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PATTERNS OF BODY MASS CHANGE DURING MOULT IN THREE DIFFERENT GOOSE POPULATIONS

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We used measurement of wing feather length as an index of moult stage to assess body mass changes amongst samples of geese caught from three different wild populations during the period of regrowth of flight feathers. Amongst male and female Greenland White-fronted and Canada Geese captured in west Greenland, there were no significant correlations between body mass and wing length. This pattern fits the generally accepted theory that moulting geese do not suffer nutritional stress during the regrowth of remiges (ie that nutritional and energetic needs of the geese during moult can be met from exogenous sources). In contrast, average body mass of Greylag Geese on the Danish island of Saltholm fell by between 12 and 26% during moult, confirmed by field observations of consistent reductions in abdominal profile scores (a field assessment of the extent of abdominal fat stores). It would appear from these data that moulting Greylags on Saltholm do utilise body stores accumulated prior to the flightless period to sustain birds through the moult period, and the significance of these findings are discussed in the light of existing information.

Keywords: Goose Populations, Mould, Body Mass, *Anser albifrons*, *Anser Anser*, *Branta canadensis*

Introduction

In attempting to identify critical periods in the annual life cycle of migratory waterbirds, it is convenient to focus upon those events which place additional nutritional demands upon the individual over and above the normal demands of general maintenance. Such nutritional 'bottle-necks' might include over-winter survival, reproduction and long-distance migration (eg Ens *et al.* 1994). All represent periods of nutritional stress, that is, when a bird's nutrient demands exceed the supply derived from ingestion,

resulting in catabolism of body tissue to meet that demand, *sensu* Ankney (1979). Because the body stores (ie nutrients accumulated in advance of periods of shortage, *sensu* van der Meer & Piersma 1994) and ultimately body reserves (ie body parts metabolised only in emergencies), of an individual face depletion at such times, they represent periods in the annual cycle when malnutrition is most likely to occur, and hence are likely to have fitness consequences for the individual.

Whether the flightless moult period of migratory geese represents such a period of

stress in their annual cycle has been the subject of considerable debate (see Hohman *et al.* 1992 for discussion). All northern hemisphere geese undergo simultaneous moult of flight feathers that renders them flightless for 21-35 days (Hohman *et al.* 1992). Since feather keratin contains high levels of sulphur-rich amino acids which are relatively scarce in their plant food, it is perhaps not surprising that some authors have considered wing moult to be a period of stress in herbivorous geese (eg Hanson 1962). Laboratory studies have shown that wing moult in Greylag Geese is energetically costly (eg van der Wal 1992) and it is well demonstrated that the soluble protein contents of monocotyledonous plant species are generally low (eg compared with soft-bodied invertebrates, Hohman *et al.* 1992). Hence, restriction of foraging choice (through flightlessness), combined with both the energetic and separate nutritional demands of feather replacement are highly likely to demand high intakes rates of exogenous nutrients to avoid nutritional stress. Despite this, Hohman *et al.* (1992, p.149) report that 'all studies of body mass change done to date indicate that body mass in postbreeding geese is constant or increasing through the wing moult', excepting the captive studies of Canada Geese by Hanson (1962).

In this paper, we report progress on the study of body mass loss in moulting Greylag Geese *Anser anser* on the Danish island of Saltholm, contrasting evidence from two other studies of body mass dynamics in free-living goose populations during moult in West Greenland. We also speculate upon the possible mechanisms responsible for the observed differences.

Methods

Data are presented from three different moulting goose populations, two sympatric low-arctic populations, the Greenland White-fronted Goose *Anser albifrons flavirostris* and the Canada Goose *Branta canadensis* from west Greenland together with the temperate Greylag Goose from Denmark. Greenland Whitefronts were captured in the Isungua area of Sisimiut Kommune, west Greenland

(67°00'N, 50°30'W) during the flightless period in July of 1989 (26 adult birds), 1992 (59) and 1997 (9). Geese were forced onto lakes, a funnel of nets was erected along the lakeshore leading to a corral on land and geese were then driven off of the water using boats (Wright & Mitchell 1993, Kristiansen 1998). Canada Geese were captured in the same area using the same techniques during 1992 (10 birds) and 1997 (52). In all 50 adult male and 44 adult female Whitefronts and 32 adult male and 30 adult female Canadas were caught and full measurements taken in these seasons. Measurements from all birds were taken of standard wing-length (Dzubin & Cooch 1992) to measure the extent of growth of the longest primary. Although growth of remiges in ducks is apparently affected by nutrition and date of replacement (Smart 1965, Pehrsson 1987) and it known that the growth rate is not linear with time (Owen & King 1979, van Dijk & van Eerden 1991), we have been forced by necessity to use this measure as an index of flight feather moult progression. Body mass was also determined for all geese captured to the nearest 50 g using Pesola scales.

