IBIS The International Journal of Avian Science
BOU
Ibis (2011), **153**, 868–874

Short communication

Greater energy stores enable flightless moulting geese to increase resting behaviour

STEVEN J. PORTUGAL,[1*†] JONATHAN A. GREEN,[2] THEUNIS PIERSMA,[3,4] GÖTZ EICHHORN[5,6] & PATRICK J. BUTLER[1]
[1]*Centre for Ornithology, School of Biosciences, University of Birmingham, Edgbaston, Birmingham B15 2TT, UK*
[2]*School of Environmental Sciences, University of Liverpool, Liverpool L69 3GP, UK*
[3]*Animal Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, PO Box 11103, 9700 CC Groningen, The Netherlands*
[4]*Department of Marine Ecology, Royal Netherlands Institute for Sea Research (NIOZ), PO Box 59, 1790 AB Den Burg, Texel, The Netherlands*
[5]*Université de Strasbourg, IPHC–DEPE, 23 rue Becquerel, 67087 Strasbourg, France*
[6]*CNRS, UMR7178, 67037 Strasbourg, France*

Many species of waterfowl undergo a post-breeding simultaneous flight feather moult (wing moult) which renders them flightless and vulnerable to predation for up to 4 weeks. Here we present an analysis of the correlations between individual time-budgets and body mass states in 13 captive Barnacle Geese *Branta leucopsis* throughout an entire wing moult. The daily percentage of time spent resting was positively correlated with initial body mass at the start of wing moult. Behaviour of individual birds during wing moult is dependent on initial physiological state, which may in turn be dependent on foraging ability; the storage of energy before the start of wing moult will help birds to reduce exposure to the dangers of predation.

Keywords: anti-predator behaviour, Barnacle Geese, body mass loss, simultaneous wing moult, storage strategies, structural size.

Most species of waterfowl and several groups of waterbird undergo a complete near-simultaneous moult of their flight feathers after breeding, rendering them flightless for 3–4 weeks (Piersma 1988a, Jehl 1990, Hohman *et al.* 1992). Wing-moulting birds may display marked changes in their behavioural time-budgets during periods of flightlessness, possibly in response to the increased risk of predation and restriction of foraging opportunities (Owen & Ogilvie 1979, Piersma 1988b, Panek & Majewski 1990, Hohman *et al.* 1992, Kahlert *et al.* 1996, Adams *et al.* 2000, van de Wetering & Cooke 2000, Kahlert 2006a, 2006b). For example, birds may become inactive and rest more, devoting less time to foraging and maintenance such as preening (Thompson 1992, Thompson & Drobney 1997, Adams *et al.* 2000). In addition, moulting birds may switch from diurnal to crepuscular or nocturnal foraging (Piersma *et al.* 1988, Kahlert *et al.* 1996), reduce dive depths if they feed underwater (Piersma 1988b), increase vigilance (Kahlert 2003, Döpfner *et al.* 2009) and/or reduce vocalizations to avoid detection by predators (Bailey 1981). Apart from changes in behavioural time-budgets,, many physiological changes also occur. Studies on wild waterfowl have shown that during this wing moult period, birds can lose body mass (Geldenhuys 1983, Sjöberg 1986, van der Jeugd *et al.* 2003), increase metabolic rates (Guozhen & Hongfa 1986) and experience atrophy of the flight muscles but hypertrophy of the leg muscles (Ankney 1984, Piersma 1988b). Similar behavioural and physiological changes have also been documented in captive waterfowl (Portugal *et al.* 2007, 2009a,b, 2010, in press).

