codes readable in the field at up to 250 m with the aid of a telescope. In 1977 the number of ringed birds rose to over 2000 (more than 25% of the population) but, despite this, the annual resighting rate of geese alive and ringed has been maintained at around 95%.

As many adults and goslings as possible were caught when flightless in July and August 1986, usually when the goslings were 3–5 weeks old. Adults and many of the young were sexed by cloacal examination, a reliable method in geese (Hanson 1967). Full-grown geese were separated into adults (2 or more years old) and yearlings (just over 1 year). Yearlings were identified by the presence of a few unmoulted juvenile (brownish) feathers on the wing coverts. Adult females were examined for the presence of a 'brood patch', an area plucked bare of feathers and down during incubation. The patch had refeathered in most cases at the time the geese were caught, but the new feathers could be distinguished either because they were not fully grown or because they were cleaner than the other

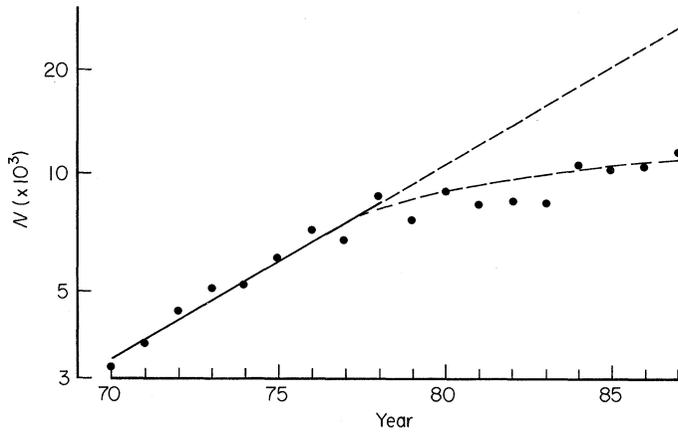


FIG. 2. The size of the population between 1970 and 1987 plotted on a logarithmic scale.

feathers on the belly and not abraded. The goslings were aged to the nearest week according to a prepared guide based on plumage development (Owen 1980), and many were weighed.

As many geese as possible were measured. The length of the skull (head + bill) was the most reliable and repeatable measure of body size; the length of the tarsal bone was also recorded if time allowed. The length of the second primary feather (usually eventually the longest) was measured by inserting a ruler between the first and second primary and recording the length of the second. This gave an indication of the state of moult. Catches were made in several breeding areas separated by fjords or glaciers, so that survival could be related to the area of origin, and to age and mass when caught.

The geese were followed to a staging area on Bear Island ($74^{\circ}30'N$, $19^{\circ}10'E$) and finally to the wintering grounds, where a number of observers monitored the geese throughout the winter. Records were also included from the early part of 1987–88, so that any birds missed in 1986–87 could be included. It was assumed that birds not recorded in either winter had died on the journey south in autumn 1986. This gives a minimum estimate of survival, but since more than 80% of the birds are recorded in the first 3 months after arrival, when they are largely on an area protected from shooting and when mortality is low, the underestimate is likely to be slight (Owen 1982, 1984). The possibility of mistakenly reporting a bird as dead because it has emigrated is negligible. The actual number of emigrants can be ascertained since researchers studying the other barnacle goose populations also resight the majority of individually marked birds each year; the first records of our geese in the Siberian and Greenland populations were in 1980 and 1984, respectively. Since 1973 a total of 5264 individual Svalbard barnacle geese has been ringed. Only twenty-three (0.4%) have been seen in either of the other populations and seven of these (30%) found their way back to the Svalbard population in later years. The chances of survival, and certainly of breeding, outside a flock of the same species, are minimal. Results of following unmarked and marked geese at both ends of the migration route in previous years are also presented.

TABLE 1. Number of geese caught in Spitsbergen in July–August 1986 and the number that were weighed and measured

Age-class	Total	Mass	Primary	Skull	Tarsus
Adult/full grown*	1672	854	738	1026	682
Yearling	156	69	62	139	62
Goslings	485	263	45	73	55
Total	2313	1186	845	1238	799
% measured		52.3	36.5	63.5	34.5

* Includes some repeat catches of the same individuals. In some catches yearlings were not separated from adults and all non-goslings were included in the adult category.