The study of moulting Greylag Geese on the island of Saltholm since 1993 (situated in The Sound between Swedish Skåne and Danish Sjøælland) has already been described (Fox *et al.* 1995, Kahlert *et al.* 1996). Here, the body condition of moulting geese was assessed using a field assessment of the abdominal profile (Owen 1981) of large samples of free-living birds. We used the modified scoring methods of van Eerden *et al.* (1991) scaling profiles between 0.5 (very lean, equivalent to van Eerden *et al.* score 1) to 3 (very fat, equivalent to van Eerden *et al.* score 6) to the nearest 0.5 during the years 1993 to 1998 inclusive, deriving daily mean scores from as many individuals as possible (always >15 on any one date). Mean profile scores were used in preference to median scores because these provide a smoother summary of the behaviour of the samples, and because no attempt has been made to analyse differences statistically in the present paper. Since it was not possible to determine sex of focal birds with any certainty, no attempt was made to segregate these data

by sex classes. In addition, we used cannon-nets to capture Greylag Geese during the moult period in 1998 to (i) relate wing feather regrowth directly to body mass and (ii) calibrate the visual abdominal profile score to body mass. A total of 24 geese were captured (seven birds on 26 May prior to the onset of flightlessness, 12 on 11 June in the middle of the moult period and five on 26 June when birds could just fly). In this sample of birds, geese were placed in a pen constructed of wire netting and their abdominal profile determined by experienced observers using the same techniques as used in field determinations, viewed from >30 m distance. The length of the longest (9th) primary from the remige calamus at the skin surface to the distal end of the feather was measured (using a graduated rule placed between the 8th and 9th primaries) as an index of feather growth and body mass was determined to the nearest 50g using a Pesola balance.

Note that the caught samples from all three species includes some birds which were capable of flight towards the end of moult, but which chose not to do so during the catching process, such that this factor does not lead to bias in the distributions of weights and wing lengths in the data presented.

Results

Greenland White-fronted Geese

There were no significant differences between the wing length and body mass distributions for the three years (*t*-tests, $P > 0.05$), so all data were combined. There were no significant correlations between wing length and body mass in data from all years combined for either males ($r = 0.044$, $n = 50$, $P > 0.05$) or females ($r = 0.395$, $n = 44$, $P > 0.05$, **Figure 1**).

Canada Geese

There were no significant differences between the wing length and body mass distributions for the two years (*t*-test, $P > 0.05$), so the data were combined. There were no significant correlations between wing length and body

mass in both years combined for either males ($r = 0.175$, $n = 32$, $P > 0.05$) or females ($r = 0.132$, $n = 30$, $P > 0.05$, **Figure 2**).

Greylag Geese

There were consistent declines in mean daily abdominal profile scores with time in all six years of the study (**Figure 3**). There were significant differences in weights of birds ascribed to differing abdominal profile score, there being an average of 320g difference between successive 0.5 increments in profile score (**Figure 4**). We therefore infer that there were significant losses of weight in all six years of the study, although in the absence of direct body mass determinations, this cannot be stated categorically. Although there were apparent differences between the sexes within API score classes, since the sex ratios approximated to 1:1 in most classes and field assessments made no sex distinction, we have used the calibration for a crude assessment of the relationship between body mass and time during the moult. Amongst the caught sample in 1998, there were significant negative correlations between wing length and body mass in both males ($r = -0.842$, $n = 13$, $P < 0.001$) and females ($r = -0.615$, $n = 11$, $P < 0.05$, **Figure 5**). However, if the birds caught full winged prior to moult are omitted (which are here plotted in **Figure 5** as zero feather length because these birds were on the point of shedding flight feathers), these relationships fail to attain statistical significance due to small sample sizes (males $r = -0.718$, $n = 9$, $P > 0.05$ and females $r = -0.678$, $n = 6$, $P > 0.05$).

Discussion

The use of such regression analysis of body mass changes with moult stage should, of course, be viewed with some caution. The use of wing length (using some measure of the longest primary as presented here) as a measure of moult stage is complicated by the non-linear nature of the growth rate with time, and the effects of external constraints upon feather growth. However, there is such individual variation in the timing of moult that

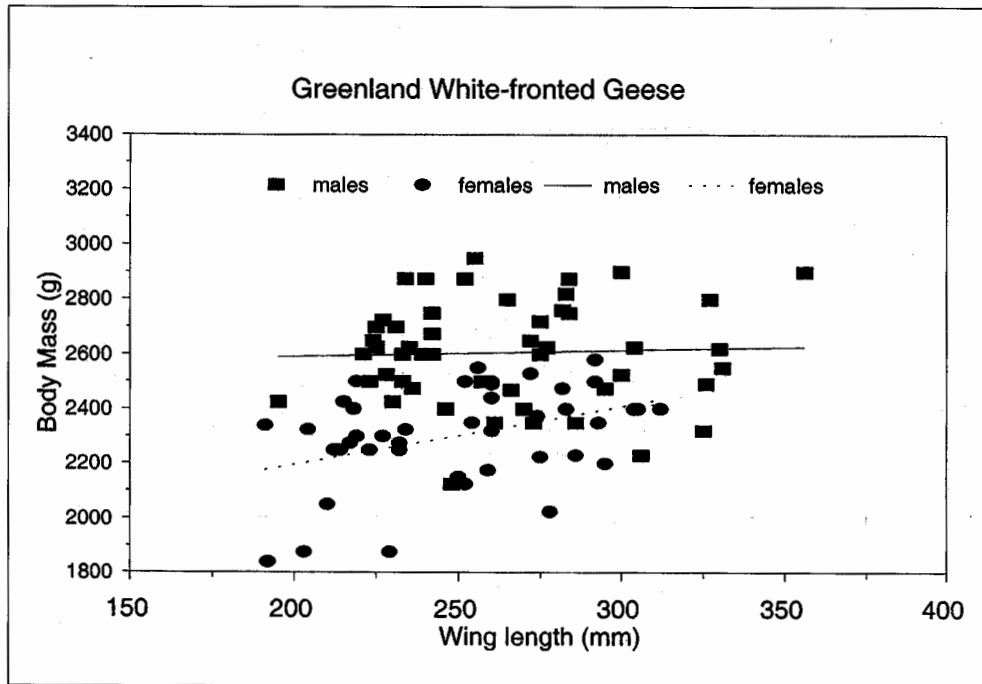


Figure 1. Changes in body mass with wing length (as a measure of moult progression stage) in adult male and female Greenland White-fronted Geese captured in Isungua, west Greenland in the summers of 1989, 1992 and 1997. Fitted least-squares regression lines are shown, although there are no significant correlations between the parameters.