Van de Wetering and Cooke (2000) observed that the degree of physiological change during moult may differ between individuals within a population of the same species depending on the physiological state (in this case, body mass) in which an individual bird had entered wing moult. Their study showed that heavier male Barrow's Goldeneye *Bucephala islandica* had greater remigial growth rates and experienced more substantial declines in body mass (standardized) than lighter birds, suggesting that body stores may be used to increase the rate of remigial growth. A higher body mass may enable the birds not only to divert more resources to feather growth, but also to reduce foraging during wing moult and live off fat and protein stores, which in turn may reduce energy expenditure and allow the bird to remain alert for predators (van de Wetering & Cooke 2000). Moreover, Portugal *et al.* (2007, 2009a, 2009b, 2010, in press) demonstrated that in wing-moulting captive Barnacle Geese *Branta leucopsis*, heavier individuals also lost more body mass per day for the duration of the flightless period. This suggests that there may be individual differences in moulting strategies and that such differences could be a function of physiological state (*sensu* McNamara & Houston 1990) at the start of wing moult.

*Corresponding author.
Email: sportugal@rvc.ac.uk

†Present address: Structure and Motion Lab, Royal Veterinary College, Hawkshead Lane, North Mymms, Hatfield, Hertfordshire AL9 7TA, UK.

In this study, we build on the data presented in Portugal *et al.* (2007, 2009a, 2009b, 2010, in press), who showed that at a population level, captive Barnacle Geese increase body mass prior to wing moult, and subsequently spend more time resting. During the wing moult period, the Geese lost on average 500 g over a 3-week period (Portugal *et al.* 2007). Here we investigated, at the individual level, the relationship between physiological state (in this case, body mass) at the start of wing moult and the amount of time spent resting during the flightless moult period. We assess whether individuals with the highest initial body mass spend more time resting during wing moult. Because a high body mass can be the result of large structural size or large body stores, or both, we also test for the relative effect of each of these variables while controlling for the other. We propose that limiting activity during wing moult is an adaptive strategy to reduce the risk of predation, while minimizing energy expenditure.

METHODS

Weighing, moult score and structural size

Thirteen Barnacle Geese were obtained as 3-week-old goslings and maintained under natural light in large outdoor aviaries at the University of Birmingham, UK. The goslings were obtained from Bentley Waterfowl Park (Sussex, UK), which has held a self-sustaining captive population of this species since 1982. 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 libitum*. The aviary (30 × 25m) consisted of three pools, areas of shrubs, and trees and open grass. Full details of animal husbandry are described in detail in Portugal *et al.* (2007, 2009a, 2009b, 2010, in press).

Throughout 2006, the Geese were weighed at 1- or 2-week intervals to the nearest 5 g. At the time of the study, the Geese were 2 years old. The flock consisted of four male birds and nine females, and none of the birds had ever bred. During weighing, birds were hooded to reduce stress and placed in a darkened plastic box. Handling was kept to a minimum. The stage of wing moult was determined using a six-point classification moult score system as defined in Portugal *et al.* (2007, 2009a, 2009b, 2010, in press). Structural size was assessed using a principal components analysis of 11 morphological measurements (not including mass; Piersma & Davidson 1991) taken from the same individual Geese. The 11 measurements were based on those described in Wiklund (1996), but see also Proctor (1993) for definitions and diagrams of body parts. Parts measured were: *tibiotarsus* from the joint with the femur to the joint with the tarsometatarsus; *foot span*, the distance on the ventral side between the tip of the hind toe and the tip of the middle toe, not including claws; *middle toe* (digit 3) from the joint with the tarsometatarsus (visible when the toe was bent slightly downward) to the posterior end of the middle toe (digit 3) not including the claw (the toe was bent downward and gently stretched and measured on the dorsal side); *head width*, measured across the dorsal surface between the two eyes; *bill length*, measured from the base of the maxilla to the tip of the premaxilla; *bill depth*, depth of the bill from top to bottom at the nasal aperture; *neck circumference*, measured at the base of the neck around fused thoracic vertebrae; *tail length*, from the pygostyle to the tip of the central feathers; *wing*, measured from the chest flank at the joint between the wing and body (glenoid fossa), and the radiale/ulnare region; *primary*, measured from the radiale/ulnare region to the tip of the 9th primary; and *body length*, from the tip of the beak to the tip of the central feathers of the tail. All measurements were made to the nearest mm, using callipers, a ruler or a tape measure. As well as calculating structural size, we also determined a measure of initial body stores (van der Meer & Piersma 1994). This was calculated as the residual of the relationship between structural size and initial body mass (van der Meer & Piersma 1994, Hayes & Shonkwiler 2001).

