Annual changes in body mass and resting metabolism in captive barnacle geese (*Branta leucopsis*): the importance of wing moult

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Summary

Many different physiological changes have been observed in wild waterfowl during the flightless stage of wing moult, including a loss of body mass. We aimed to determine whether captive barnacle geese (*Branta leucopsis*) would show the characteristic decrease in body mass during their wing moult, even though they had unlimited and unrestricted access to food. Fourteen captive geese were weighed at 1–2-week intervals for two complete years. During the flightless period of the moult, body mass decreased by approximately 25% from the pre-moult value. To understand the basis of this change, the rate of oxygen consumption was measured during daytime and nighttime at six points in the second year, and at three points (before, during and after wing moult) behavioural observations were made. Measurements of the rate of oxygen consumption showed an 80% increase above that of the nonmoulting periods of the year. We propose that metabolism was increased during moult because of the cost of feather synthesis. Although food was available, the captive birds chose not to forage and instead increased the proportion of time spent resting. It is likely that this behaviour in response to wing moult is a strategy to avoid predation in the wild. Thus, the innate nature of this behaviour has potential survival value for wild birds of this species. We conclude that the increase in metabolism led to the use of endogenous energy reserves because the birds reduced rather than increased their food intake rates, and as a result, the barnacle geese lost body mass during wing moult.

Key words: moult, barnacle goose, metabolism, annual cycles, foraging behaviour.

Introduction

Timing of the annual moult is an important component of energy allocation in birds (Hohman et al., 1992; Gates et al., 1993). Barnacle geese *Branta leucopsis*, like almost all waterfowl, undergo a simultaneous wing moult that renders them flightless for the duration of the regrowth of the flight feathers, just prior to their autumn migration (Owen and Ogilvie, 1979). In the wild, this period of flightlessness could present several problems for the geese, such as restricting their normal capacity to forage and escape predation. Therefore, it is apparent that shortening of the flightless period has a selective value (Douthwaite, 1976; Owen and Ogilvie, 1979; DuBowy, 1985; Pehrsson, 1987; Fox and Kahlert, 2005).

Mass loss during wing moult has been documented in several waterfowl species, including the Russian breeding population of barnacle geese (van der Jeugd, 2003), Barrow's goldeneye *Bucephala islandica* (Van de Wetering and Cooke, 2000), greylag geese *Anser anser* (Fox and Kahlert, 2005), mallard *Anas platyrhynchos* (Pehrsson, 1987), Eurasian teal *Anas crecca* (Sjöberg, 1986) and South African shelduck *Tadorna cana* (Geldenhuys, 1983).

A loss in body mass during moulting might be adaptively advantageous, since a lighter bird may be able to fly again sooner than a heavier bird, and therefore be able to escape predators or move sooner to a more suitable habitat (Geldenhuys, 1983; DuBowy, 1985; Sjöberg, 1986). Hanson (Hanson, 1962), Ankney (Ankney, 1979) and Dolnik and Gavrilov (Dolnik and Gavrilov, 1979) suggested that moult is nutritionally stressful and energetically demanding, and increases in metabolism of up to 40% have been recorded in moulting waterfowl (e.g. Guozhen and Hongfa, 1986). Energetic costs of moult may include nutrient demands for feather components, increased amino acid metabolism, changes in water balance, an increase in blood volume and enhanced heat loss (King, 1980; Lovvorn and Barzen, 1988).

As well as physiological changes, many species of waterfowl also display a marked difference in behaviour during the flightless moult period (Owen and Ogilvie, 1979; Murphy, 1996; Adams et al., 2000; Van de Wetering and Cooke, 2000). Birds often become inactive, spending longer periods resting or hauled out of the water, devote less time to foraging and general maintenance and may switch to nocturnal feeding (Thompson, 1992; Adams et al., 2000; Kahlert et al., 1996).

Panek and Majewski proposed that these changes in behaviour are a result of the increased risk of predation as a result of being flightless, and this behavioural change results in a loss of feeding opportunities, and consequently a drop in body mass (Panek and Majewski, 1990).

Relatively little is known about the effects of captivity on wing moult in waterfowl (e.g. Hanson, 1962). By having birds in captivity and removing predation pressure and restrictions on foraging, it is possible to establish how innate these moult rhythms and associated behaviours are and to investigate their possible causes. Thus, we asked the following questions: (1) Do captive barnacle geese lose mass during the wing moult, despite having unrestricted access to food and no predation pressure? (2) Does resting metabolic rate (measured as the rate of oxygen consumption during rest) increase during the flightless period of the moult? (3) How do captive barnacle geese alter their time budgets in response to wing moult? (4) Do heavier birds lose proportionally more mass during moult, perhaps to minimise the duration of the flightless period?

