



Nordic Society Oikos

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Reviewed work(s):

Source: *Ornis Scandinavica*, Vol. 23, No. 4 (Oct. - Dec., 1992), pp. 451-458

Published by: Blackwell Publishing on behalf of Nordic Society Oikos

Stable URL: <http://www.jstor.org/stable/3676676>

Accessed: 09/06/2012 02:59

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Energy budgets of wintering Barnacle Geese: the effects of declining food resources

Myrfyn Owen, Richard L. Wells and Jeffrey M. Black

Owen, M., Wells, R. L. and Black, J. M. 1992. Energy budgets of wintering Barnacle Geese: the effects of declining food resources. – *Ornis Scand.* 23: 451–458.

This paper documents the daily activities and feeding rates of Barnacle Geese *Branta leucopsis* through the autumn and winter in relation to changes in biomass of their food supply. Energy intake and expenditure were estimated and energy surplus or deficit for each month calculated. A net surplus was achieved in the months of October (+ 235 kJ d⁻¹) and November (+ 247 kJ d⁻¹) when most food was available. Geese suffered a net deficit in December (- 225 kJ d⁻¹) and January (- 113 kJ d⁻¹) when biomass and food quality were lowest. In February, when grass began to grow again, the birds achieved a surplus once again (+ 167 kJ d⁻¹). Body mass changes through the winter were modelled using observed intake rates and estimated energy expenditure. Body mass predictions were consistent with observed mass and body condition changes. It is argued that mass loss in midwinter in this species is enforced by the limited feeding opportunity and declining food supply rather than an adaptive response to reduce predation risk. Geese gain substantial body reserves in autumn prior to this predictable mass loss. As soon as daylength and food biomass allow, lost reserves are replaced and mass increases rapidly in preparation for migration and breeding.

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Introduction

Many studies have described changes in body mass in wintering waterbirds, which in most cases conform to a pattern of mass accumulation during autumn, followed by a decline in winter and an increase in spring (see e.g. Owen and Cook 1977, Pienkowski et al. 1979, Ankney 1982, Ebbing 1989). Most workers have reasoned that the loss of body mass, in particular of lipid stores, is imposed by restricted food availability or feeding opportunity. These limitations become more severe when combined with increased energy demands in cold weather. An alternative explanation is that the birds are predisposed through selection to gain and lose weight at particular times of year irrespective of food availability. Loss of unnecessary body reserves may be advanta-

geous to reduce the risk of predation, as heavier birds are probably less agile. Thus birds might lay down reserves in preparation for the lean periods, and then only maintain sufficient to guarantee against predictable adversity.

There is some evidence in support of this in Dunlin *Calidris alpina* during winter (Pienkowski et al. 1979). Following a period of severe weather, when body mass was lost, the birds regained mass, even under the restricted conditions of daylength and tides. An experimental study with Greenfinches *Carduelis chloris* found that they maintained minimal body reserves during periods with abundant food supply. In this species at least, the extent of reserves depended more on predictable future needs than on current foraging opportunity (Ekman and Hake 1990).

Received 22 July 1991

Revised 4 March 1992

Accepted 22 March 1992

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There is evidence from waterfowl during the flightless moult that loss of body reserves is physiologically predisposed rather than a result of energetic hardship; Mallard *Anas platyrhynchos* (M. Owen unpubl.), Red-billed Teal *Anas erythrorhynchos* (Douthwaite 1976), Barnacle Geese *Branta leucopsis* (Owen and Ogilvie 1979) and Snow Geese *Anser caerulescens* (Ankney 1979). Other work in captivity support the hypothesis that body mass changes follow an endogenous cycle rather than being imposed by environmental constraints (Hepp 1986, Perry et al. 1986).

Many species of wild geese feeding in terrestrial habitats are herbivorous, have rather inefficient digestive systems compared with other grazers, and are almost exclusively diurnal (review in Owen and Black 1990). They also deplete their food supply, whose quality also declines, in winter. Food quality and quantity do not increase until spring in normal weather conditions. Wild geese might, therefore, be expected to suffer energetic deficits during the short days of midwinter (Owen 1981).

Studies have shown that geese compensate to some extent for declining food stocks by pecking more rapidly and increasing the proportion of time spent feeding. The birds also change feeding patch or diet if better quality areas are available (Madsen 1985, Ydenberg and Prins 1985). However, the biomass (as it affects the amount ingested per bite), and the quality (protein content and digestibility) of food are crucial to the net energy a bird obtains per unit of foraging time (Prop and Deerenberg 1991).