date alone is very poor index of the stage of moult in any one individual, and hence feather regrowth must represent a more appropriate measure. In addition, the use of samples from geese rounded up during the flightless period compared to birds caught with cannon nets prior to and during the moult also complicates analysis. No full-winged geese were caught in the Greenland samples immediately prior to moult which may have demonstrated the high body mass found in the cannon-netted Greylag Geese. Nevertheless, White-fronted and Canada Geese caught in the latter stages of moult (which had the power to fly) showed no sign of being lighter than at other stages of the moult. Some of the female birds of both species showing low body mass early in the moult may well have been breeders or failed breeders, commencing moult at particularly low body mass levels after incubation weight loss, but elimination of these individuals has no

effect on the relationship between body mass and wing length. Hence despite these limitations, we consider there is evidence that there are real differences in body mass dynamics during moult in these two populations and in Greylag Geese.

Ankney (1979) considered that the ability of adult Lesser Snow Geese to meet the nutrient demands of wing moult through their diet was hardly surprising given that during the same period, and in the same area, growing goslings increased their body weight 20 fold, developed leg and breast musculature to almost adult size, grew and ossified a skeleton to almost body size and grew a complete set of body, tail and wing feathers. This logic has undoubtedly shaped much of the discussion relating to body mass dynamics of moulting geese ever since, even though Owen & Ogilvie (1979) showed significant declines in body mass with moult stage in arctic Barnacle Geese *Branta leucopsis*

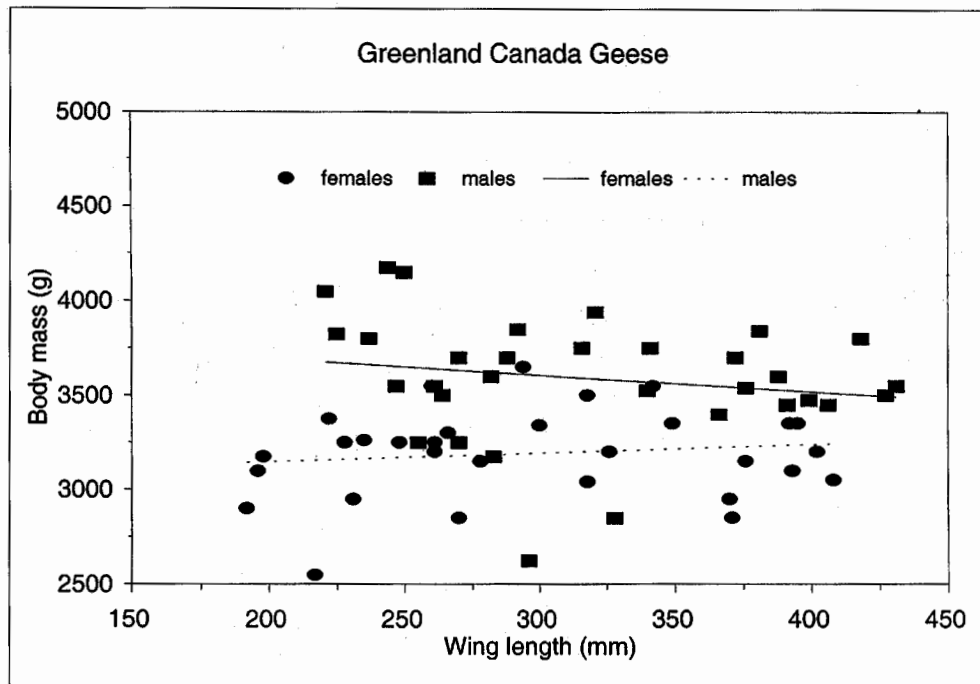


Figure 2. Changes in body mass with wing length (as a measure of moult progression stage) in adult male and female Canada Geese captured in Isungua, west Greenland in the summers of 1992 and 1997. Fitted least-squares regression lines are shown, although there are no significant correlations between the parameters.

amongst adult males and yearling females. Those authors considered that mass loss was adaptive, geese lay down body reserves as an insurance against adverse conditions during flightlessness. Owen & Ogilvie (1979) argue that if conditions are favourable, body mass is lost to speed up the onset of flight, which could be interpreted as being advantageous to minimise predation risk and (certainly in the case of Owen and Ogilvie's Barnacle Geese) enable access to richer feeding grounds which are essential for pre-migratory fattening. However, Ankney's (1979) carcass analysis suggested geese were close to lean weight, since there were no fat depots in his birds at any time during moult. Furthermore, the captured Greenland White-fronted Geese weighed in this study were close to the lowest weights recorded at any stage in their annual cycle (unpublished data). Hence, it seems unlikely that this explanation applies to weight

loss in all goose species.