Materials and methods
Birds

A captive population of 14 barnacle geese obtained as 3-week-old goslings was maintained under natural light in a large outdoor aviary at the University of Birmingham. The goslings were obtained from Bentley Waterfowl Park (Sussex, UK), which has held a self-sustaining captive population of this species since 1982. Although the origin of this population is unknown, the geese have therefore not migrated for at least 25 years. The geese were fed with a 50–50 diet (Lilico, Surrey, UK) of mixed poultry corn (4% fat, 12% protein and 71% carbohydrate) and poultry growers pellets (3% fat, 16% protein and 61% carbohydrate), and water was available *ad lib*.

Weighing

Throughout a 2-year period (2004, 2005), the geese were weighed at one- or two-week intervals to the nearest 5 g. Birds were hooded to reduce stress and placed in a darkened plastic box for weighing. Handling was kept to a minimum. All regulated procedures were performed by British Home Office-licensed personnel in possession of a Personal License, and working under the auspices of a corresponding Project License, as set out in the Animals (Scientific Procedures) Act 1986.

Moult score

The stage of wing moult was determined using a six-point classification moult score system (e.g. Geldenhuys, 1982; Ankney, 1984; Bridge, 2004): (0) pre-wing moult, (1) primaries and secondaries remain, new primary pin visible, (2) primaries missing and most secondaries remain, (3) all primaries and secondaries missing, (4) new primaries emerged just beyond primary coverts, (5) primaries visible well beyond primary coverts and secondaries visible beyond secondary coverts, and (6) post-wing moult.

Time–activity budgets

The activity budgets of the captive barnacle geese were recorded during 2005 at three points during the year (June, August and November). Behaviour was recorded onto paper at three different times of the day: morning (07:00–12:00 h GMT), afternoon (12:00–17:00 h GMT) and evening (17:00–22:00 h GMT). Observations were made from a shed a short distance (approximately 6 m) away from the birds and were restricted to periods of good weather. An individual goose was selected and watched for a total period of 5 min, with activities being recorded at 15-s intervals. If there was any disturbance during the 5-min observation, the data were not used. The number of individuals sampled each day ranged from 7 to 14. In total, 105 observation sessions were performed.

Twenty separate behaviours were recorded during the study and pooled into six general categories (Austin, 1987; Adams et al., 2000): foraging (including feeding and pausing), resting (which includes loafing and sleeping), maintenance (including preening, scratching, stretching and splash bathing), locomotion (including tail wagging, walking, swimming, wing-flapping and scooting), social (agonistic and courtship), and alert (including head raising and inactivity to scan the immediate area).

Resting rate of oxygen consumption measurements

Resting rate of oxygen consumption ($\dot{V}_{O_2}$) was measured overnight in darkness between the hours of 23:00 h and 07:00 h, and during the day in the light between the hours of 11:00 h and 14:00 h. Birds were placed inside a Perspex box (74 cm high $\times$ 58 cm long $\times$ 47 cm wide) and $\dot{V}_{O_2}$ measured using open circuit respirometry (Withers, 2001). Air temperature within the chamber was 19–21°C, which is within the thermoneutral zone for the geese (Calder and King, 1974). Food (not water) was withheld from the birds for 8 h before they were placed in the respirometer box. Resting rate was calculated from the lowest value when averaged over 5-min periods (Withers, 2001). Thus, those data collected during the night are equivalent to basal rates of oxygen consumption, or basal metabolic rate (BMR) (McNab, 1997; Frappell and Butler, 2004). The data were collected during the second year of the study (2005), in February, May, July, August, September and November, and the same six birds were sampled in each session.

Respirometry equipment

Two respirometry systems were used simultaneously to record resting $\dot{V}_{O_2}$, in order to minimise the duration of the sampling sessions. Information regarding the set-up and equipment for system 1 are described elsewhere in detail (Green et al., 2001) and for system 2 by Wilson et al. (Wilson et al., 2006). The extent to which each respirometry system leaked was determined by pumping oxygen-free nitrogen gas (BOC Gases, Guildford, UK) into the chamber at a known rate (Fedak et al., 1981). The calculated values of gas exchange were adjusted to compensate for the loss of chamber gas.

