

WING MOLT AND WEIGHTS OF BARNACLE GEESE IN SPITSBERGEN

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Feather growth and changes in body weight during the molt of geese have been little studied. Hanson (1962) found that Canada Geese (*Branta canadensis*) of the Mississippi flyway weighed least during the flightless period; he identified this as the time of greatest stress. Caged birds lost between 5% and 12% of body weight during molt and females lost more weight than males. The energetic costs of molting are rather small compared to other activities of the annual cycle (Payne 1972) although most data are from passerines, which molt more gradually than geese. Hence, weight loss, if it occurs in the wild, may be adaptive because lighter birds are able to fly earlier than heavy ones.

This paper examines the process of wing molt in wild Barnacle Geese (*Branta leucopsis*) caught during the flightless period, and unless otherwise stated, "molt" refers to that of the primary remiges. These geese are part of a small (7,200 individuals in 1976-77 winter) discrete population with a circumscribed winter range (within 50 km) in northern Britain and a breeding range in western parts of the Spitsbergen (Svalbard) archipelago between 77° and 80°N (Boyd 1961, Owen and Norderhaug 1977). This work formed part of an international project in 1977 to study the behavior and energetics of the population at all stages of its life cycle.

STUDY AREA AND METHODS

The work was carried out at Nordenskiöldkysten (between 77°40'N and 78°00'N), one of the most densely populated breeding and molting areas for these geese (Owen and Norderhaug 1977). This is a flat coastal plain some 50 km long and 1.5 to 11 km wide (below 25 m contour). Many small lakes lie within a few hundred meters of the coast and were ice-free by mid-June 1977. Larger, deeper inland lakes were frozen until mid-July and most molting geese concentrated on coastal pools.

A 2-4-m high storm beach runs along the coastline and members of the catching teams (usually 6 or 7 people) were able to walk along the shore unseen by geese on nearby lakes. We surrounded flocks on pools and drove them into a pen with the aid of an inflatable dinghy. All full-grown geese were sexed by cloacal examination and weighed. The chord length of the wings, including the primary feathers and the wing joint itself, was measured. Repeated wing measurements provided information

on feather growth. The length of the wing without feathers ($n = 10$ males without feather stubs) was between 138 and 162 mm (mean = 149); 10 females ranged from 130 to 147 (mean = 141). Means of 150 and 140 mm for male and female wing length were assumed so that feather length could be estimated. The lengths of the skull and tarsus were measured on all but a few birds. Yearlings (hatched in 1976) could be distinguished from adults by a few unmolted brownish juvenile feathers on the wing coverts. Adult females were examined for brood patches (Hanson 1959). Goslings were caught about 4-5 weeks after hatching and were only sexed and weighed.

The geese were marked with coded plastic leg bands (Ogilvie 1972) identifiable at up to 250 m, as well as metal bands, allowing pairs and breeding status to be identified when the geese returned to the wintering grounds. Earlier observations on geese caught in 1973 indicated that re-sighting rates in excess of 90% annually were possible.

RESULTS

Of 1,333 individuals present on the coast during the molting period, 1,241 (93%) were caught. These included 416 adult males, 380 adult females, 188 yearling males, 213 yearling females and 44 goslings. Of the adult females, 125 had brood patches but a count of used nests on all available breeding islands indicated that this may have underestimated the number of attempted breeders. Thus the "non-breeding" group may include a few birds who had attempted to nest but deserted or lost their clutches early, probably before the start of incubation. The proportion of birds identified as yearlings on the coast, 32% of full-grown geese, was higher than the 28% juveniles recorded in the population in the previous season but as it is more likely that yearlings are mistaken for adults than vice versa, yearlings are considered to have been identified reliably.

Mortality of goslings of this population before arrival on the wintering grounds is very small (Owen and Norderhaug 1977). Thus we assumed that pairs arriving in Scotland without young were non-breeders or geese earlier identified as unsuccessful breeders. The breeding status of males was assumed to be that of their mates in autumn. This is a reasonable assumption because pairs rarely, if ever, separate except on the death

TABLE 1. Weights and measurements of Barnacle Geese caught in 1977.

Age	Sex	Breeding	Body weight (g)			Skull length (mm) ¹			Tarsus length (mm) ²					
			n	Mean	s.e.	Range	n	Mean	s.e.	Range	n	Mean	s.e.	Range
A ³	M	B ⁴	48	1972 ± 23.3		1600-2440	48	88.1 ± 0.35		83.5-93.5	48	73.1 ± 0.20		65.0-78.5
A	M	NB ⁴	366	1788 ± 8.5		1350-2230	336	88.5 ± 0.15		81.0-95	335	71.8 ± 0.46		60.5-80
Y ³	M	-	188	1669 ± 10.6		1280-1990	177	88.1 ± 0.18		83.5-95	177	72.2 ± 0.27		63.5-81
All	M	-	602	1765 ± 7.2		1280-2440	561	88.1 ± 0.11		83.5-95	560	72.1 ± 0.15		60.5-81
A	F	B	125	1656 ± 11.2		1330-1880	120	84.6 ± 0.20		81.0-90	120	68.9 ± 0.31		62.5-81
A	F	NB	253	1586 ± 7.7		1210-1950	218	84.1 ± 0.16		78.0-90	219	68.2 ± 0.23		58.5-77
Y	F	-	212	1471 ± 9.2		1120-1820	203	83.9 ± 0.16		78.0-89	202	67.8 ± 0.22		58.5-75.5
All	F	-	590	1560 ± 6.0		1120-1950	541	84.2 ± 0.10		78.0-90	541	68.2 ± 0.14		58.5-81

¹ Skull length is the distance from bill tip to back of head.