The findings presented here confirm that there was no body mass loss associated with the moult in two populations of geese occurring in the low arctic region of west Greenland, where both species are able to exploit the nitrogen-rich youngest growth of graminoid species in sedge-rich meadows and late-snow patches associated with their moulting lakes (see Madsen & Fox 1981 and Fox *et al.* 1983 for White-fronts, personal observations for Canada Geese). It is known that non-breeding moulting White-fronts spend approximately one-third of the 24 hours of daylight feeding in west Greenland (Madsen 1981) and preliminary data suggest non-breeding Canada Geese show very similar patterns there (J.N. Kristiansen unpubl. data). Since most of the remaining time is spent by both species resting or preening on, or extremely close to, their feeding habitats, it

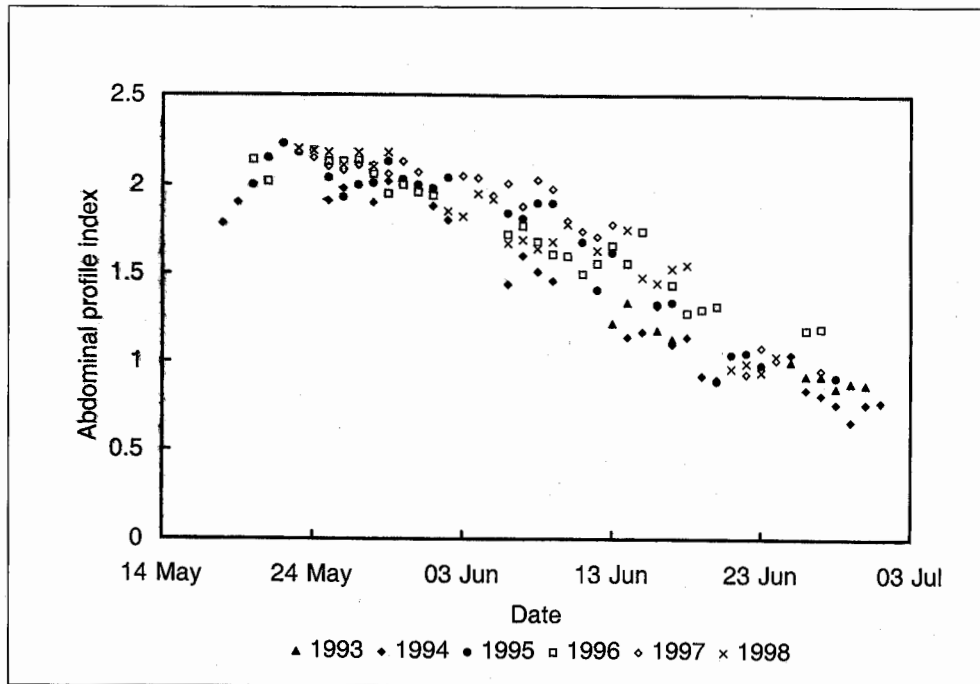


Figure 3. Mean daily abdominal profile scores of Greylag Geese moulted on the Danish island of Saltholm from 1993-1997 inclusive.

seems clear that there is potential for these birds to devote an even greater proportion of their daily activity to foraging if there was a nutritional need so to do. Hence, despite the relatively recent arrival of the Canada Goose to this part of west Greenland (Fox *et al.* 1996) and the potential for exploitative competition with White-fronts (Kristiansen 1997), it would appear that in this particular study area at the present time, neither species has difficulty meeting the energetic and nutritional demands of wing moult in habitats which are shared with breeding populations. This presumably has fitness implications, in that both species (post moult) are not then required to rebuild depleted body stores/reserves in preparation for autumn migration to wintering areas, a distance of 3000-3400 km via staging areas in the Atlantic provinces of Canada to wintering areas in the United States between Massachusetts and Pennsylvania for Canada Geese (Glahder *et al.* 1996, Kristiansen 1998) and 2500-3100 km via Iceland to western

Britain and Ireland for White-fronted Geese (Fox *et al.* 1994).

In marked contrast, however, we document the first clear evidence of a substantial loss of body mass associated with moult in individual non-breeding Greylag Geese on Saltholm. The mean body mass of males caught towards the end of the 1998 moult period represented a loss of 25.7% of those caught prior to dropping their old flight feathers, with females showing a 12.0% loss over the same period. Although the sample size of weighed individuals was small (and the condition of birds attracted to bait perhaps reflects a biased sample of the population overall not present in samples of geese rounded up during moult), the pattern of reduction in abdominal profile in free-living geese has been consistent over the past six years of the study, suggesting that this is a regular phenomenon associated with this moulting aggregation. There are strong indications that the same is also true of Greylags moulting at Oostvaardersplassen in