In their study on Barrow's Goldeneyes, van de Wetering and Cooke (2000) measured feather length during wing moult and showed that birds that entered the flightless phase in a better state (i.e. with greater fat stores) had higher remigial growth rate. It was not possible directly to measure feather growth rate in the current study, as during the previous year (2005) it was found that regular handling of the Geese to measure flight feathers caused abnormalities in the feather growth rate, with growth rate slowing. This response was not noted when birds were caught to take body mass measurements, but only when direct measurements of feathers were attempted.

The activity budgets of the captive Barnacle Geese were recorded at three points during the year (June, August and November). Behaviour was recorded at three 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). Here, only behaviour regarding resting during the wing moult period (27 July–6 August) is assessed (see Portugal *et al.* 2007, 2009a, 2009b, 2010, in press). Observations were made from a shed a short distance (approximately 6 m) away from the birds and were restricted to periods of good weather. Geese were individually marked with Darvic rings, and 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 discarded. Seven to 14 individuals were sampled each day. 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). Mean values were determined for percentage of time spent resting during the wing moult period for each individual Goose.

Statistical analysis

The proportion of time spent resting during the wing moult was investigated as a function of initial body mass, measured at the commencement of wing moult (moult score 2) as a linear regression. Secondly, we assessed whether any effect of mass was due to differences in structural size or body stores by partial correlations between percentage of time spent resting during wing moult and initial body stores and structural size in a multiple linear regression model. All correlation and regression analyses, using least-squares linear regression, were conducted in MINITAB (v. 16; Minitab Inc., Progress Way, Coventry, UK). In each case, visual inspection of various residual plots indicated that the assumptions of linear regression regarding normality and heteroscedasticity were met.

RESULTS

All Geese increased their body mass in preparation for wing moult and used their initial body stores during moult to a varying extent (Fig. 1). Mean body mass at the start of wing moult was 2015 ± 72 g, and dropped to a mean body mass of 1567 ± 38 g at the end. Geese that were heavy at the start of wing moult rested more (Fig. 2), although this alone did not tell us whether heavy Geese had large initial body stores or simply a large structural size The model containing both initial body stores (i.e. residual initial body mass) and structural size showed a significant effect on time spent resting by each of these explanatory variables while controlling for the other (initial body stores: $t = 3.03$, $P = 0.013$, structural size: $t = 2.74$, $P = 0.021$, model $R^2 = 0.626$). To investigate this further, a partial correlation revealed that 47.9 and 42.9% of the variance in time spent resting during wing moult was accounted for by initial body stores and structural size, respectively (Table 1).

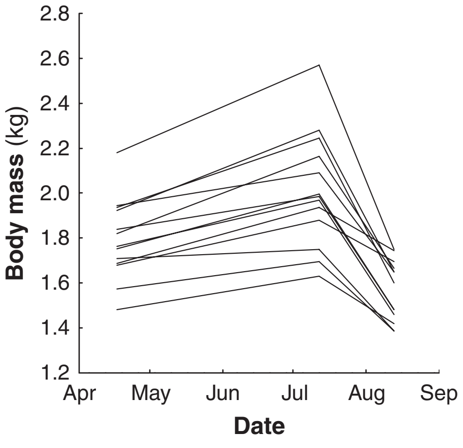

Figure 1. Individual body mass of 13 Barnacle Geese during a stable period of body mass (April), at the start of wing moult (early July), and at the end of wing moult (late August).