² Tarsus length is the distance from the top of the ankle to the bottom of the foot when bent at right angles to the leg.

³ A = adult, Y = yearling.

⁴ "Breeding" males are those caught in catches 8-12, where 46 out of 48 females had bred. Non-breeding males include some (about 80 out of 368) that have attempted to breed (none successfully). These birds were caught at different times but at a similar stage of the molt.

of one partner, and pair formation takes place in winter and spring (Owen, unpubl. data).

Our data were collected after an unusually late spring in Spitsbergen. Nearly all the land was snow-covered on 6 June and some snow still remained on breeding islands. Only 4.4% of the coastal population were goslings—lower than any proportion in the winter population since 1958 (Owen and Norderhaug 1977). Thus it is likely that feeding conditions were worse than usual in the early molt period. The summer was exceptionally warm and later food supplies may have been as good or even better than average. Data from the more normal season of 1973 indicate that weight and molt patterns were broadly similar, although these were collected from another part of the breeding range (Jackson et al. 1974).

MEAN WEIGHTS AND MEASUREMENTS

Means and ranges of weights and body measurements of adult geese are given in Table 1. The sample of "breeding" males was from catches where all but two of the females were classified as breeding. The non-breeding group thus contains at least 77 males that had attempted to breed. The breeding status of females is more reliably determined.

Yearling females molt at weights 115 g (9%) less than non-breeding females and males show a similar pattern. This is probably because adult females accumulate larger body reserves in anticipation of the demands of breeding. Owen, N. Gullestad, and A. K. M. St. Joseph (unpubl.) observed that the abdominal profile [an indication of the amount of fat in the abdominal depot (Hanson 1962)] of yearlings was less convex than that of paired adults at a migration staging area in May. We suggest that these birds were un-

able to store greater reserves because most had, by then, lost parental protection and were harassed by their male parents and other paired males. Since some yearlings were molting at less than 60% of winter weight for their sex, this seems a more likely explanation than the alternative, i.e. molting at lower weight is adaptive for yearlings. Body measurements of yearlings are similar to those of adults of the same sex.

Breeding females were 4% heavier than non-breeders, and males were 10% heavier (*t*-test for both sexes $P < 0.001$). Although both groups were caught at the same stage of molt, the "breeding" sample was caught about two weeks later than non-breeders. The difference may thus be due to better feeding conditions during their molt (see below). This is surprising as Hanson (1962) found that captive geese lost weight during molt and that females did so to a greater extent than males. He suggested that the difference was due to the stresses of breeding; however the breeding females here (both successful and unsuccessful), had partially compensated for loss of reserves about a month after leaving the nest.

The skull and tarsal measurements did not differ significantly between birds of different breeding status.

EFFECT OF CAPTURE

A total of 238 birds were captured more than once and most had lost weight following capture (Fig. 1). Greatest loss was recorded three days after original capture in a group of geese that had travelled 6 km in the intervening period. Birds caught at intervals longer than four days lost little weight, on average 4 g/day, which is no different from normal weight loss during the molt (see below, Fig. 3). Only one sample contained

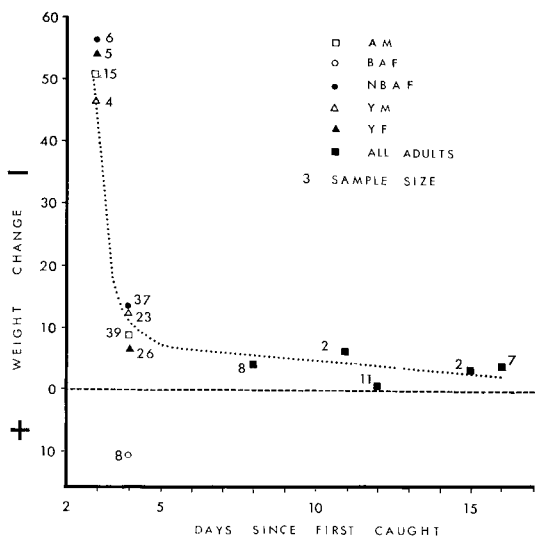


FIGURE 1. The change in weight of birds caught more than once and the number of days between capture. The horizontal dotted line indicates no change, with losses above and gains below. AM, adult males; BAF, breeding adult females; NBAF, non-breeding adult females; YM, yearling males; YF, yearling females.

a sufficient number of females that had bred; eight birds in this sample had on average gained 11 g/day whereas other age and sex groups had lost about 10 g/day.