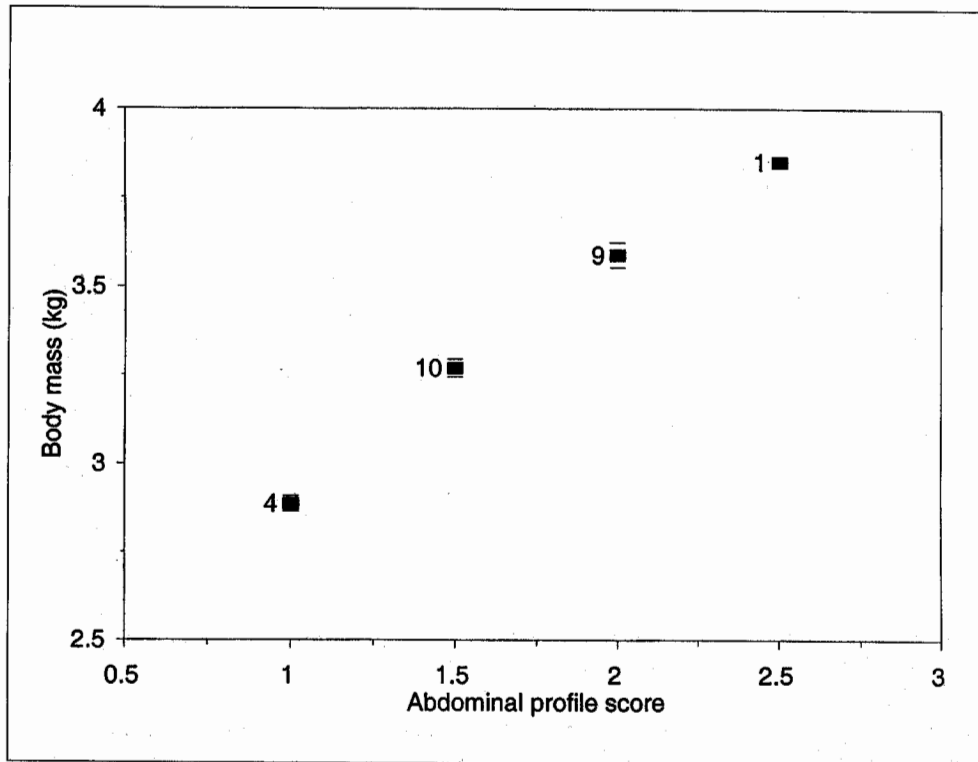


Figure 4. Mean body mass values (\pm standard errors) of captured Greylag Geese assigned to abdominal profile index size classes. Note no birds amongst the caught sample were considered to be of classes 0.5 or 3.0.

The Netherlands, where individually marked geese showed an average decline in abdominal profile index from 2.3 to 1.6 (using the scale presented here), although some individuals did show no change at all (Loonen *et al.* 1991). Based on the calibration curve presented in **Figure 4**, such a mean reduction in abdominal profile would equate to a reduction from 3.75 kg to 3.30 kg (a mean reduction of 12% of the starting body weight), of similar magnitude to that observed amongst the female sample captured here. In captive studies, a female Greylag Geese also showed loss of body mass from 3.3 to 2.8 kg during moult (van der Waal 1992).

So why the difference in body mass change during moult between species? It is clear that geese can derive adequate nutrients to meet the demands of flight feather regrowth in arctic situations, so why then should Greylag Geese

fail to do so in more temperate conditions? In considering the nutritional demands of the moult, it is important to focus on two differing elements: protein balance and energy requirement. Feathers are largely composed of protein, yet this resource is stated to be of restricted availability to herbivores in the environment relative to other nutrients and energy (Hohman *et al.* 1992) and the capacity of birds to store protein is generally considered to be very limited (Blem 1976). It is also thought that the sulphur-rich amino acids typical of feather protein are relatively scarce in the environment (Hanson 1962) and the conversion of dietary protein into feathers is energetically costly in waterfowl (Murphy & King 1984). Hence, the availability of dietary protein rich in sulphur-bearing amino-acids may place a constraint upon the ability of a goose to complete moult without catabolism of body

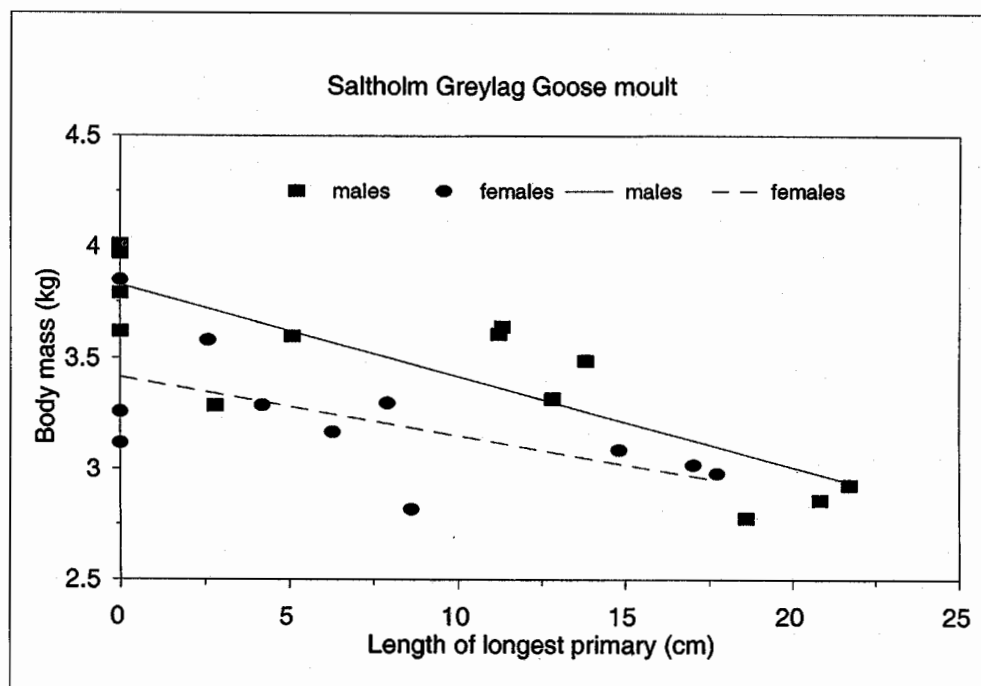


Figure 5. Changes in body mass with length of 9th primary feather (as a measure of moult progression stage) in adult male and female Greylag Geese captured on Saltholm, Denmark in May/June 1998. Fitted least-squares regression lines are shown, there being significant negative correlations between the parameters amongst both sexes.