The rate of oxygen consumption was calculated using the equations of Depocas and Hart (Depocas and Hart, 1957), as modified by Withers (Withers, 1977) and Koteja (Koteja, 1996). As CO_2 was not measured in system 1, for these experiments equation 3a (Withers, 1977) was used to calculate $\dot{V}_{O_2}$ (Ward et al., 2002), where the respiratory exchange ratio (RER) was assumed to be the mean value measured in the birds in system 2. This procedure would introduce an error of less than 1% into the calculated $\dot{V}_{O_2}$ (Koteja, 1996), given the measured variation in RER. For system 2, equation 3b from Withers was used (Withers, 1977). Data from both systems were pooled.

Statistical analysis

Repeated-measures analysis of variance (ANOVA) was performed to compare the mean values for each weighing session, and on measurements of resting $\dot{V}_{O_2}$. Post-hoc Bonferonni corrected paired *t*-tests were used to compare resting $\dot{V}_{O_2}$ between sampling sessions ($P<0.003$). Analysis of covariance (ANCOVA) was used to compare rate of mass change during the wing moult period between the 2 years, and to investigate the relationship between body mass and $\dot{V}_{O_2}$.

Linear regression was used to examine the influence of body condition on rate of body mass change during the moult. For this, mass was adjusted for structural size [size-adjusted body mass=body mass (g)/tarsus length (cm)] (Van de Wetering and Cooke, 2000).

Percentage data for each behavioural category from each sampling session was arcsin transformed and a two-way ANOVA (time of day and month) with post-hoc Tukey's honest significant difference (HSD) tests ($P<0.05$) was performed to determine whether there were differences in the mean proportion of time dedicated to each category of behaviour between the three different times of year, and between morning, afternoon and evening observations.

All tests were considered significant at $P<0.05$. Values given are means ± s.e.m.

Results

Annual cycles in body mass and moult

Mean body mass of the 14 captive barnacle geese (Fig. 1) changed significantly throughout the annual cycle for both years of the study ($P<0.0001$). As might be expected, the birds were significantly heavier in year 2 than year 1 ($P<0.0001$) as they had reached sexual maturity.

Peaks in body mass were observed in January 2005 (2143±89 g) and early July (1951±62 g and 2034±75 g for 2004 and 2005, respectively), followed by a significant drop in body mass of approximately 430 g during the moult periods in both years ($P<0.0001$). In 2005 the first flight feathers were dropped during the last week of June, and by July 14th, all bar-one of the birds was classified as moult score 3 or higher. The flightless period was estimated to be 38 days. The lowest body mass was recorded towards the end of the wing moult (moult score 5), in mid-August (1528±41 g and 1596±53 g for 2004 and 2005, respectively). There was no significant difference between the 2 years in mean body mass at this time ($P=0.09$), although body mass prior to moult was significantly different between the 2 years (paired *t*-test, $P<0.001$). Rate of mass change during the wing moult was not significantly different between the 2 years (ANCOVA, $P=0.850$).

Following the completion of moult (moult score 6), mass increased significantly ($P<0.001$) over the following 7–8 weeks before reaching a plateau in mid-October. Body mass remained stable throughout the winter months until an increase in December and January, when the highest mass of year 2 was recorded. From the middle of January, mass declined to reach a level similar to that in the autumn (1820±12 g and 1850±32 g for 2004 and 2005, respectively), from which it began to increase in May and June.

There was a significant relationship between decrease in body mass during moult and size-adjusted initial body mass ($r^2=0.37$, $y=-0.0269x+0.25$, Fig. 2). After adjusting for body size, heavier birds still lost body mass at a proportionately greater rate.
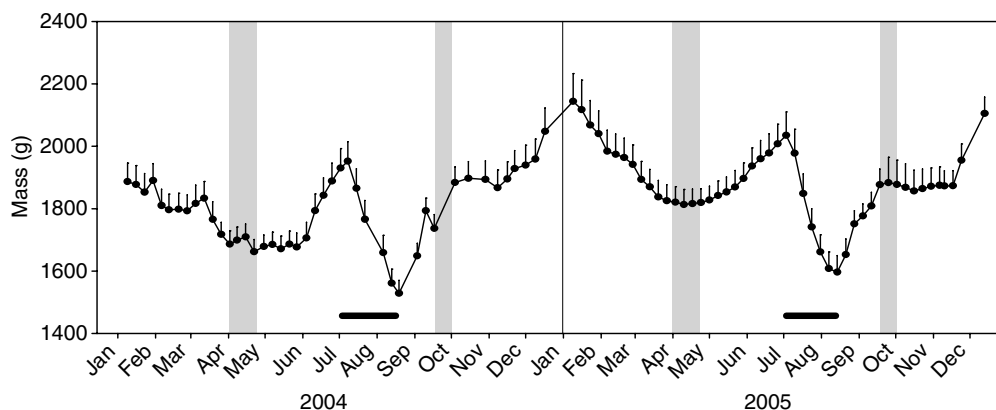