Since most individuals represented in Figure 1 had travelled some distance between captures (no attempt was made to catch individuals more than once and rarely was the same bird captured at the same site), their weight losses would be expected to be greater than for the majority of the geese, which remained in the capture site. Thus, although the disruption of the feeding pattern during and shortly after capture did cause some weight losses, the overall effect of catching operations was negligible in 1977.

GROWTH RATE OF FEATHERS

Average growth rates of primary remiges, calculated on feather growth per day, irrespective of the number of days between captures (minimum 3 days, maximum 16) are given in Table 2. The rate of feather growth for geese of different age and sex is remarkably constant. Only the breeding females are substantially different, and this is probably because many of them were caught before feather stubs had appeared and there may be a lag between the loss of old primaries and the appearance of the new.

Original feather length was not correlated with growth rate in any group, i.e. feather

TABLE 2. Means and ranges of primary feather growth per day for geese of different age and sex.

Age	Breeding status	Sex	n	Mean	s.e.
A	-	M	88	7.62	± 0.22
A	NB	F	47	7.62	± 0.22
A	B	F	25	7.00	± 0.45
Y	-	M	41	7.42	± 0.29
Y	-	F	37	7.62	± 0.34
Overall			238	7.52	0.13

growth was constant throughout the flightless period.

DURATION AND TIMING OF MOLT

The eventual length of the primary feathers is about 260 mm for males and 250 mm for females. If growth rate were constant, the molt period would last 33–34 days. Allowing for some time lag before the appearance of new feathers and the probable slowing down of growth in the latter stages, the true figure is likely to be 35–40 days. Some birds were seen to fly when their primaries were 80–100 mm less than their expected length so the flightless period can be estimated as about 25 days. Direct observation of marked geese confirmed this, the mean for four individuals being 26 days (J. Prop, T. M. van Spanje, unpubl. data). This agrees well with the value of 3–4 weeks for this and other species of similar size given in Cramp and Simmons (1977).

In order to compare the molt stage of birds of different ages and breeding status, it was necessary to "correct" the wing lengths of individuals measured on different dates to a common reference point. July 23 was arbitrarily chosen; all birds caught before that date had 7.5 mm/day added to their wing length and those caught after had 7.5 mm/day subtracted. A few individuals were caught while still flying on old primaries; their wing length was taken as the mean minimum (without feathers) of 150 mm for males and 140 mm for females. Mean corrected wing lengths are given in Table 3. There is no significant difference between yearling and non-breeding females. We attribute the difference between yearling and "non-breeding" males to the fact that some in the non-breeding group had, in fact, attempted to breed, which depressed the mean wing length. Nesting geese began molting 9–10 days later than non-breeders. Successful birds (subsequent observations from the wintering ground) had significantly shorter wings than unsuccessful ones ($P < 0.001$ for both sexes), and the difference represented

TABLE 3. Mean wing lengths of birds of different ages, sexes and breeding status, "corrected" to 23 July 1977 (see text).

Age	Sex	Breed- ing status ¹	n	Mean wing length (mm)	s.e.	C ²
A	M	B	48	127.9	± 5.1	27.6
A	M	NB	368	214.8	± 2.1	16.3
A	F	B	125	147.6	± 2.5	23.9
A	F	NB	200	219.3	± 2.4	15.5
Y	M	-	188	228.3	± 1.8	10.5
Y	F	-	212	220.8	± 1.5	10.0

¹ Breeding status as in Table 1.² C = Coefficient of variation; % = standard deviation/mean × 100.

7–8 days. The coefficient of variation (Table 3) shows that yearlings were more synchronized in their timing of molt than non-breeders and that the latter were less variable than nesting birds. This would be expected since the non-breeders may include a group that spent some time prospecting for nests and the breeders include geese which failed (and subsequently molted) at different times. A similar pattern of molt of geese of different breeding status has been observed in most species of geese and swans (see Palmer 1976).

Although yearlings were not distinguished in 1973, some were subsequently classed as probable yearlings because they remained unpaired through the following season and then became paired to unbanded individuals. There were 15 males and 16 females in this category; by applying the feather growth rate of 1977 we calculate that this group began molting on 6 or 7 July 1973 (the same date for both sexes). This compared with a mean starting date of 12–13 July for both sexes in 1977, six days later than in 1973. Parental geese, the only other comparable group caught in 1973, started their molt on 28 July (males) and 27 July (females), compared with 28 July and 29 July respectively in 1977. The date of hatching was similar or a very few days earlier in 1973 and 1977, which accounts for the

similar molting time of parents. In 1973 yearlings were caught on offshore islands safe from foxes whereas those in 1977 were on the mainland. Their molt was probably late in 1977 because the lakes were not sufficiently free of ice until the first week of June. Stirling and Dzubin (1967) stated that the molt period of Canada Geese is directly controlled by ice break-up and that the timing can vary up to two or three weeks.