Routine observations included classifying the geese according to the profile of their abdomen (Owen 1981). This gives a crude estimate of the extent of fat reserves on arrival on the Solway, for comparison with other years.

RESULTS

Catching and condition during moult

The number of geese caught, weighed and measured in Spitsbergen is shown in Table 1. The size of the various catches and the conditions under which they were made determined how many measurements could be taken; overall more than half the geese were weighed and had at least one measurement taken to indicate body size.

Table 2 shows the mass and moult stage (primary length) of adults (not including yearlings) from seven areas, listed from south to north, in 1986. In a previous study barnacle geese lost some mass during moult (Owen & Ogilvie 1979); however, the

TABLE 2. The body mass and primary length of adults caught in seven different areas of Spitsbergen in 1986. Primary feather length is corrected according to the date caught, to the estimated value on 1 August (see text)

Area	Body mass (g)				Primary length (mm)			
	Male		Female		Male		Female	
	<i>n</i>	Mean ± S.E.	<i>n</i>	Mean ± S.E.	<i>n</i>	Mean ± S.E.	<i>n</i>	Mean ± S.E.
Dunoyane	110	1843 ± 17	103	1553 ± 16	109	85.1 ± 3.7	103	72.7 ± 3.4
Tjornsetta	72	1756 ± 15	75	1516 ± 15	73	64.3 ± 4.6	75	46.3 ± 4.6
Nordenskiold S	54	1823 ± 21	51	1578 ± 16	55	63.4 ± 6.4	53	66.0 ± 6.0
Nordenskiold C	47	1838 ± 22	54	1618 ± 17	46	64.0 ± 8.0	55	48.5 ± 6.3
Nordenskiold N	72	1934 ± 18	77	1716 ± 15	40	52.7 ± 7.2	42	53.1 ± 7.7
Daudmannsoyra	28	1914 ± 41	35	1658 ± 26	27	96.6 ± 8.9	35	100.8 ± 7.6
P.K. Forland	15	1740 ± 45	12	1488 ± 41	15	37.0 ± 8.3	12	24.9 ± 7.0

TABLE 3. The mean age and body mass of goslings from the different areas where substantial numbers were caught. The data were weighted so that they approximated to the values at the median catching date, 1 August (see text). Also given are the numbers that reached the wintering grounds from each area (see below)

Area	Age (weeks)	Mass (g)	Seen	Not seen	% seen
Tjornsetta	3.5	707	10	17	37.0
Nordenskiold S	4.1	735	81	40	66.9
Nordenskiold C	3.4	745	29	28	50.9
Nordenskiold N	4.0	950	106	42	71.6
Daudmannsoyra	2.8	795	54	26	67.5

relationship was far from clear in the present study. There were much larger differences (up to 300 g) between areas on the same dates than between dates in the same area. It seemed safer, therefore, not to correct body masses of adults for the date when they were taken. Primary lengths were, however, corrected to the median catch date, 1 August, by adding or subtracting 7.5 mm per day—the average growth rate of feathers (Owen & Ogilvie 1979).

For adult males there was a significant negative correlation between body mass and primary length in six of the seven areas. The slope of the regression line varied, however, from the equivalent of 0.73 g mm^{-1} in central Nordenskioldkysten to 3.41 g mm^{-1} in Prins Karls Forland. The interpretation of the trends was not straightforward. On the one hand, the maintenance of body condition depends on local feeding conditions. On the other it has been argued that mass loss during moult has adaptive advantages (Owen & Ogilvie 1979). Overall, for adult males, the negative regression represents 1.4 g mm^{-1} of primary length ($r = 0.42$, $P < 0.01$).

For females the interpretation was more complex. In only one area was there a significant relationship between feather length and body mass. Samples were small within areas but, overall, females without brood patches showed a significant negative relationship ($r = 0.27$, $P < 0.01$) amounting to 2.8 g mm^{-1} of feather length. Females with brood patches, however, showed no such significant relationship.