Fig. 1. Year-round mean weekly body mass for 14 captive barnacle geese for 2004 and 2005. Horizontal black bars indicate approximate period of wing moult. Shaded areas relate to migratory periods in wild barnacle geese. Mass changed significantly throughout the year for both years sampled (repeated-measures ANOVA $P<0.0001$ for years 1 and 2, respectively).
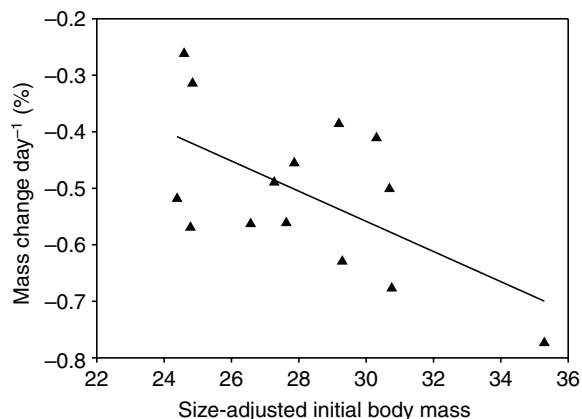
Fig. 2. Relationship between mass change and size-adjusted initial body mass of 14 captive barnacle geese during wing moult ($r^2=0.36$, $P=0.02$). After adjusting for body size, heavier birds still lost body mass at a proportionately greater rate. Size-adjusted body mass is calculated as body mass (g) divided by length of the tarsus (cm).
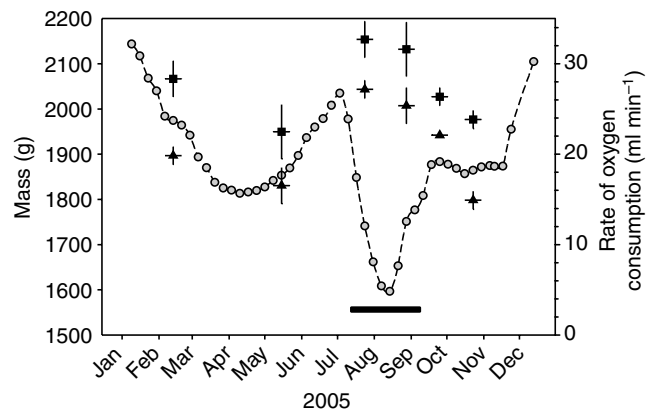

Fig. 3. Year-round average weekly masses for 14 barnacle geese (grey circles) with rates of oxygen uptake measurements ($N=6 \pm$ s.e.m.) at six points of the year. Triangles represent night resting values and squares day resting values. X error bars represent duration of sampling period. Both day and night resting rates varied significantly throughout the year (repeated-measures ANOVA, $P<0.001$ and $P<0.004$, respectively) and followed a similar pattern. Black bar indicates the wing moult period.

Resting rate of oxygen consumption

There was significant variation throughout the year of both day and night resting $\dot{V}_{O_2}$ (Fig. 3, $P<0.001$ and $P=0.004$, respectively). Maximum night and day resting $\dot{V}_{O_2}$ were observed during the moult in a period of mass change, and averaged 27.2 ± 1.4 ml min^{-1} and 32.7 ± 2.0 ml min^{-1}, respectively. The minimum nighttime value (14.91 ± 1.2 ml min^{-1}) was recorded in November, a period of stability when body mass did not change significantly. The minimum daytime value was observed in May ($22.5.\pm3.0$ ml min^{-1}). Oxygen uptake measurements taken during moulting periods (July–August) were significantly higher than those measured during the pre- and post-moult periods. Mass-specific $\dot{V}_{O_2}$ followed a similar pattern, with values during the moult period of 16.2 ± 1.2 ml min^{-1} kg^{-1}, compared with, for example, 8.9 ± 0.3 ml min^{-1} kg^{-1} for May. There was no significant relationship between body mass and $\dot{V}_{O_2}$.