The timing of the molt differs little between the sexes (Table 4). The coincidence in timing of the members of a pair is strongest in unsuccessful breeders, highly significant in non-breeders but not significant in successful pairs. A higher correlation for pairs that had nested unsuccessfully might be expected because both members would molt as soon as possible after leaving the nest. The slight correlation in pairs with young (coefficient of dependence $r^2 = 0.20$) is rather surprising. Figure 2 relates the molt stage of parents to the mean weight of their goslings (identified in autumn) when caught. Since the weights of goslings of different sexes did not apparently differ within broods, both sexes are combined. There is significant correlation between the molt stage of the male parents and gosling weight (and therefore gosling age), $r = 0.753$, $P < 0.01$, but not of females, $r = 0.192$. Thus the timing of the molt of parental males depends on the age of their goslings. The regression in Figure 2 is projected to 0 on the Y axis (the start of the molt), and this occurs when the young weigh 740 g. Young Barnacle Geese reared in captivity in Britain, on grass and high protein supplement, reach this weight at 25–30 days of age (Owen, unpubl. data) and the figure for wild geese is likely to be within these limits.

Comparable data on molt timing of members of 11 parental pairs were obtained in 1973 although their goslings could not be identified. Parental males molted about one

TABLE 4. The stage of molt of pair members when caught. Feather length is wing length minus 150 mm for males, 140 mm for females.

Sex	Breeding status	n	Mean feather	M – F mean	Mean diff. (days)	r M/F feather
M	Non	39	68.0	- 6.5	-0.9	0.688 $P < 0.001$
F	Non	39	74.5			
M	Fail	18	46.2	7.4	1.0	0.926 $P < 0.001$
F	Fail	18	34.3			
M	Succeed	11	58.3	-10.9	-1.5	0.436 NS
F	Succeed	11	69.2			

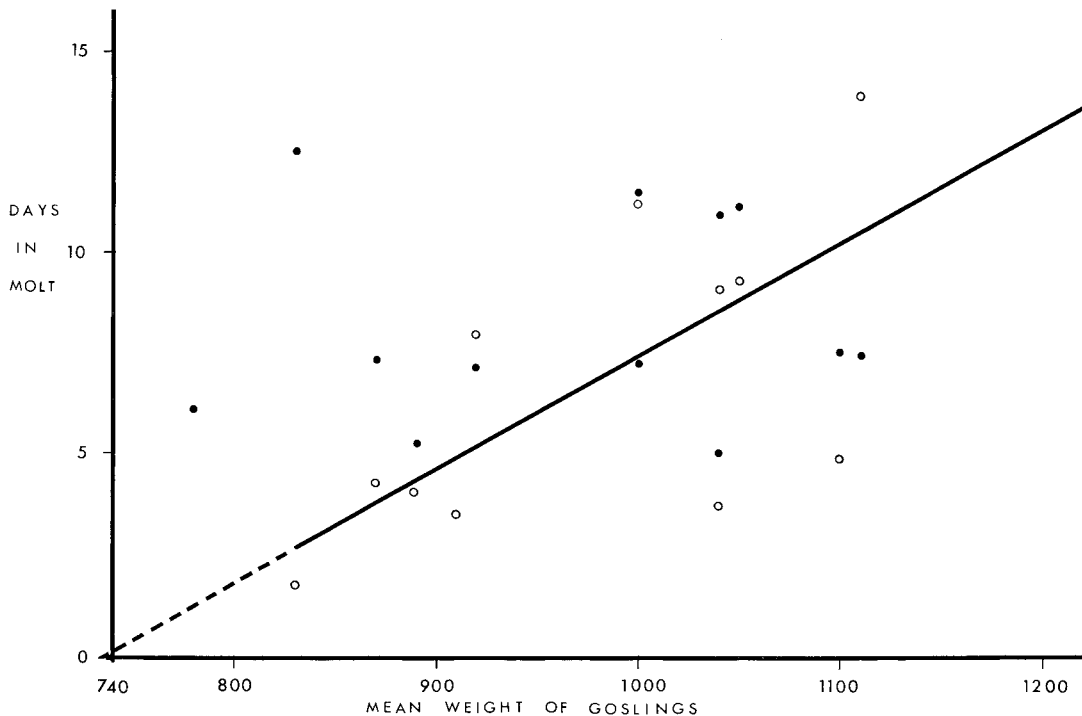


FIGURE 2. The molt stage of parental geese in relation to the weight of their goslings. Open circles: males $r = +0.753$ $P < 0.01$. Closed circles: females $r = 0.192$ N.S. The solid line gives the regression of male molt on gosling weight, projected as a dotted line to the beginning of the flightless period.

day earlier than females and there was similarly no significant correlation ($r = 0.030$).

WEIGHT CHANGES DURING MOLT

The relationship between body weight and molt is given in Figure 3. In order to detect possible changes in weight according to feeding conditions, the data are separated into two periods: before and after 23 July. Before 23 July catches were of dense concentrations of geese in areas where feeding conditions were poor, whereas afterwards the molting groups were smaller, and lakes had better feeding areas adjacent. In all adults, mean weights were higher at the later date although these birds were at least as advanced in molt. An insufficient number of yearlings was caught after 23 July to test for differences. All correlations were slight ($r = -0.077$ to $+0.326$), and only three were significant: adult males 18–23 July, $r = -0.213$, $P < 0.001$; adult breeding females 18–23 July, $r = +0.312$, $P < 0.01$; and yearling females $r = -0.326$, $P < 0.001$. The fact that breeding females molting early (all were unsuccessful breeders) were able to regain some of the weight lost during incubation (see also Fig. 1) may mean that losses in other groups were either adaptive or not directly attributed to molt but to some factor associated with it.