This paper examines data on energy intake and expenditure in wintering Barnacle Geese to test the hypothesis that loss of body mass in winter is imposed by a failure to meet energy requirements rather than being the result of an endogenous condition cycle.

Methods

A small, closed population of Barnacle Geese breeds in the Svalbard (Spitsbergen) archipelago and spends the months of October through April in a restricted area of the Solway Firth in north western Britain. Much of the winter feeding of the geese takes place on the Wildfowl & Wetlands Trust reserve at Caerlaverock in south west Scotland (Owen et al. 1987). This study was carried out while the birds were feeding on inland pastures on the reserve. The diet obtained by grazing on the pastures consists almost exclusively of grass leaves (mainly *Lolium perenne* with some *Agrostis* and *Poa* spp.) and the leaves of white clover *Trifolium repens*. The behavioural and ecological data were collected in the 1976–77 season, whereas it took several years (between 1975–1982) to obtain adequate samples of body measurements.

Between October and February the time budget of the geese was monitored by scanning large flocks and

recording the activity of a large sample of birds (at least 75% of the birds in flocks which numbered 300 or more). Because the birds range over a very small area, their activities during the whole of the daylight period were known. At least 10 samples were made for each hour of the day within each month. The absolute time spent in various activities was calculated from the proportion of individuals that were grazing, vigilant (all head-up postures), resting (all sitting and sleeping), flying and a lumped category of other activities in each hour of the day.

The geese roost on sandflats 1–2 km away from the feeding fields. The normal pattern is for them to retire to the roost just after sunset and return to the feeding areas just before sunrise. The flocks are very vocal and they can clearly be heard when active at night; repeated checks during the hours of darkness indicated that nocturnal foraging in fields was negligible during these studies. Although it is possible that a small amount of feeding could have taken place near the roost before the birds flew to the fields, we assume that any "extra" feeding was constant throughout the study period. Other observations, on position of flocks at the roost in the evening and in the following morning, and the presence of roosting piles of droppings there indicating that the birds had stayed in the same position all night, support the supposition that nocturnal feeding was rare during the study.

Pecking and walking rates were determined for each daylight hour for each month between October and February. The defaecation interval is very short in geese (Owen 1971), and can be easily measured. The interval was measured directly in this study by timing the period between individual droppings. The viewing conditions were such that individual birds could be followed for lengthy periods. Droppings are not produced in the first hour of feeding, while the gut fills up with food. No data on dropping interval were collected during this period. The geese leave the feeding grounds with full guts; we assumed that this balances out the early morning period and we calculated intake over the whole period on the feeding grounds. The ingestion rate of food was estimated from the mass of excreta by correcting for assimilation efficiency using crude fibre as a natural marker (Drent et al. 1979). At least two samples of grass and droppings were collected for analysis each month. The amount of food obtained per peck was estimated by dividing the amount of ingesta by the number of pecks taken per day or per hour.

Green biomass (g m^{-2}) was evaluated from biweekly grass clippings (to ground level) that were sorted into green and dead leaves, dried (at 90°C overnight) and weighed. The calorific value of paired grass and dropping samples (droppings collected after the birds had been in the field for a least 90 minutes – the throughput rate of food) from the same fields was measured using an adiabatic bomb calorimeter.

Total body mass was obtained from live birds, caught

Table 1. The length of the active day and the proportion and absolute amount of time spent actively foraging by adult Barnacle Geese. At least 40 flock scans spread throughout the daylight hours were made in each month.

Month	Active (h)	Percent foraging	Hours foraging
October	10.1	83	8.38
November	8.6	86	7.41
December	7.2	92	6.62
January	7.6	95	7.22
February	9.0	94	8.46

at various times through the winter for ringing, over a period of years, or (once) from samples of dead birds illegally shot and confiscated by the police. Because live birds were held for about 30 minutes or more before being weighed, and because the throughput rate of food is extremely rapid in geese (Owen 1975), they were empty of gut contents or nearly so. Dead geese were full of food; the mass value used for them is the total fresh weight minus the food in the whole gut.

Results

Foraging effort

The length of the active day and the relative and absolute amount of time spent in active foraging are shown in Table 1. Since the geese fly to the fields at approximately the same time relative to dawn and dusk each day, the length of the active day closely matches that of the daylight period. There is clearly some compensation for declining daylength; the variability in the absolute amount of time on the feeding grounds (C.V. = 13.6%) is greater than that in the amount of time spent feeding (C.V. = 10.3%). Complete compensation is impossible, however, without nocturnal activity; for example, the time spent feeding in October is greater than the entire active period in December.