The age and body mass of goslings are given in Table 3. There was no significant difference between the sexes so males and females were combined. Catches including goslings were spread over 15 days, 24 July–8 August. Goslings caught 4 or more days from the median date (1 August) had one week added to or subtracted from their ages. Goslings grew rapidly; in the middle of the growth period when growth was linear the increase in mass was around 30 g per day for both sexes (M. Owen, unpublished data from captivity where the fledging period was similar to that in the wild). For each day a gosling was caught before or after the median date, 30 g was subtracted from or added to its mass. The values in Table 3 represent comparable figures for 1 August.

As might be expected, differences in age between goslings in different areas were rather small, at most about 10 days. The differences were likely to be due to the exact time at which nesting islands were free of snow and ice since the geese nest as soon as the snow clears (Prop, van Eerden & Drent 1984). The relationship between age and body mass was

not consistent in the different areas. Most clear was the difference between the northern and southern parts of the Nordenskiöld Coast; goslings of the same age were more than 200 g (29%) heavier in the north. This difference was consistent with the richness of the vegetation; the northern part of this coastline contains the richest feeding grounds of any on the whole western coast of Svalbard (Norwegian Polar Institute, in lit.). Despite being almost a week younger, the goslings reared on Daudmannsoyra were heavier than those reared on Tjornsletta and Prins Karls Forland. At both sites most of the ground is gravel desert and there are few feeding places.

These data show that there was considerable variation in the condition of goslings at the age of 3–4 weeks. The birds fledged at about 6 weeks of age, at which time they gained access to rich feeding grounds under bird cliffs (Prop, van Eerden & Drent 1984). The differential in body mass is likely to be maintained to this stage and perhaps to the time of autumn migration.

Autumn migration

The geese normally leave northern parts of Svalbard in September and more than half of them gather on Bear Island during the latter half of the month (Owen & Gullestad 1984). Winter came exceptionally early in 1986; there was a heavy snowfall and strong winds during the second week of September. Observers who arrived on Bear Island on 25 September found it covered with snow; the geese had already migrated through the area.

The median date for mass arrivals of geese on the Solway is 3 October (range 25 September–13 October, see Owen & Gullestad 1984). The first geese arrived in 1986 on 19 September, a day earlier than ever recorded previously (30 years of observation). The migration was completed by 1 October, about a week earlier than usual.

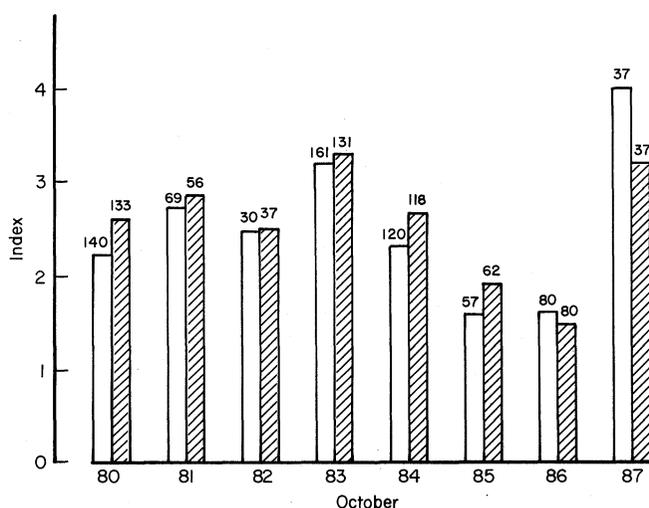


FIG. 3. The weighted median (see text) abdominal profiles of paired adult males (□) and females (▨) in the first 10 days after arrival in Scotland, 1980–81 to 1987–88. Numbers above the columns are sample sizes.