Ankney (in press) similarly found that weights of Lesser Snow Geese (*Anser c. caerulescens*) did not decline during molt and concluded that the molt "is not a great nutritional stress" for that species. His sample is equivalent to ours after 24 July and does not include early molting non-breeders.

AUTUMN WEIGHTS

Of 194 geese caught in Scotland on 4 October 1977, a few days after arrival on the wintering grounds, 26 had previously been caught during the summer molt. All groups except adult males had gained weight even though the geese had undergone a 3200-km migration between captures (Table 5). Although the birds may stop to rest for a few hours en route they do not feed (N. Gullestad, pers. comm.; M. Norderhaug, pers. comm.). The energy cost of migratory flights of Canada Geese has been predicted by Raveling and LeFebvre (1967) and later confirmed in other studies (Berger and Hart 1974) as $12 \times$ Standard Metabolic Rate (SMR). The SMR of a 1.7 kg goose is approximately 125 kcal/day or 5.2 kcal/h (from the equation of King and Farner 1961). At an average speed of 64 km/h (40 mph) (Blokkpoel 1974) the journey would take 50 hours and 3,120 kcal, equivalent to a weight loss of about 320 g (King and

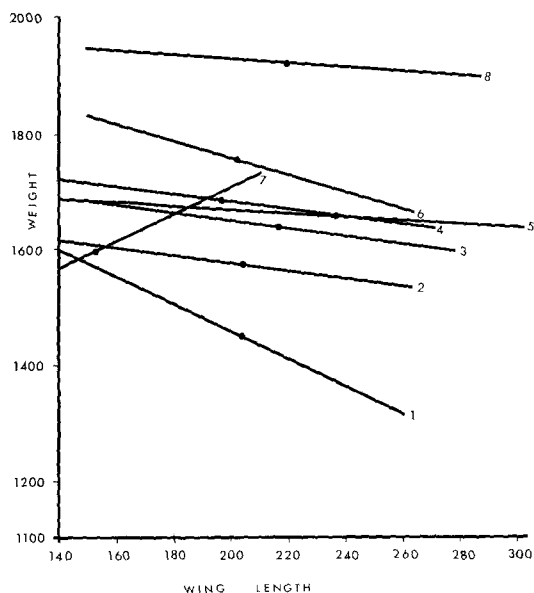


FIGURE 3. Regressions of body weight on wing length of geese of different age, sex and breeding status. The solid dots indicate means for the relevant classes. 1: YF 18–23 July, 2: ANBF 18–23 July, 3: YM 18–23 July, 4: ABF 24 July–6 August, 5: ANBF 24 July–6 August, 6: AM 18–23 July, 7: ABF 18–23 July, 8: AM 24 July–6 August.

Farner 1961). Since Barnacle Geese with full guts have on average 13.5 g of dry food (about 70 g wet; Owen 1975), gut contents are unlikely to account for more than 50 g of body weight of the geese captured in autumn. The geese were caught only a few days after arrival so the weight gain in Scotland would be expected to be small. It is likely that the birds leave Spitsbergen 200–300 g heavier than their autumn weights (Table 5).

Weight gains in the six to eight weeks after the birds regain their powers of flight are considerable (300–500 g [5–9 g/day] for yearlings). Richer feeding areas such as grassy slopes below seabird cliffs are available to flying birds and large flocks concentrate in such areas in late August and September (Owen et al., unpubl.). Weight gains here are less than the 10 g/day recorded for Brant Geese (*Branta bernicla bernicla*) on spring migration (Ebbinge 1977). Since yearlings and adults of both sexes have similar weights in autumn (Table 5) optimum weights for autumn migration are probably achieved before departure. Body weights of nine full-grown males and nine females shot in Scotland a month after arrival in 1972 were respectively 320 g and 200 g more than those weighed in October 1977 (Owen, unpubl. data).

TABLE 5. Mean weights (g) of 26 birds caught in summer in Spitsbergen and recaptured on arrival in Scotland, 4 October 1977.

Age	Sex	n	Summer	Autumn	Difference
A	M	9	1844.4	1828.8	– 15.6
A	F	4 ¹	1648.0	1720.0	+ 72
Y	M	7	1718.6	1871.3	+153
Y	F	6	1513.3	1695.0	+182

¹ Two with and two without brood patches.

These figures probably represent peak winter weights for geese of this population.

DISCUSSION

FEATHER GROWTH RATE

Little is known about the growth rate of primary remiges in large samples of wild waterfowl. Mathiasson (1973) recorded 6.5 mm per day for a few Mute Swans (*Cygnus olor*) and H. Boyd (pers. comm.) quoted a figure of 6.0 mm/day for Brant, with a wide scatter of apparent rates among individuals. Hanson and Jones (1976) gave values ranging from 8.2 to 6.4 mm per day for several races of Canada Geese in captivity. Their values of 7.7 mm for a male and 7.5 mm for a female *B. c. hutchinsii*, a race of similar size to our Barnacle Geese, are close to our values (Table 2) for wild geese. This suggests that feathers may grow at similar rates in wild and captive birds. Further studies of captives would add to our knowledge of growth rates and flightless periods in geese.