While on the feeding grounds the birds increase foraging effort at the expense of other activities. The proportion of time spent alert declines from 12% to 5% between October and January; the proportion spent resting from 1.4% to zero and the time in other activities from 4 to 0.5% (Wells 1980, Black 1987).

Feeding rate changes with biomass and time

Although there is some cold weather mortality of grass, biomass of vegetation declines mainly due to removal by the geese (data from exclosures show that standing crop is maintained in the absence of grazing, Wells 1980). There was sometimes vegetation growth during mild weather, and there were differences between fields depending on the timing of the goose visitation. How-

ever, since geese tend to harvest fields in rotation (Prins et al. 1980), and periods of substantial growth are uncommon, biomass usually declines steadily as winter progresses. In this study the standing crop (20 measures from 4 fields) fell from 19.4 g m^{-2} (SE = 2.1) in October, to 8.2 g m^{-2} (SE = 1.4) in December, and reached its lowest in February, at 4.8 g m^{-2} (SE = 0.8) (see also Black and Owen 1989a).

The relationship between peck rate and time of day, biomass and time of year are shown in Fig. 1. Although the relationship with time of day is not particularly close (Spearman Rank Correlation, $r_s = 0.441$, $P < 0.05$), peck rate tends to increase towards evening (Fig. 1a). Late in the day, food is ingested more rapidly than it is processed, so that it accumulates in the oesophagus,

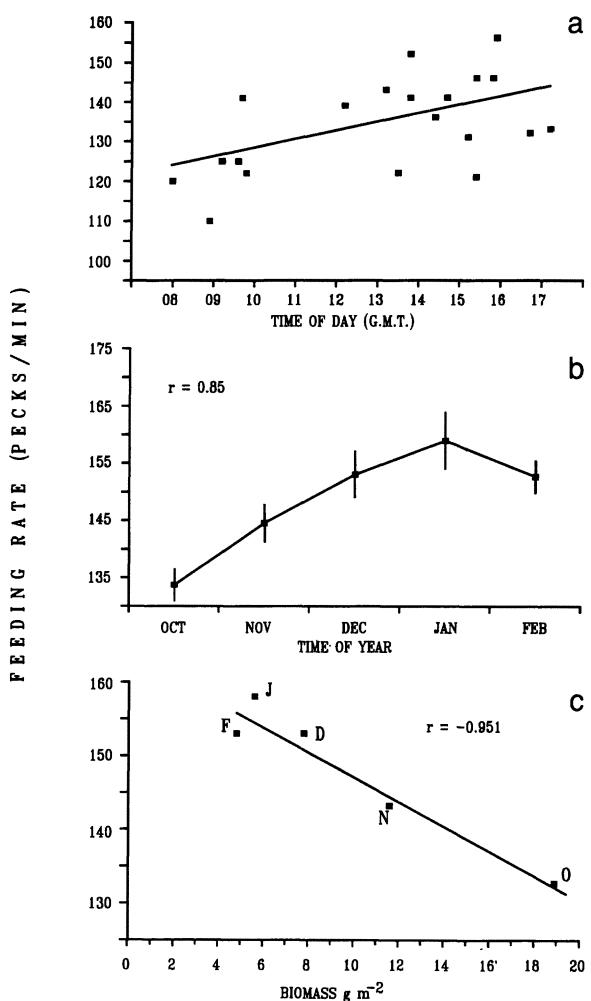


Fig. 1. (a) the variation in feeding rate (pecks per minute, points are means of 10–20 observations from one week in February) with time of day, (b) the mean feeding rate (with standard errors) in each month from October through March and (c) the relationship between feeding rate and biomass of vegetation (g m^{-2}). Sample sizes for (b) and (c) as follows: Oct – 39; Nov – 46; Dec – 17; Jan – 17; Feb – 47.

Table 2. Seasonal net energy intake of Barnacle Geese during the wintering period. Net energetic intake (NEI) calculations use the total dry weight of ingested food minus the amount in the droppings (calculations are listed below). Daily energy expenditures were calculated from the overall time budgets for each month using multiples of BMR after Wooley and Owen (1978). Based on active daylengths in Table 1.