Survival of geese caught in Spitsbergen

Table 4 shows the survival rates of geese of different ages and sexes between the time of catching and arrival at the wintering grounds. These could have been underestimated for two reasons: (a) geese could lose their rings and thus be assumed to be dead, and (b) birds could arrive and die before being seen. The first possibility is unlikely, since losses of rings were extremely rare in the first 5 years. The minimum time between ringing and the loss of a ring was 2.5 years (M. Owen, E C Rees & S Warren, unpublished data). The effect of the second on the survival estimate is small, since most of the geese are seen very soon after they arrive. For example in 1986, 81% of geese were seen in the first month after arrival and 98% in the first winter (Table 4). Since the mortality rate during the winter is only around 5% (Owen 1982), the underestimate of survival is likely to be negligible.

The survival rate of yearling and adult geese was very high in 1986, and comparable with that in previous years (Owen 1982); although the yearlings' survival was slightly higher than that of adults it was not significantly different (see also Owen 1984). Goslings, however, survived poorly: 35% died between the age of 4 weeks and arrival in Scotland. It is possible that, despite evidence to the contrary in previous years, catching the birds puts sufficient stress on young goslings to affect their subsequent survival. This was checked by comparing the proportion of young birds in flocks in the two places. The sample from the breeding grounds represented about a third of the population; it was from a range of sites and so could be regarded as a reliable sample. This sample gave an estimate of 2200 goslings on the breeding grounds in late July. Aged samples on arrival in Scotland indicated that only 1250 (57%) of these were alive in October. This indicated that mortality of ringed geese was no greater, and perhaps less, than average for the population at large. Because of its relative richness, survival from Nordenskioldkysten, where most of the goslings were marked, may be higher than average.

Adult and well grown goslings are occasionally taken on the breeding grounds by arctic foxes *Alopex lagopus* L.; the main losses of goslings, however, are during the first week of life, when they are vulnerable to chilling and to predation by glaucous gulls *Larus hyperboreus* Gunnerus as well as foxes. Later, between 3 weeks and fledging, losses of young are negligible (Ebbinge & Ebbinge 1976; Owen & Norderhaug 1977; Prop, van Eerden & Drent 1984), so we assumed that the vast majority of gosling losses in 1986 occurred on migration.

*Factors affecting survival**Age*

In the sample as a whole the estimated age of the youngest and the oldest goslings differed by 4 weeks. Thus, the earliest brood hatched around 15 June and the latest not until 15 July; the laying of the first egg would have occurred about a month earlier, since it takes 5 days to lay the clutch and the incubation period is 24–25 days (Owen 1980). Such a large difference is probably unusual but 1986 was an exceptionally early season and the geese migrated to the breeding grounds a week earlier than normal (unpublished data). Some geese, nesting on the more open islands on which the snow had melted, started their nests in mid-May, at least a week before the normal median laying date. Beginning a clutch in mid-June is not unusual, especially in late seasons (Prop, van Eerden & Drent 1984).

The survival of goslings of different ages is shown in Table 5. The method of assessing age assumed that feather development was dependent on age. Whilst this may not be

TABLE 5. The survival of barnacle goose goslings according to their estimated age (according to plumage development) on 1 August 1986

Age	Seen	Not seen	% Seen
Week 2	18	15	54.5
Week 3	101	60	62.7
Week 4	92	54	63.0
Week 5	65	22	74.7
Week 6	10	2	83.3
Total	286	153	65.1

strictly true, feather development is somewhat independent of mass, or even body size in waterfowl (e.g. Smart 1965). The estimate is crude and for some young probably in error, since they were improbably heavy for their stated ages. However, we decided to include all the data since we wanted to examine mass and age as independently as possible of each other. The samples aged and weighed were not, of course, identical.

The proportion of goslings that survived increased with age (Spearman rank correlation on percentage seen values, $r_s=0.90$, $P<0.05$, one-tailed test), although about half of even the youngest group survived.

Body mass and condition

Table 6 shows the survival of goslings of different body masses (weighted to 1 August). There is a clear relationship between body mass on 1 August and subsequent survival; the goslings that returned to Scotland were significantly heavier than those that did not. This was not surprising given that body mass must be closely correlated with age. To separate these effects, the masses of surviving and non-surviving geese were examined within the three most common age groups (Table 7). For each of the age groups the survivors were significantly heavier than the non-survivors, though there was a considerable overlap.