WEIGHT CHANGES AND TIMING OF THE MOLT

We have shown that there are differences of up to two weeks in the molt dates of individuals of different age and status. Birds that had nested in 1977 were flightless when the vegetation was growing and they were better able to use rich areas around lakes farther inland and slower thawing, than were non-breeders. Why then do non-breeders not delay their molt until these lakes become available? They do not undergo the stresses and energy demands of breeding, and the evidence suggests that they molt as soon as the shallow coastal pools are ice-free, although feeding areas around some of these pools are relatively poor. Nevertheless, the birds lose little weight during the molt.

The energy cost of feather replacement can be calculated from the weight of the feathers being molted (Kendeigh et al. 1977). Further, the daily cost of molting can be calculated if the duration of the molt period is known. The

total weight of the primaries, secondaries, and tertiaries of a Barnacle Goose was 21 g. Since the wing coverts and some body feathers are molted at the same time as the flight feathers, the total weight of feathers being replaced is likely to be approximately 25 g. Using the conversion of Kendeigh et al. (1977) the total cost is 2675 kcal, or 70 kcal per day over a 38-day period. This is equivalent to about 25% of daily energy expenditure in winter (Ebbinge et al. 1975).

Molting birds often compensate for the increased energy demand by remaining inactive and these Barnacle Geese spent eight hours feeding, eight hours resting and eight hours swimming, preening, etc. (R. Wells, P. Reynolds, unpubl. data). This time budget resembles that at other times of the year except that the birds do not fly and do less walking while foraging. Wintering geese spend upwards of 30 min flying (unpubl. data), so the energy "saving" through relative inactivity during molt is about 50 kcal/day. Other compensating factors in molting birds (Kendeigh et al. 1977) probably reduce the energy burden of wing molt to less than 10% of the daily energy requirements.

By molting early, non-breeders can increase the time available to lay down premigratory reserves. Not only can they take advantage of increased quantity of food but they can use previously unexploited areas, free from competition with nesting birds and their families. Some of these areas, such as the slopes beneath seabird cliffs, are extremely lush. Similarly, geese that have nested unsuccessfully become flightless shortly after they leave the nest.

Palmer (1972) stated that a female Lesser Snow Goose drops her quills approximately 21 days post-hatching and a male 3-4 days later. He further observed that "the molting of the gander quite likely is triggered some time beforehand by visual and/or auditory cues from the goose." Our data conflict with this suggestion, as female Barnacle Geese molted on average a day earlier than males in 1977 and a day later in 1973, but individuals varied greatly, from 11 days earlier to 5 days later than their mates. Parental females in 1977 began their molt on average three weeks after hatching. Before molting, nesting females must replace some of the body reserves lost during laying and incubation and the attainment of a minimum weight may control the timing of their molt. The molt of males is correlated with the size of their young; males become flightless when young are about a month old. Since Barnacle goslings fly at

40-45 days (Cramp and Simmons 1977) and the flightless period of adults is about 25 days, these males will be flightless for one or two weeks after their goslings are able to fly. This suggests that the delayed molt of males is more important for enabling them to protect the young goslings than for synchronizing their attainment of flight with fledging of the young. This is contrary to Ryder's (1967) suggestion that synchronization with the goslings' flight is most important in Ross' Geese (*Anser rossii*). Hanson (1965) stated that the wing molt of breeding females preceded that of their mates by a week to 10 days, but quoted Balham (1954) as presenting conflicting results indicating that adults of both sexes molted 20-30 days after hatching. If our hypothesis on the regulation of molt timing in parental females is correct, these observations need not conflict since seasonal differences, as they affect the post-hatching condition of breeding females, could induce different molt patterns in different years and in different areas.

Cooch (1958) and Inglis (1977) observed that the male is almost completely responsible for protecting the young, and the adaptive value of the delay of molt is obvious. Month-old goslings are safe from aerial predation, against which the male's ability to fly is most important.

Our finding that little weight is lost during molt agrees with that of Ankney (in press) but conflicts with Hanson's (1962) data on *B. canadensis* at lower latitudes. He found that females lost relatively more weight than males and adults more than yearlings. He attributed the greater weight loss of females to their greater initial fat deposits. This suggests that weight losses may not be a direct effect of molting but may have adaptive advantages. We have argued that the energetic costs of molting are probably below 10% of daily energy requirements. Thus geese in captivity should be able to maintain weight easily since our geese make weight gains equivalent to an excess of 10% of daily requirements immediately following molt. We noticed that the lightest birds were able to fly on undeveloped wings. Thus the effective shortening of the flightless period has selective value, as the remains of flightless geese were recovered from the dens of Arctic foxes (*Alopex lagopus*). We suggest, therefore, that non-breeding birds who begin the molt with large fat deposits are at an advantage if they deplete these, whereas lighter individuals attempt to maintain their body weight slightly above critical level to provide some insurance

against unfavorable feeding conditions and low temperatures during the molt period. Non-breeders and immatures who molt at low weights early in the season could be stressed if feeding conditions were poor. Immatures may also suffer in feeding competition with adults at the same molting site (it may be significant that the lightest individuals, the yearling females, showed the steepest decline in weight; Fig. 3).