Month	Energy intake and expenditure	Energy surplus or deficit
October	Net energetic intake Daily energy expenditure	1193 kJ 959 kJ + 234 kJ d ⁻¹
November	Net energetic intake Daily energy expenditure	1225 kJ 980 kJ + 247 kJ d ⁻¹
December	Net energetic intake Daily energy expenditure	805 kJ 1030 kJ - 225 kJ d ⁻¹
January	Net energetic intake Daily energy expenditure	842 kJ 955 kJ - 113 kJ d ⁻¹
February	Net energetic intake Daily energy expenditure	1122 kJ 955 kJ + 167 kJ d ⁻¹

October NEI = (182 g intake \times 18.0 kJ energetic content) - (131 g droppings \times 15.9 kJ energetic content) = 1193 kJ d⁻¹

November NEI = (164.5 g \times 18 kJ) - (112 g \times 15.5 kJ) = 1225 kJ d⁻¹

December NEI = (125 g \times 17.6 kJ) - (90 g \times 15.5 kJ) = 805 kJ d⁻¹: cost of thermoregulation was 11.3 kJ d⁻¹ (after Lefevre and Raveling 1967; Owen and Reinecke 1979).

January NEI = (126 g \times 17.6 kJ) - (96.6 g \times 14.2 kJ) = 842 kJ d⁻¹: (cost of thermoregulation = 8.8 kJ d⁻¹)

February NEI = (164 g \times 4.1 kJ) - (115.5 g \times 3.5 kJ) = 1122 kJ d⁻¹: (cost of thermoregulation = 4.6 kJ d⁻¹)

thus effectively lengthening the feeding day (Owen 1972). In this case, increased pecking rate is translated into increased intake rate.

The mean peck rate also increases through the season (Fig. 1b, $r = 0.85$, $P < 0.01$), owing to the close negative relationship between peck rate and biomass (Fig. 1c, $r = -0.951$, $P < 0.001$). Drent and Swierstra (1977) showed a very close relationship between peck rate of a captive Barnacle Goose and grass height, which they manipulated by clipping to various heights. Similar relationships have also been found with sheep (Allden and Whittaker 1970).

Walking rate was variable but not significantly correlated with time of day, season or biomass (range 27–42 steps min⁻¹, $N = 160$). This is probably because movement to some extent interferes with the ability to select green leaves, especially at peck rates of up to 200 min⁻¹.

Seasonal changes in foraging performance and Net Energetic Payoff

We have shown that Barnacle Geese compensate for lack of feeding opportunity and for declining biomass by increasing their foraging effort, but what is the net result of this? We calculated the net energy intake and expenditure per day in each month and calculated the net energetic surplus or deficit during the winter season.

An estimate of the energetic cost of daily existence was calculated by attributing a cost to each activity as a multiple of the Basal Metabolic Rate (BMR), as calculated by Wooley and Owen (1978) for semi-captive Black Ducks *Anas rubripes*. The BMR was calculated from the equation of Lasiewski and Dawson (1967) based on a mean winter body mass of an adult goose of

1790 g (data from this study). While on the roost, the birds were assumed to be resting.

The most costly activity was flying, calculated as 14 \times BMR (King 1974, modified from Hart and Berger 1972). The energy expenditure multiple for feeding was 2 \times BMR, alert 2.1 \times BMR, resting 1.3 \times BMR and other activities, including preening and social behaviours 2.3 \times BMR. An additional cost of thermoregulation was added when the temperature was below the Lower Critical Temperature (LCT). The coefficient of heat loss was calculated from its relationship with body mass given in Lefebvre and Raveling (1967), and the LCT was calculated from its relationship with body mass in Owen and Reinecke (1979).

Energy intake was calculated on a daily and hourly basis from the mass of food assimilated (Ebbinge et al. 1975, Drent et al. 1979) and its energetic value; the energy budget in each month of the winter is given in Table 2. The net energy intake per peck (calculated from the data in Tables 1 and 2) declines from 18–19 kJ in October and November to 12 kJ in January. The short daylength in midwinter also curtailed foraging time so that the geese suffered a net loss of energy. They had, however, built up a reserve of fat in the early winter which allowed them to survive a period of energetic stress. If the figures given here held for each day of each month, the birds made an energetic surplus of 14664 kJ in October and November. The deficit in December and January amounts to 10478 kJ, so the birds made a surplus of 4186 kJ up to the end of January, after which they were once again in positive energy balance. This is equivalent to about 75 g of lipid (bomb calorimetry of Barnacle Goose fat yielded 42 kJ g⁻¹ and the conversion efficiency is assumed to be 75%, from Drent et al. 1979). Clearly, however, different weather