TABLE 6. The survival of goslings according to their body mass on 1 August, the median catching date. Masses of geese caught before or after 1 August were corrected by adding or subtracting 30 g per day (see text)

Mass (g)	Seen	Not seen	% Seen
< 500	0	4	0.0
501-600	3	8	27.3
601-700	18	29	38.3
701-800	42	12	77.8
801-900	20	9	69.0
901-1000	42	28	60.0
> 1000	37	11	77.1
Total	162	101	61.6

Mean mass of survivors = 866 ± 12.4 g, non-survivors 754 ± 15.6 g $t=5.62$, $P<0.001$.

TABLE 7. Effect of body mass on survival within the three most common age-classes

Mass (g)	Age group					
	Week 3		Week 4		Week 5	
	<i>n</i>	% Seen	<i>n</i>	% Seen	<i>n</i>	% Seen
< 600	10	20.0	3	33.3	1	0.0
600–700	30	46.7	12	8.3	3	33.3
700–799	44	65.9	16	50.0	7	42.9
800–899	25	80.0	16	68.8	11	81.8
900–999	5	40.0	15	73.3	7	71.4
≥ 1000	1	100.0	27	70.4	17	82.4
Mean ± S.E. (number seen)	759.9 ± 10.6 g (<i>n</i> = 68)		926.8 ± 19.0 g (<i>n</i> = 51)		969.7 ± 26.2 g (<i>n</i> = 32)	
Mean ± S.E. (number not seen)	689.4 ± 16.4 g (<i>n</i> = 47)		810.3 ± 26.6 g (<i>n</i> = 38)		839.6 ± 46.7 g (<i>n</i> = 14)	
<i>t</i> (seen/not)	3.96 <i>P</i> < 0.001		3.66 <i>P</i> < 0.001		2.59 <i>P</i> < 0.02	

The mass increment for the interval between 3–4 and 4–5 weeks represented 24 g per day, not very different from the 30 g per day predicted (see above). The interval between the 4–5 and 5–6 week age groups, however, represented only 6 g per day. The growth rate was slowing down at this stage, and age determination was not exact, but this may also have indicated that competition for food might be limiting the growth rate of older goslings.

Area of origin

Since age and body mass differ between rearing areas we might expect differences in survival. The survival rates from the different areas are given in Table 3. There were significant differences (chi-square = 17.45, d.f. = 4 *P* < 0.01), and these were clearly related to the age and, particularly, the body mass of the birds from different areas.

The survival rate of adults was so high that no significant differences could be detected between areas of origin.

Breeding effort

Of 127 females from a single area that were checked and had detectable brood patches, 115 (90.6%) survived to reach Scotland. Of forty-seven non-breeders, forty-six (98%) survived; this difference was not significant.

Mean body masses of females seen in Scotland (*n* = 714) were 50 g lower than those not seen (*n* = 42), but the difference was not significant.

Of the 142 females from all areas that had brood patches and sufficient resightings in Scotland, thirty-seven (26%) were accompanied by broods, and these were significantly heavier (*t*-test, *P* < 0.05) than those without families.

Information from previous years

Table 8 presents information on gosling mortality on migration from other years when breeding areas were visited. In some years mortality was determined by resighting in Scotland goslings that were ringed on the breeding grounds. Losses were also determined

TABLE 8. Survival of goslings after autumn migration in different years

Year	Breeding area	Total goslings	Number of deaths	% Survival	Method
1977	Nordenskiold N&C	44	9	80	a
1978-80	Nordenskiold S&C	378	78	79	b
1983	Whole range	—	—	87	c
1984	Nordenskiold S	195	23	88	d
1986	Areas in Table 2	439	153	65	a

a, Determined from catch and resighting of ringed goslings.

b, Pooled data from Prop, van Eerden & Drent (1984).

c, Determined from reduction in the mean brood size (see text).

d, From losses of goslings from broods with ringed parents.

by assessing brood reduction between 1 and 2 weeks of age and fledging or arrival in Scotland. This is feasible since there are very few losses of entire broods after families arrive on their tundra feeding areas (Ebbinge & Ebbinge 1976; J. M. Black & M. Owen unpublished data).