Breeding geese, molting later, did not conform to this pattern for we have evidence that they are substantially heavier at the same molt stage than non-breeders. Similarly Marris and Ogilvie (1962) found that adult Barnacle Geese caught with goslings in Greenland late in the season were 8-9% heavier than non-breeders caught earlier. This suggests that for the later molting birds, the requirement for building up premigratory reserves overrides the advantages of reducing the flightless period. Barry (1962) found that non-nesting Brant Geese were heavier than nesting females at least until mid-molt although his samples were small. Ankney (in press) found a 16% increase in the weight of females between late incubation and early molt, whereas the weight of males remained constant. Neither sex lost weight subsequently. Ankney's generalization that molting is not stressful for Snow Geese is not fully justified since he examined only those birds which were flightless when food supplies were adequate. The fact that females lay down body reserves before becoming flightless suggests that in certain circumstances these reserves may be necessary to complete molt satisfactorily.

THE MOLT MIGRATION

The immatures and non-breeders of most goose species undergo a molt migration, sometimes to sites several hundred miles from the breeding area. Salomonsen (1968) observed that all known cases in geese were northward, in many cases to areas beyond the boundary of the breeding range of the species. This does not hold in a few cases, e.g. the probable migration of East Siberian Brant to more southerly molting sites in Alaska (Palmer 1976) and the southwesterly migration of small numbers of Graylag (*Anser anser*) and Canada geese in Europe (Ogilvie 1978). Salomonsen suggested that one reason for the northerly migration was to avoid competition with breeding birds "enabling the breeding population to raise its productivity." For any such habit to be perpetuated, it must confer advantages to the birds undergoing it rather than to another segment of the same

population. Avoidance of competition is advantageous, but this would operate whatever the direction of movement or, as with geese in this study and several breeding groups of Lesser Snow Geese (Palmer 1976), where non-breeders molt in discrete groups within the breeding area.

Ebbinge and Ebbinge-Dallmeijer (1977) have attempted to explain the northerly movement by suggesting that the geese profit from the longer days and lessened vulnerability to predators. Some goose molt migrations, however, are northward from areas of continuous daylight (see Salomonsen 1968 and Palmer 1976). They argued that predation of Pink-footed Geese (*Anser fabalis brachyrhynchus*) in the Icelandic breeding grounds is higher than in Spitsbergen. Gardarsson (1975), however, following several years of intensive study at Thjorsarver, the main colony, assumed that "casualties among adult birds during this (summer) period are so few that it is not necessary to take them into account." Inglis (1977) found no evidence of fox predation on adults and very little on goslings in the same area.

Stirling and Dzubin (1967) suggested that reduced vulnerability to predators is the main reason for northerly migration to safe areas where human and predator pressure is low and where waters for escape are available. This cannot be true, for example, with the Pink-footed Geese of Iceland. Stirling and Dzubin further suggested that northerly migrations "may be associated with traditional areas of use during past climatic optimum." However any movements that are costly in energy and that do not benefit those undergoing them, would cease through natural selection.

We suggest that non-breeding geese migrate northward because feeding conditions are better, not only because there is no competition with breeding conspecifics but because the vegetation is at an earlier stage of growth and hence more nutritious and more easily digested. The results presented in this paper indicate that the geese were under little stress while molting but conditions could be envisaged where small weight losses during molt following a poor winter and late spring and a lengthy migration might be critical. Because immatures molt at lower weights than adults they would be the most likely to suffer from adverse conditions and to benefit from a move to a better molting area. Very occasional conditions that eliminated the immatures molting within the breeding area would ensure the continuance of the movement. Large and unexplained apparent adult mortalities have

been recorded in this Barnacle Goose population in the past and it has been suggested that these could have been brought about through mass deaths of non-breeders during molt (Owen and Campbell 1974). Before we can better understand the importance of molt stresses we need to know more about annual variations in body condition on arrival at the molting area and about the range of environmental conditions likely to be encountered by molting geese.

In southern populations, increased day-length for feeding may give an added benefit. Our observation that Barnacle Geese do not eat much during molt—if it held true for other species—would mean that the advantage of avoiding predators would be negligible. The birds could retreat onto water or fox-free islands to rest during the dark period, or when predators were nearby, without affecting their demand for feeding. Indeed, Ekman (1922; quoted in Salomonsen 1968) stated that Lesser White-fronted Geese (*Anser erythropus*) move to the uppermost parts of mountains. Movement up an altitudinal gradient is equivalent to increasing latitude and such movements may occur in other species whose habits are not yet well known.