Behaviour

Two-way ANOVA revealed no significant difference in time budgeting between morning, afternoon and evening observations within each sampling period. During August (i.e. wing moult), the geese spent $64\pm1.9\%$ of their time resting, which was significantly greater than the $45\pm2.4\%$ and $43\pm1.6\%$ of their time spent resting in June and November, respectively (Fig. 4). Foraging dropped during wing moult, from $23\pm2.0\%$ in June and $24\pm1.7\%$ in November to $7\pm0.6\%$ in August ($P<0.001$). Maintenance behaviour increased significantly during wing moult ($P<0.001$) from $12\pm1.4\%$ and $9\pm1.1\%$ in June and November, respectively, to $20\pm1.6\%$ when the birds were flightless.

Discussion

Body mass and behavioural changes during wing moult

Despite having constant access to food, the captive barnacle geese lost approximately 25% of their body mass during the wing moult in both years of the study. A similar degree of mass loss was recorded in wild non-breeding waterfowl – such as male greylag geese moulting on Saltholm, Denmark (Fox et al., 1998). Sjöberg found that teals lost between 10–20% of their body mass during the flightless period (Sjöberg, 1986), a similar figure to that noted in red-billed teal and South African shelduck (Douthwaite, 1976; Geldenhuys, 1983). Sjöberg noted that many species of wild waterfowl moult in extremely favourable habitats and can therefore compensate for the energetically demanding wing moult period by increasing their daily food intake (Sjöberg, 1986). As such, he concluded that any observed mass loss must be an adaptation for decreasing the flightless period by enabling the bird to fly on partially regrown flight feathers. However, atrophy of flight muscles in moulting waterfowl (e.g. Ankney, 1979; Marden, 1987), and a lack of consistency in mass loss during wing moult between populations of the same species (Fox and Kahlert, 2005), suggests this is unlikely to be broadly applicable.

Panek and Majewski proposed that the cause of mass loss during wing moult in wild waterfowl was the change in behaviour and loss of foraging opportunities, brought about by an increased risk of predation (Panek and Majewski, 1990). Therefore, birds were not able to compensate for the increased energetic demands during moult by increasing their food intake. They noted that mallards with only 1–3 flight regimes missing still continued to exhibit what they described as 'secretive behaviour', and still continued to lose body mass, indicating that the birds were aware of their vulnerability to predation whilst flightless (Pehrsson, 1987; Adams et al., 2000). The captive geese showed a marked difference in behaviour during the flightless period of the wing moult,
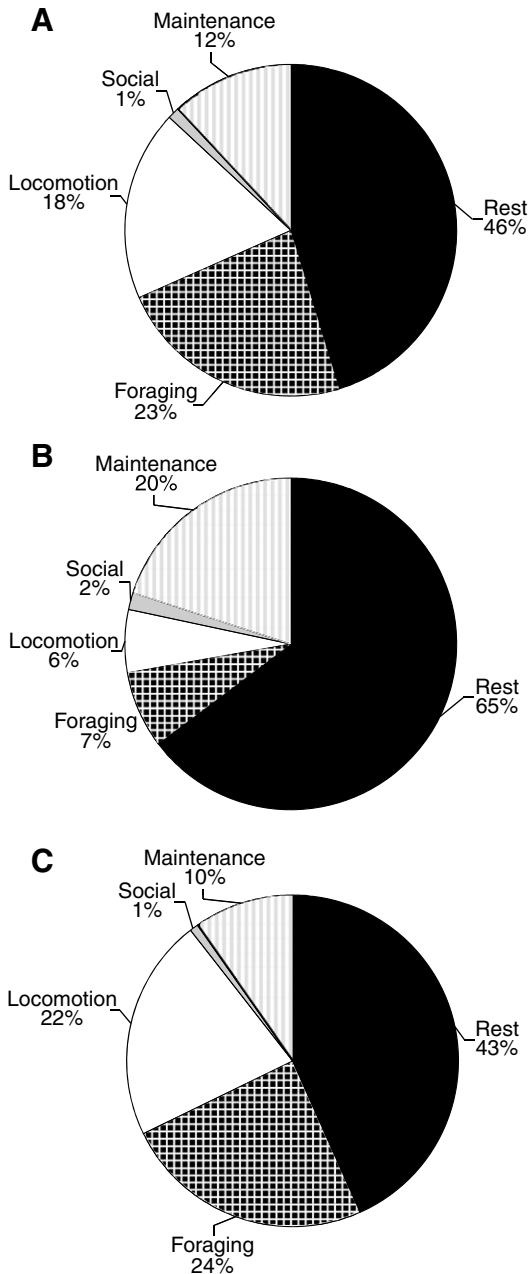
Fig. 4. Time–activity budgets (%) for 14 captive barnacle geese, for pre- (A, June), during (B, August) and post- (C, November) wing moult. The time dedicated to alert behaviour was less than 1% and is not shown.