In 1983 ($n=29$) and 1984 ($n=62$) brood size was 3.4 goslings on average in the first few days of gosling life. In both years there were on average 2.3 goslings per brood ($n=47$ and 509, respectively) on Bear Island, the last staging area before migration. In Scotland, mean brood size was 2.0 ($n=171$) in 1983, suggesting a 13% loss of young on migration. In 1984 direct evidence was available of losses in eighty-four broods whose parents were marked (195 young). After correction for orphans (young not in families), gosling loss between Bear Island and Scotland was estimated at 12%. In both years, adult migration losses were reliably estimated (individually marked birds) at 2.0% ($n=293$ and 492, respectively).

Although from the table it appears that the high mortality in 1986 is unusual, less detailed information from other recent years when numbers were high (the information that prompted the present study) suggest that it is not unique.

DISCUSSION

Whereas estimating hatching success and survival prior to fledging is relatively easy, post-fledging survival, and particularly survival to enter the breeding population, which is the crucial test of reproductive success, is very difficult. To our knowledge, in only two other non-passerine birds has a relationship been demonstrated between fledging mass and subsequent survival. In the manx shearwater, *Puffinus puffinus*, heavier young had a 50% chance of returning to the colony in subsequent years compared with only 10% for lighter chicks (Perrins 1966; Perrins, Harris & Britton 1973). In the gannet *Sula capensis*, birds recovered dead close to the breeding grounds had significantly smaller fledging masses than average (Jarvis 1974).

Other non-passerine species show no significant effect of body mass or fledging time on subsequent survival. The lack of relationships is attributed either to an extended period of parental feeding of chicks (in the guillemot *Uria aalge*, Hedgren 1981), or to short migration distances (puffin *Fratercula arctica*, Harris & Rothery 1985; sparrowhawk *Accipiter nisus*, Newton & Moss 1986). As more information is collected on long-distance

migrants, we expect that post-fledging mortality on migration will be seen as an important source of loss in these species.

In most studies of migratory populations of geese, survival is assessed from recoveries, recaptures or return rates to nesting colonies that are open to immigration and emigration (see e.g. Boyd, Smith & Cooch 1982; Rockwell *et al.* 1985). There is good evidence of a similar autumn migration mortality in the light-bellied brent goose *Branta bernicla hrota* breeding in northern Canada and wintering in Ireland (O'Briain 1987, personal communication). In each of 2 years when birds of all ages were marked, survival of young was significantly poorer than that of adults. The loss rate of young was greater than 25% in each year, and averaged 33%, compared with an average of 5% for adults. Data on factors influencing survival are not yet available from that study but similar effects would be expected since the young geese undertake a (presumably non-stop) migration over the Greenland icecap to Iceland in September, a distance of at least 2500 km.

Once fledged, geese have rather low mortality rates; even in quarry species wintering in Britain, the annual mortality rates are less than 15% (Owen, Atkinson-Willes & Salmon 1986). In these barnacle geese, the annual mortality rate (calculated as in Owen 1982) of young after arrival on the wintering grounds averaged 10.3% (data from 6 years combined, $n = 418$). The mortality rate of yearlings (15–27 months of age) is even lower, at 7.3% (data for 7 years combined, $n = 1054$). The average rate for all ages is around 11% and varies little between years (Owen 1982). Thus, once a gosling survives to reach the wintering grounds in its first year, it has an 83% chance of becoming a potential breeder, at 2 years of age. Clearly, the scale of the migration mortality that can occur in years with a short rearing period and a high density of geese can have a substantial effect on recruitment into the breeding population. In summary for the year 1986, of every 100 potential eggs (twenty-five mature females \times clutch size of four), only eight resulted in fledged young reaching the wintering grounds.