stores or reserves. Secondly, the conversion of dietary protein into feather mass is thought to be energetically costly (Murphy & King 1984), confirmed in the Greylag Goose by recent laboratory studies (van der Wal 1992). Although not as rich a source of energy as fat, dietary protein offers a potential c.18 kJ g⁻¹ energy content, which exceeds that of structural and soluble carbohydrates (Schmidt-Nielsen 1975). If dietary protein is used preferentially for production of feather material and typically comprises 15-25% dry weight content of the diet during the moult (Loonen *et al.* 1991, Fox *et al.* 1998), this loss of a potential source of energy from the diet has additional consequences for moulting geese if that diet is already relatively energy-poor (given that diet selection already favours a high protein content, eg Fox *et al.* 1998). Analysis of uric acid content of droppings from Greylag Geese on Saltholm shows that uric acid secretion is

reduced by 50% during moult compared to the period prior to flightlessness (Fox & Kahlert *in press*) suggesting major modifications to protein metabolic pathways (such as higher retention rates of dietary protein in the body) do indeed occur during the period of flight feather production.

It is perhaps no coincidence that both these moulting aggregations where loss of body mass have been observed are newly established (at Oostvaardersplassen since its creation in 1968 and Saltholm which was probably established in the late 1980s) in novel habitats. Both concentrations have built rapidly to relatively large numbers over a relative short period (35,000 and 13,000 respectively) and consist primarily of birds of sub-adult and failed breeder classes from throughout the western European breeding range (Zijlstra *et al.* 1991, Fox *et al.* 1995). In both situations, extensive undisturbed and predator-free habitat is available to the

geese, along with food items which are available in some abundance (primarily *Phragmites australis* at Oostvaardersplassen and *Puccinellia maritima* on Saltholm). However, studies have shown that the protein content of these food supplies declines throughout the course of the moult period (Loonen *et al.* 1991, Fox *et al.* 1998), which, together with the expansion in the numbers exploiting the habitat, could limit the dietary availability of nutrients necessary for the successful completion of regrowth of flight feathers. Furthermore, on the island of Saltholm, despite the absence of terrestrial predators, flightless geese forage only at night (almost certainly as a result of their responses to phantom and predator-like stimuli) in contrast to during the prelude to moult when they feed by day and night, a feature which reduced their time potentially spent on the feeding areas from 16.2 to 8.9 hr d⁻¹ day (Kahlert *et al.* 1996). Although this approximates to the same absolute time spent foraging as in the other two species, the period spent feeding is constrained by the movement of the Saltholm Greylags to safe offshore islands where feeding is not possible (Fox *et al.* 1995, Kahlert *et al.* 1996).

It seems unlikely that protein limitation *per se* would cause the loss of 12-26% of the body-mass of moulting Greylag Geese, especially since it is clear from the visual observations that substantial loss of tissue occurs in the vicinity of the abdomen, known to be an important depot for fat deposition (Owen 1981, Mainguy & Thomas 1985). Excepting male Lesser Snow Geese *Anser caerulescens*, protein reserves of all studied Northern Hemisphere geese remain unchanged or actually increase during moult (Hohman *et al.* 1992, Table 5-4). However, low level catabolism of protein is known to occur during the moult in Spur-winged Geese *Plectropterus gambensis* in Africa (Halse & Dobbs 1985) and this could contribute a small proportion to the general loss of mass during the moult period in Greylags on Saltholm. However, it seems more likely that the Greylag Geese at Saltholm undergo a period of rapid fat accumulation prior to moult prior to the energetic demands of wing moult (as recognised in other species,

see review of Hohman *et al.* 1992), and that stores are depleted in order to meet these demands (as recognised in other species eg Halse & Dobbs 1985), given that dietary selection may be the result of a trade-off which satisfies specific amino-acid requirements rather than maximising energy gain. Indeed, van Eerden *et al.* (1998) calculated that Greylag Geese moulting at Oostvaardersplassen could generally only derive 50% of their estimated daily energy requirements from their diet there because of intraspecific competition. This fell to 22% of their energy requirement when feeding conditions deteriorated in a particular year, an event that led to between 7,000 and 15,000 geese leaving the site to moult elsewhere.