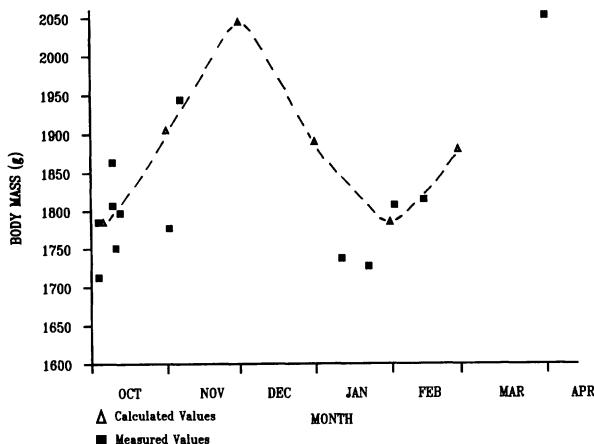


Fig. 2. The predicted mass changes in each month through the winter (triangles linked by a dashed line) and body mass of live Barnacle Geese caught at different times (squares, mean of all adults, sample sizes range between 83–222 birds per point), or dead birds (one case, $N = 17$).

and feeding conditions in early and mid winter could easily mean that there was a net deficit between October and January.

Predicted and actual mass changes during winter

We used the data to model the body mass changes that would be predicted in each month of the winter. Body mass at the beginning of October was set at the mean body mass of adult male and female geese caught between 1 and 10 October, which was 1785 ± 9.4 g ($N = 536$). We predict changes in this mass according to the energy surplus or deficit in each month given in Table 2. We assumed that all the variation in body mass was accounted for by changes in lipid. There are few data on changes in body composition in wintering geese, but Ely and Raveling (1989) found that changes in body mass during the winter were very largely attributable to changes in lipid reserves. The efficiency of fat deposition is assumed to be 75% (see above). The predicted changes are plotted in Fig. 2, together with the mean mass values for geese caught at different times during the wintering period.

Although the actual mass data are from a number of winters, and there are clearly annual differences, the changes are consistent with the predicted changes based on the model. We have no energetic data for March and April but the observed mass and condition changes are clearly related to increasing daylength and biomass in those months. The change in abdominal profile in the winter of 1977–78, given in Owen (1981) also showed a similar pattern, although the timing of peak condition was earlier in that analysis. Abdominal profile changes in other years show variations in relation to the birds' condition on arrival, food availability and winter weather, but they do conform with the general pattern

of improvement in condition to late November, a drop to a low in late January and a rapid increase as the grass begins to grow in February and March (Black and Owen 1988, Owen et al. unpubl. data).

The variations in the mass changes between years mean that the exact timing of changes in condition varies annually, and these variations are related to temperatures and the availability of food (Owen 1981, Black and Owen 1988). More data are needed to establish whether the pattern shown here is consistent from year to year though evidence from unpublished data on abdominal profile does support this.

Discussion

The evidence presented here supports the hypothesis that food availability causes loss of body mass during winter. This does not, however, exclude entirely the idea that endogenous cycles also control body mass. For example, we cannot exclude the possibility that in autumn, mass gain may not be as rapid as the food supply would allow.

It is well known that wintering birds suffer in severe weather and in very hard winters there can be mass deaths of geese from starvation (review in Owen and Black 1990). There is little information, however, on the energy balance, feeding opportunity and mass changes in a normal winter. The data presented in this paper suggest that geese are unable to maintain their energy balance in midwinter. The most important factor in limiting feeding opportunity is the short daylength; since they do not normally forage at night, the geese are unable to compensate by increasing intake rate on depleted food stocks.

The energy balance calculated for other goose species from published sources are compared with that from this study in Table 3. There have been few studies during the winter, but the studies of South American Ruddy-headed Geese *Chloephaga rubidiceps* indicate another case where an energy surplus is not achieved.

Bedard and Gauthier (1989) found that the diet of Snow Geese varied in different habitats. In one area the birds fed on nutritious *Scirpus* and in the other on poor quality *Spartina* roots. Although the expense of feeding in these areas was similar, only the geese using the more nutritious foods had a net surplus of energy from the foods (Table 3) which means that they were able to gain some weight prior to departure for northern breeding areas. Bedard and Gauthier (1989) also categorised three diet types of geese using agricultural land adjacent to the marshes: 90% grass or 90% grain or a mixture of grass and grain. The energy intake from these diets was 107 kJ h^{-1} , 228 kJ h^{-1} and 112 kJ h^{-1} , respectively. Because the foraging cost (in energetic terms) is much less for agricultural plants than on the marsh, they

Table 3. Estimates of daily food intake and energy balance for different goose species, feeding on a variety of foods at different times of year. Scientific names of goose species are given in the text.