increasing the time they spent in maintenance and resting and decreasing the time spent foraging.

Kahlert et al. found that only flightless wild greylag geese would respond to grey herons *Ardea cineria* and helicopters overhead by returning to water for safety, whereas fully flighted birds would not respond (Kahlert et al., 1996). In addition, these moulting geese spent on average 19 min resting on the water after a 'spook' event, potentially losing valuable feeding time (Kahlert, 2006). During wing moult, the greylag

geese spent just 8.9 h foraging compared with 16.2 h when fully flighted (Fox and Kahlert, 1999). Furthermore, these birds did not compensate for this reduction in foraging time by increasing peck rate (Fox and Kahlert, 1999).

Studies performed on other wild moulting waterfowl have shown varying changes in resting levels and feeding effort during the flightless period. Austin reported a 10% increase in time spent resting during the flightless stage in lesser scaup *Aythya affinis* (Austin, 1987), and mottled ducks *Anas fulvigula* spent only 9% of their time feeding during wing moult compared with 65% of their time before and after, a trait also observed in harlequin ducks *Histrionicus histrionicus*, black ducks *Anas rubripes* and canvasbacks *Aythya valisineria* (Paulus, 1984; Bowman, 1987; Thompson, 1992). Other species exhibited different compensatory behaviours. For example, redheads *Aythya Americana*, red-crested pochards *Netta rufina* and greylag geese fed primarily at night during wing moult (Bailey, 1981; Van Impe, 1985 Kahlert et al., 1996).

Despite having constant access to food and no obvious predators, the captive barnacle geese in the present study still changed their behaviour during the flightless period of wing moult and did not increase their food intake rate. These findings suggest that increased resting during a potentially vulnerable stage of the bird's annual cycle is an innate behaviour.

Rate of mass loss and body size

In the present study heavier geese lost mass faster than lighter geese; a similar observation was noted in the Russian breeding population of barnacle geese and Barrow's goldeneye (van der Jeugd, 2003; Van de Wetering and Cooke, 2000). This may explain the peak in body mass prior to wing moult. If, as hypothesised by Owen and Ogilvie (Owen and Ogilvie, 1979), Sjöberg (Sjöberg, 1986) and Douthwaite (Douthwaite, 1976), mass loss during the flightless period is an adaptation to regain flight sooner, gaining mass prior to this period would appear to be a waste of energy. If, however, being in good condition before the onset of wing moult enables a bird to achieve higher remigial growth rates and thus shorten the flightless period compared with birds in poorer condition, there is an obvious advantage to gaining mass before wing moult. Using endogenous reserves (mainly fat) during wing moult can be a behavioural strategy that allows birds to spend less time feeding and to occupy safer habitats that reduce the risk of predation (Thompson, 1992; Van de Wetering and Cooke, 2000). This will enable birds in better condition to reduce activity more so than those in poorer condition and possibly reduce the chance of being predated upon. Comparing two Russian breeding populations of barnacle geese, van der Jeugd et al. found birds in one population to be 200 g heavier at the onset of wing moult. During the flightless period, however, body mass in these heavier birds declined three times more rapidly compared with that of the other population, and the flightless period was shorter (van der Jeugd et al., 2003).