The implications from these studies are clear, in that although moulting geese can derive their nutritional demands for wing moult from their diet under ideal conditions (as generally described in the existing literature), the imposition of external constraints, such as limits to food quality or access to adequate resources, may result in the adoption of alternative strategies to balance nutritional requirements, some of which may involve catabolism of fat stores to meet short-term needs. In the case of the Greylag Geese moulting on Saltholm and Oostvaardersplassen, it may be that at the time of initial settlement, geese took advantage of predator-free environments which provided an adequate source of protein, but insufficient energy. The strategy would necessitate the accumulation of fat stores, derived from energy-rich food sources prior to moult, which are depleted during moult and reconstructed again post-moult (in preparation for an autumn migration of up to 2,500 km to southern Spain, Nilsson & Persson 1996). This is probably achieved by exploiting energy rich food sources inaccessible during the flightless period, and in areas unsuitable as moulting habitat. Whether the adoption of such a strategy has a cost in terms of subsequent fitness is impossible to assess, but it must be assumed that a bird which loses body mass during moult is less likely to be able to meet its present and future nutritional needs than an equivalent individual that does not, making

geese adopting such a strategy more vulnerable to further future energetic stress (eg as a result of disturbance).

In their analysis of Greylag Geese at Oostvaardersplassen, van Eerden *et al.* (1998) demonstrated an effect on energy balance as the result of increasing numbers of moulting geese exploiting a finite resource. As most goose populations continue to increase, the use of new, novel and extra-limital moulting habitats will also increase, as will the pressure of numbers on existing moulting areas (Ankney 1996). Indeed, it has been considered that the Saltholm moulting birds derive from local breeding sites which formerly also supported moulting non-breeders, but which have now increasingly become occupied by expanding numbers of breeding pairs which have then displaced the non-breeding element (see discussion in Fox *et al.* 1995). Hence, intra-specific competition may place additional constraints upon nutrient acquisition during moult when geese are confined by flightlessness to a specific locality. The numbers of Greylag Geese moulting on Saltholm have increased dramatically since the late 1980s and it will be interesting to see if the ability of moulting birds to acquire nutrients at the site will become a density-dependent mechanism which regulates numbers settling to moult in a manner similar to that observed at Oostvaardersplassen (van Eerden *et al.* 1998).

Increasingly, range overlap of expanding goose populations also brings inter-specific competition (eg between increasing numbers of breeding and moulting Brent *Branta bernicla* and Barnacle Geese in the Kanin peninsula exploiting habitats formerly used by staging Barnacle Geese breeding further north and east, Vinogradov 1994). Hence, it is to be expected that further constraints on the ability of moulting geese to meet the nutritional demands of the wing moult will be encountered as their numbers increase. For that reason, it is prudent to at least presume that not all moulting concentrations of geese are able to complete moult without nutritional stress and that more and more in the future, with increasing goose populations and human

pressure on wetlands used by moulting geese, the flightless wing-moult period of geese will become recognised more as a potential nutritional bottleneck in their annual cycle. It will be interesting to see also, whether loss of body mass will become apparent in the future amongst moulting Whitefronts and Canada Geese as a consequence of the increase in numbers (and hence densities) of both species in west Greenland.

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References

- Ankney, C.D. 1979. Does the wing molt cause nutritional stress Lesser Snow Geese? *Auk* 96:68-72.
- Ankney, C.D. 1996. An embarrassment of riches: too many geese. *J. Wildl. Manage.* 60:217-223.
- Blem, P.R. 1976. Patterns of lipid storage and utilisation in birds. *Am. Zool.* 16:671-684
- van Dijk, K. & van Eerden, M.R. 1991. Biometrics and timing of moult of non-breeding Mute Swans *Cygnus olor* at Lake IJsselmeer, the Netherlands. *Wildfowl Supplement* 1:296-303.