Species	Season	Food type	Gross intake (g)	Net surplus or deficit (kJ)	Reference
Uppland Goose	winter	old pastures <i>Poa</i>	200 260	+150 Female +450 Male	Summers and Grieve (1982)
	summer	old pastures <i>Poa</i>	261 338	+550 Female +1000 Male	Summers and Grieve (1982)
Ruddy-headed Goose	winter	old pastures <i>Poa</i>	132 132	+0 Female +100 Male	Summers and Grieve (1982)
	spring	old pastures <i>Alopecurus, Poa</i>	159	+179	Madsen (1985)
Greater Snow Goose	spring	newly sown barley	230	+1544	Madsen (1985)
	spring	marsh <i>Scirpus, Phleum, Trifolium</i>	249 ^a	+137 ^b	Bedard and Gauthier (1989)
Barnacle Goose	autumn	marsh <i>Spartina, Phleum, Trifolium</i>	188 ^a	-276 ^b	Bedard and Gauthier (1989)
	winter	old pastures <i>Lolium, Poa</i>	165	+247	this study
	winter	old pastures <i>Lolium, etc</i>	125	-125	this study

^a Calculated values for the third week of spring

^b Average of all values in spring period

found that all three diets were more profitable than food gathered from the marshes.

It is often argued that animals should shift to new areas in response to decreased food availability (Krebs 1978, Goss-Custard 1985). Barnacle Geese do this to some extent, but the whole population of Barnacle Geese on the Solway have a winter range extending no more than 50 km between the furthest points (Owen et al. 1987). Whereas, in the present day landscape, there are ample open areas elsewhere in which the birds could settle, they evolved in a situation where food patches were few and far between and survival chances were presumably better by staying rather than moving to unknown conditions. We know that these geese tend to be site faithful, sometimes continuing to visit the same areas even when the habitat has become temporarily degraded (Black et al. 1991).

In favourable seasons, grass may be incompletely exploited in autumn and may be available later in the winter. However, at our study site this cannot make a substantial contribution to winter feeding for the geese, since the quality of grass declines rapidly as winter progresses. Food quality has a considerable effect on the rate of nutrient assimilation by geese (Prop and Vulink in press). The quantity of grass also declines through the winter in the absence of exploitation because leaves are killed in hard weather. If there is no opportunity to migrate, the birds become "prisoners of their food supply" (Drent and Prins 1987).

The effect of energetic deficit is different on different individuals; young birds, which begin the winter with

smaller reserves than adults (Owen and Black 1989), are inexperienced feeders and subordinate to adults (Black and Owen 1989a). Elsewhere, we have shown that feeding is about 27% more profitable in the edges of the flock where birds have first choice of plants (Black et al. in press) and that dominant goose units tend to monopolise these positions (Teunissen et al. 1985, Black and Owen 1989a). In goose flocks, dominance rank is ordered according to the number of birds in the unit; families are dominant over pairs and pairs over singles (Boyd 1953, Raveling 1970). Single birds are at a competitive disadvantage and are known to gain body condition at a slower rate than those in a family unit (Black and Owen 1989b). Ebbing et al. (1991) have shown that in some winters survival is worse in juvenile than adult geese. In the mass die-off of Atlantic Brant *Branta bernicla hrota* in eastern USA in the severe winter of 1976-77, there was a much higher proportion of juveniles in the birds picked up dead than in the population at large; nearly all the young succumbed (R.E. Kirby pers. comm.).

Whether mass changes in winter affect breeding success in geese has yet to be determined, although there are clear links between breeding success and body condition in late spring, just before departure for the breeding area (Ebbing 1989, Black et al. 1991). Future research should focus on mass and condition changes in winter in relation to food supply and weather, and the effects of those changes and on individual performance on reproduction and survival.

Acknowledgements – We thank the staff of the Wildfowl and Wetlands Trust at Caerlaverock and Slimbridge for cooperation in this study, and to the many students and volunteers who helped in the collection of the data. Jouke Prop and Tony Fox and Jesper Madsen made constructive comments on a draft.

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