Rate of oxygen consumption measurements

There was a distinct annual cycle in resting $\dot{V}_{O_2}$ in the captive geese used in the present study (Fig. 3). The night resting $\dot{V}_{O_2}$, which is equivalent to basal $\dot{V}_{O_2}$ (a proxy for BMR), increased by approximately 80% during the wing moult when compared with the post-moult period in November. Ward et al. sampled night resting rates of oxygen consumption in early September (Ward et al., 2002), and recorded a mean night resting $\dot{V}_{O_2}$ of 25.3 ml min^{-1}, compared with values from the present study of 25.3 ml min^{-1} for late August and 22.0 ml min^{-1} for mid-September. Nolet et al. took measurements of rate of oxygen consumption from captive barnacle geese during the late winter (Nolet et al., 1992), and reported a mean night resting $\dot{V}_{O_2}$ of 16.9 ml min^{-1}, compared with values from the present study of 19.8 ml min^{-1} for early February and 14.9 ml min^{-1} for late November (17.3 ml min^{-1} winter mean). These comparisons suggest that there is an annual cycle in BMR in captive (and potentially wild) barnacle geese. This conclusion is supported by seasonal variations in night resting heart rate in macaroni penguins *Eudyptes chrysolophus* (Green et al., 2005), wild cormorants *Phalacrocorax carbo* (C. R. White, D. Gremillet, P. J. Butler and G. R. Martin, unpublished data) and eider ducks *Somateria mollissima* (M. Guillemette and P. J. Butler, unpublished data).

This increase in BMR during moult is greater than that reported for most species (Payne, 1972). For example, Lindström et al. reported a 35% increase in BMR in captive moulting redpolls *Carduelis f. flammea*, when compared with pre-moult and post-moult values (Lindström et al., 1993). However, the majority of studies have been on passerines that have a sequential moult, often lasting several months as opposed to waterfowl with their simultaneous wing moult, and this may explain the higher values recorded in the captive barnacle geese. By contrast, Guozhen and Hongfa reported increases in $\dot{V}_{O_2}$ of only 25% and 35% for Eurasian teal and European shoveler *Anas clypeata*, respectively (Guozhen and Hongfa, 1986). This discrepancy may be due in part to the timing of metabolic measurements with respect to the duration of the moult. Penguins also have a rapid moult during which they are unable to forage and rely on endogenous reserves. Green et al. found that the metabolic rate of macaroni penguins increases from, then decreases to non-moulting levels during this moult fast, with a peak approximately 40% above non-moulting levels (Green et al., 2004). In the present study, wing-moult measurements were taken in the middle of the wing-moult period (Fig. 3), but this may not have been the case in other studies.

Are data from the present study applicable to wild geese?

No published study has previously recorded the year-round mass of barnacle geese, wild or captive, although other studies have weighed wild barnacle geese at various times of the year (Owen and Ogilvie, 1979; Tombre et al., 1996; Phillips et al., 2003).

Tombre et al. captured female geese in Ny-Ålesund, Svalbard, within three days of their arrival from their spring staging posts in Norway (Tombre et al., 1996). Masses recorded were 2099±55 g and 2219±44 g for 1993 and 1994, respectively (N=13 and 11, respectively), and these are heavier than masses taken from the captive geese in the present study at around the same time (e.g. 1827±37 g, 5th May 2005, Fig. 1). Phillips et al. caught birds at their wintering grounds on the Solway Firth between December 1999 and January 2004 and recorded a mean body mass of 2000 g (N=20, no s.e.m. provided) (Phillips et al., 2003), which is similar to the winter masses in the captive geese during the second year of the present study (e.g. 2105±53 g, 12th December 2005). Mean body mass of moulting adult birds in Svalbard was 1788±8 g and 1586±7.8 g for non-breeding males and females, respectively (Owen and Ogilvie, 1979), compared with a combined mean of 1596±53 g for the captive geese during moult. van der Jeugd et al. recorded body masses of barnacle geese during wing moult of 2002±169 g and 1769±177 g for males and females, respectively, although they noted that approximately 20% of the birds caught were non-breeders and had completed wing moult (van der Jeugd et al., 2003).

Thus, despite their not migrating or breeding, and having constant access to food, captive barnacle geese show a distinct annual cycle in body mass that is generally similar to measurements recorded at various points in the year from wild populations of barnacle geese.

Summary

Data presented here provide evidence that captive barnacle geese follow a distinct annual cycle in BMR and body mass. During wing moult, the geese show a significant drop in body mass, as a result of reducing time spent foraging and the observed increase in BMR associated with the costs of moulting. Despite having constant access to food, the captive birds did not increase time dedicated to foraging to compensate for the increase in metabolism. Although food was available, the captive birds chose not to forage and instead increased the proportion of time spent resting. It is likely that this behaviour in response to wing moult is a strategy to avoid predation in the wild. As the captive barnacle geese exhibit such behaviour, it suggests this behavioural response to being flightless in this species at least is innate.

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