Prop, van Eerden & Drent (1984) have shown that most juvenile mortality occurs before goslings reach the brood rearing areas on the tundra, especially in years when nest initiation is delayed by snow. However, they failed to find a density-related effect in gosling survival between 1978 and 1980. In 1977 when the population was much smaller and competition on the breeding grounds was presumably much less severe, gosling survival was not related to mass at fledging as it was in 1986. We suggest that the substantial increase in potential breeders in 1986 (over 1300 individuals more than ever before), coupled with the shortened brood-rearing season, was responsible for the high gosling mortality in that year.

Our finding that some goslings from even the youngest age categories survived suggests that the shorter brood-rearing period was not the complete reason for increased gosling mortality. The fact that survival was strongly related to gosling body mass, and that this was true for birds of the same age, suggests that heavier goslings acquired more or better food than lighter goslings of the same age. Prop, van Eerden & Drent (1984) showed that gosling survival increased with the food intake of their mothers (though there were, unfortunately, only five points plotted). This may mean that parents who take their goslings to feed in better areas survive better. Elsewhere we have shown that the dominance rank of families (ranked according to family size) is positively correlated with the time spent in areas with the most grass biomass (Black & Owen 1989a). Limitations on food during the rearing period, acting through mortality of young on migration, is likely to have a considerable limiting effect on geese breeding in these sparsely vegetated areas. Barnacle goose females have a higher annual mortality rate than males and this is related

to poor breeding seasons (Owen 1982). Owen (1982) suggested that some females may not be able to regain body condition to complete autumn migration successfully. In 1986 there was no difference in survival for females that did and did not attempt to breed nor were the females that survived autumn migration heavier (in summer) than those that did not survive. However, females that laid and incubated eggs (those in the catch with brood patches) and were successful in bringing families to Scotland were heavier than those that had also been through a period of incubation but failed to bring young to Scotland.

There are several possible reasons for this difference between females. Firstly, as has been shown for snow geese *Anser caerulescens*, unsuccessful females may emerge from incubation lighter than successful ones (Ankney & MacInnes 1978) and this difference may carry over to the time of autumn migration. Secondly, females that fail may be less successful foragers (Prop, van Eerden & Drent 1984), and this may also limit their ability to lay down premigration fat reserves.

A third reason may be related to the fact that late hatching young have less chance of survival (this study). The time of hatching clearly determines the length of the fattening period for the pair; females incubating late would thus be lighter than early breeders.

A fourth reason may be related to a pair's ability to rear young. There may be a conflict between feeding to replenish fat reserves and parental care during the brood-rearing period (see e.g. Ankney 1977). Experience in breeding may be a factor both in the maintenance of body reserves and in success in rearing young. For example, families with less experienced parents break up sooner than those with more experienced ones (Black & Owen 1989b).

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REFERENCES

- Ankney, C. D. (1977). The use of nutrient reserves by breeding male lesser snow geese (*Chen caerulescens caerulescens*). *Canadian Journal of Zoology*, **55**, 1985–1987.
- Ankney, C. D. & MacInnes, C. D. (1978). Nutrient reserves and reproductive performance of female lesser snow geese. *Auk*, **95**, 459–471.
- Barry, T. W. (1962). Effect of late seasons on Atlantic brant reproduction. *Journal of Wildlife Management*, **26**, 19–26.
- Birkhead, T. R. & Furness, R. W. (1985). Regulation of seabird populations. *Behavioural Ecology: Ecological Consequences of Adaptive Behaviour* (Ed. by R. M. Sibly & R. H. Smith), pp. 145–167. Blackwell Scientific Publications, Oxford.
- Black, J. M. & Owen, M. (1989a). Agonistic behaviour in barnacle goose flocks: assessment, investment and reproductive success. *Animal Behaviour*, **37**, 199–209.