Non-breeding and immature Barnacle Geese in this study do not undergo a molt migration apparently because little habitat is not already occupied by breeding and molting flocks (Owen and Norderhaug 1977). Instead they molt early and regain the powers of flight as close as possible to the start of grass growth. Non-breeding Ross' Geese in Canada also molt with breeding birds within the breeding area (Ryder 1967). Northerly movement for them would mean movement to milder areas (Ryder 1969) and possibly into competition with the larger and more aggressive Lesser Snow Goose (MacInnes and Cooch 1963). Ryder (1967) stated that non-breeders and yearlings move into "inland lakes and water-courses," which suggests that they may be moving up a climatological gradient. Gardarsson and Sigurdsson (1972) discovered that the only major molting area of Pink-footed Geese in Iceland apart from that within the breeding colony was around a large upland lake near a major icecap. Here ice break-up would be later than in the breeding area and these geese were also molting higher up a climatological gradient. This lake is also a molting site for Graylag Geese (R. H. Kerbes and Ogilvie, unpubl. data) whose breeding grounds are in milder areas both north and south of the molting site (H. Boyd, unpubl.). All these

cases are consistent with our hypothesis as to the reasons for molt migration in geese.

The advantage of making a, sometimes long, molt migration must outweigh the costs of reaching the molting area. While many birds of North America and Eurasia travel overland and presumably stop en route, the Icelandic Pink-footed Goose makes an 800–1200-km migration, most of which is over the sea, to Greenland. The main breeding area, which is a discrete oasis of vegetation, appears, however, unable to support the large breeding population even without the molting non-breeders (Gardarsson 1975). In this situation even a long molt migration would have obvious selective advantages.

More detailed information is needed on the energetics of breeding in geese before the significance of the costs of molting in the annual energy budget can be more fully understood.

SUMMARY

This paper examines the wing molt and measurements of 1,241 Barnacle Geese caught during the flightless period in Spitsbergen (Svalbard) in 1977. Birds were individually marked and observations on the wintering grounds established pair and breeding status of individuals caught in molt.

Yearlings were about 9% lighter than adult non-breeders although other body measurements were similar. Breeding birds which molted later in the season were heavier than non-breeders, presumably because feeding conditions were better.

Repeat captures showed that the round-ups caused large weight losses in some groups, although geese caught more than four days after their original capture showed only small daily weight losses. Catching operations could, in certain circumstances, cause increased mortality of molting geese.

Primary feathers grew at the rate of 7.5 mm/day on average. This was similar in all age and sex classes and the rate was constant through the flightless period, which lasted about 25 days. Because the birds could fly before their primaries were fully grown, the period of wing molt is longer, 35–40 days.

Unsuccessful nesters molted 9–10 days later than non-breeders, who became flightless as soon as coastal pools became ice-free. Parental adults began their molt 7–8 days later than unsuccessful breeders. The timing of molt of parental males was correlated with the size of their young, and began when young were a month old. Molt of parental females was independent of that of their mates and we

suggest that the timing of their molt is determined by the need to attain a minimum body weight after the stresses of laying and incubation.

Most classes of geese lost weight gradually during molt but females who nested unsuccessfully made significant gains. We suggest that birds beginning the molt with large fat reserves are at an advantage in depleting these because lighter birds have a shorter flightless period. Geese beginning the molt in poor condition (many of the yearlings in our sample) would suffer if feeding and weather conditions were unfavorable.

We argued that non-breeders molt early in order to maximize the time available for acquiring reserves for autumn migration. Post-molting geese are able to use better feeding areas and a sample recaptured in autumn had gained up to 500 g in weight following molt.

We hypothesize that many goose species undergo a long northward molt-migration because it enables them to molt at the beginning of the growing period in these areas, when the vegetation is more nutritious and more easily digested.

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RECENT PUBLICATIONS

Never Enough of Nature.—Lawrence Kilham. 1977. Droll Yankees, Mill Road, Foster, Rhode Island 02825. 264 p. \$10.00. The reflections of a naturalist who, through sensitive and patient watching, has seen many unusual sights in the wild and who has befriended a bizarre array of "pets." Most of the writing pertains to eastern North America although there is a section on the author's adventures in the tropics and Africa. Kilham's homespun prose and unique encounters with wild animals combine to make this book different but rewarding for amateur naturalists who feel that they can have "never enough of nature."

A Year with New England's Birds: A Guide to 25 Field Trips.—Sandy Mallett. 1978. New Hampshire Publishing Co., Somersworth, NH 03878. 128 p. Paper cover. \$5.95. This book recounts a series of field trips taken by the author and her family, throughout the year, to some of the good birding areas in New England. Each chapter includes a list of the species

to be expected at that time and place. Writing for novice birders, the author pleasantly evokes her experiences and tells a little about the birds she saw. Readers may have difficulty in following her trail, however, because directions for finding several places seem inadequate. Illustrated with photographs and nice drawings by Gail Reyna.

Birds of Man's World.—Derek Goodwin. 1978. British Museum (Natural History) and Cornell University Press, Ithaca and London. 183 p. \$10.95. With all the talk about endangered species, we tend to overlook those birds which have managed to thrive alongside mankind. This book redresses the balance, describing many of the ways by which birds have adjusted to or taken advantage of man-made changes in the environment. The author gives many examples from his own experiences, mostly in Britain, Egypt, Sri Lanka, and Australia. Addressed to a general audience, the book is informative and easily readable, but loosely organized and undocumented.