- Dzubin, A. & Cooch, E.G. 1992. *Measurements of geese: general field methods*. California Waterfowl Association, Sacramento, California.
- van Eerden, M.R., Zijlstra, M. & Loonen, M.J.J.E. 1991. Individual patterns of staging during autumn migration in relation to body condition in Greylag Geese *Anser anser* in the Netherlands. *Ardea* 79:261-264.
- van Eerden, M.R., Loonen, J.J.E. & Zijlstra, M. 1998. Moulting Greylag Geese *Anser anser* defoliating a reed marsh *Phragmites australis*: seasonal constraints versus long-term commensalism between plants and herbivores. In: van Eerden, M.R. (Ed.). *Patchwork: patch use, habitat exploitation and carrying capacity for waterbirds in Dutch freshwater wetlands*. Published Ph.D. thesis. Rijkswaterstaat, Lelystad, the Netherlands. Pp.239-264
- Ens, B.J., Piersma, T. & Tinbergen, J.M. 1994. Towards predictive models of bird migration schedules: theoretical and empirical bottlenecks. *Nederlands Instituut voor Onderzoek der Zee Rapport* 5:1-27.
- Fox, A.D., Madsen, J. & Stroud, D.A. 1983. The summer ecology of the Greenland White-fronted Goose (*Anser albifrons flavirostris*). *Dansk Orn. Foren. Tidsskr.* 77:43-55.
- Fox, A.D., Norriss, D.W., Stroud, D.A. & Wilson, H.J. 1994. *Greenland White-fronted Geese in Ireland and Britain 1982/83-1993/94*. Greenland White-fronted Goose Study/Irish National Parks & Wildlife Service, Aberystwyth & Dublin.
- Fox, A.D., Kahlert, J., Ettrup, H., Nilsson, L. & Hounisen, J.-P. 1995. Moulting Greylag Geese on the Danish island of Saltholm; numbers, phenology, status and origins. *Wildfowl* 46:16-30.
- Fox, A.D., Glahder, C., Mitchell, C., Stroud, D.A., Boyd, H. & Frikke, J. 1996. The population of North American Canada Geese *Branta canadensis* in west Greenland. *Auk*. 113:231-232.
- Fox, A.D. & Kahlert, J. 1999. Adjustments to nitrogen metabolism during wing moult in Greylag Geese *Anser anser*. *Functional Ecology* 13: in press
- Fox, A.D., Kahlert, J. & Ettrup, H. 1998. Diet and habitat use of moulting Greylag Geese *Anser anser* on the Danish island of Saltholm. *Ibis* 140:676-683.
- Glahder, C.M., Fox, A.D., Stroud, D.A. & Mitchell, C. 1996. North American Canada Geese in West Greenland. *IWRB Goose Specialist Group Bulletin* 7:23-25.
- Halse, S.A. & Dobbs, J.C. 1985. Carcass composition of spur-winged geese with comments on reproduction and moulting. *Afr. J. Ecol.* 23:171-178.
- Hanson, H.C. 1962. The dynamics of condition factors in Canada Geese and their relation to seasonal stress. *Arctic Inst. N. Am. Tech. Paper* No.12.
- Hohman, W.L., Ankney, C.D. & Gordon, D.H. 1992. Ecology and management of post-breeding waterfowl. In: Batt, B.D.J., Afton, A.D., Anderson, M.G., Ankney, C.D., Johnson, D.H., Kadlec, J.A. & Krapu, G.L. (Eds.). *Ecology and management of breeding waterfowl*. University of Minnesota Press, Minneapolis. Pp.128-189
- Kahlert, J., Fox, A.D. & Ettrup, H. 1996. Nocturnal feeding in moulting Greylag Geese *Anser anser* - an anti-predator response? *Ardea*. 84:15-22.
- Kristiansen, J.N. 1997. Diet of Canada Geese and White-fronted Geese in Isungua, West Greenland. *Dansk Orn. Foren. Tidsskr.* 91:130-131.
- Kristiansen, J.N. 1998. *Report of the 1997 expedition to Isungua, west Greenland*. Greenland White-fronted Goose Study, Aberystwyth.
- Loonen, M.J.J.E., Zijlstra, M. & van Eerden, M.R. 1991. Timing of moult in Greylag Geese *Anser anser* in relation to the availability of their food plants. *Ardea* 79:253-260.
- Madsen, J. 1981. Post hatching behaviour of families and non-breeding Greenland White-fronted Geese. In: Fox, A.D. & Stroud, D.A. (Eds.). *Report of the 1979 Greenland White-fronted Goose Study Expedition to Eqaungmiut Nunaat, West Greenland*. Greenland White-fronted Goose Study, Aberystwyth. Pp. 116-122.

- Madsen, J. & Fox, A.D. 1981. The summer diet of the Greenland White-fronted Goose. In: Fox, A.D. & Stroud, D.A. (Eds.). *Report of the 1979 Greenland White-fronted Goose Study Expedition to Eqaungmiut Nunaat, West Greenland*. Greenland White-fronted Goose Study, Aberystwyth. Pp. 108-115.
- Mainguy, S.K. & Thomas, V.G. 1985. Comparison of body reserve build-up and use in several groups of Canada geese. *Can. J. Zool.* 63:1765-72.
- van der Meer, J. & Piersma, T. 1994. Physiologically inspired regression models for estimating and predicting nutrient stores and their composition in birds. *Physiological Zoology* 67:000- 000.
- Murphy, M.E. & King, J.R. 1984. Sulfur amino acid nutrition during molt in White-crowned Sparrow. 2: Nitrogen and sulfur amino acid balance in birds fed graded levels of sulfur-containing amino acids. *Condor* 86:314-323.
- Nilsson, L. & Persson, H. 1996. The influence of the choice of winter quarters on the survival and breeding performance of Greylag Geese *Anser anser*. *Gibier Faune Sauvage* 13:557-571.
- Owen, M. 1981. Abdominal profile - a condition index for wild geese in the field. *J. Wildl. Manage.* 45:227-230.
- Owen, M. & King, R. 1979. The duration of the flightless period in free-living Mallards. *Bird Study* 26:267-269.
- Owen, M. & Ogilvie, M.A. 1979. Wing molt and weights of Barnacle Geese in Spitsbergen. *Condor* 81:42-52.
- Pehrsson, O. 1987. Effects of body condition on molting in Mallards. *Condor* 89:329-339.
- Schmidt-Nielsen, K. 1975. *Animal Physiology. Adaptation and environment*. Cambridge University Press, London.
- Smart, G. 1965. Development and maturation of primary feathers of redhead ducklings. *J. Wildl. Manage.* 29:533-536.
- Vinogradov, V.A. 1994. Changes in goose status on the Kanin Peninsula. *IWRB Goose Research Bulletin* 5:26-27.
- van der Wal, R. 1992. *The energetic costs of moult in the Greylag Goose*. Unpubl. M.Sc. thesis, University of Groningen, The Netherlands.
- Wright, G. & Mitchell, C. 1993. *Report of the 1992 expedition to Isungua, west Greenland*. Greenland White-fronted Goose Study, Aberystwyth. 41pp.
- Zijlstra, M., Loonen, M.J.J.E. & van Eerden, M.R. 1991. The Oostvaardersplassen as a key molting site for Greylag Geese in western Europe. *Wildfowl* 42:45-52.