- Black, J. M. & Owen, M. (1989b). Parent-offspring relationships in wintering barnacle geese. *Animal Behaviour*, **37**, 187-198.
- Boyd, H., Smith, G. E. J. & Gooch, F. G. (1982). The lesser snow geese of the Eastern Canadian Arctic. *Canadian Wildlife Service Occasional Paper*, 46.
- Ebbinge, B. & Ebbinge, D. (1976). Barnacle geese (*Branta leucopsis*) in the Arctic summer—a reconnaissance trip to Svalbard. *Norsk Polarinstutt Aarbok*, 1975, 119-138.
- Hanson, H. C. (1967). Characters of age, sex and sexual maturity in Canada geese. *Illinois Natural History Survey Division Biological Notes*, No. 49.
- Harris, M. P. & Rothery P. (1985). The post-fledging survival of young puffins *Fratercula arctica* in relation to hatching date and growth. *Ibis*, **127**, 243-250.
- Hedgren, S. (1981). Effects of fledging weight and time of fledging on survival of guillemot chicks. *Ornis Scandinavica*, **12**, 51-54.
- Jarvis, M. J. F. (1974). The ecological significance of clutch size in the South African gannet (*Sula capensis* (Lichtenstein)). *Journal of Animal Ecology*, **43**, 1-17.
- Newton, I. & Moss, D. (1986). Post-fledging survival of sparrowhawks *Accipiter nisus* in relation to mass, brood size and brood composition at fledging. *Ibis*, **128**, 73-80.
- O'Briain, M. (1987). *Families and other social groups of brent geese in winter*. Unpublished Report, University College, Dublin.
- O'Connor, R. J. (1985). Behavioural regulation of bird populations: a review of habitat use in relation to migration and residency. *Behavioural Ecology: Ecological Consequences of Adaptive Behaviour* (Ed. by R. M. Sibly & R. H. Smith), pp. 105-142. Blackwell Scientific Publications, Oxford.
- Owen, M. (1980). *Wild Geese of the World*. Batsford, London.
- Owen, M. (1981). Abdominal profile: a condition index for wild geese in the field. *Journal of Wildlife Management*, **45**, 227-230.
- 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. *Norsk Polarinstittut Skrifter*, **181**, 37-47.
- Owen, M. & Gullestad, N. (1984). Migration routes of Svalbard barnacle geese *Branta leucopsis* with a preliminary report on the importance of the Bjornoya staging area. *Norsk Polarinstittut Skrifter*, **181**, 67-77.
- Owen, M. & Norderhaug, M. (1977). Population dynamics of the barnacle goose *Branta leucopsis* breeding in Svalbard, 1948-1976. *Ornis Scandinavica*, **8**, 161-174.
- Owen, M. & Ogilvie, M. A. (1979). Wing molt and weights of barnacle geese in Spitsbergen. *Condor*, **81**, 45-52.
- Owen, M., Atkinson-Willes, G. L. & Salmon, D. G. (1986). *Wildfowl in Great Britain*, 2nd edn. Cambridge University Press, Cambridge.
- Perrins, C. M. (1966). Survival of young manx shearwaters *Puffinus puffinus* in relation to their presumed date of hatching. *Ibis*, **108**, 132-135.
- Perrins, C. M., Harris, M. P. & Britton, C. K. (1973). The survival of manx shearwaters *Puffinus puffinus*. *Ibis*, **115**, 535-548.
- Pienkowski, M. W. & Evans, P. R. (1985). The role of migration in the population dynamics of birds. *Behavioural Ecology: Ecological Consequences of Adaptive Behaviour* (Ed. by R. M. Sibly & R. H. Smith), pp. 331-352. Blackwell Scientific Publications, Oxford.
- Prop, J., van Eerden, M. R. & Drent, R. H. (1984). Reproductive success of the barnacle goose *Branta leucopsis* in relation to food exploitation on the breeding grounds, western Spitsbergen. *Norsk Polarinstittut Skrifter*, **181**, 87-117.
- Rockwell, R. F., Findlay, C. S., Cooke, F. & Smith, J. A. (1985). Life history studies of the lesser snow goose (*Anser caerulescens caerulescens*). IV. The selective value of plumage polymorphism: net viability, the timing of maturation, and breeding propensity. *Evolution*, **39**, 178-189.
- Ryder, J. P. (1970). A possible factor in the evolution of clutch size in Ross's goose. *Wilson Bulletin*, **82**, 5-13.
- Smarth, G. (1965). The development and maturation of primary feathers in redhead ducklings. *Journal of Wildlife Management*, **29**, 533-536.

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