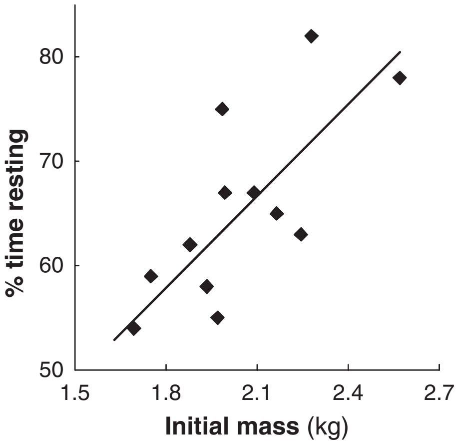

Figure 2. Percentage time spent resting during wing moult by 13 Barnacle Geese as a function of initial mass at the start of wing moult ($y = 4.941 + 0.029x$, $R^2 = 0.617$, $P = 0.001$). Two observations had an initial mass of 2.0 kg and percentage of time spent resting of 67%.

Table 1. Zero order and partial correlation statistics for percentage of time spent resting during wing moult in Barnacle Geese ($n = 13$) with body condition and structural size (see Methods). In the first-order partial correlations the effect of the other (second independent) variable is accounted for, revealing the unique relationship between percentage of time spent resting and each of the two explanatory variables.

	Zero-order (Pearson) correlations		First-order partial correlations	
	r	*P*	*r*	*P*
Body condition	0.587	0.035	0.692	0.013
Structural size	0.530	0.062	0.655	0.021

DISCUSSION

Waterfowl are at their most susceptible to predation when flightless (Moore 2001, Guillemette & Ouellet 2005) and for adult waterfowl, wing moult can be the period of highest mortality (Schmidt & Loonen 2006). Therefore, any mechanism that can decrease exposure to predators during the vulnerable flightless phase will increase the likelihood of survival. Increased vigilance during wing moult has been demonstrated in numerous species of moulting waterfowl (Kahlert 2003, Döpfner *et al.* 2009). For a visually guided forager like Barnacle Geese, predator detection will be severely reduced during foraging, and generally head-down foraging and head-up vigilance are mutually exclusive activities (Mayhew & Houston 1989, Guillemain *et al.* 2002, Portugal & Guillemain 2011). Our data show that individual Geese that enter the wing moult phase at a higher mass spent a greater proportion of their time resting. This ability was related to the size of the initial body stores and, to a slightly lesser extent, their structural size. Thus, heavier Barnacle Geese are able to spend more time resting, reducing their exposure to potential predation. The captive Barnacle Geese spent significantly more time resting during wing moult (65%) than during non-moult periods (46%). Although sleeping forms part of the resting behaviour (as described in Methods), it has been demonstrated that birds can remain vigilant while sleeping through regular 'peeking' and through monitoring the behaviour and movement of conspecifics (Lendrem 1984, Gauthier-Clerc *et al.* 1994, 2002, Gauthier-Clerc & Tamisier 2000, Beauchamp 2009). An increase in resting behaviour may be an effective energy-saving mechanism during egg production in female birds (Schifferli 1976, Ettinger & King 1979, Houston *et al.* 1995). By allocating 13% less energy to activity during the laying period, female Willow Flycatchers *Empidonax traillii* are able to compensate for the energy costs of egg production (Ettinger & King 1979). Similarly, female Zebra Finches *Taenoipygia guttata* showed a 65% reduction in activity, which could result in substantial savings during egg production and incubation (Houston *et al.* 1995).

There could be a threshold in body mass above which it is possible to live off fat stores entirely during the flightless period. In Mottled Ducks *Anas fulvigula*, stored fat provides, on average, 33% of the total estimated costs of moult, which equates to approximately 9 days of the flightless period (Moorman 1993). Therefore, moulting Mottled Ducks would have to continue foraging during wing moult to meet the requirements of feather regrowth. Wing-moulting Common Pochards *Aythya ferina*, however, spent on average 90% of their time resting, and by using fat stores were able to meet up to 94% of their daily energy requirements during wing moult (Fox & King 2011). Thus, having large fat stores at moult onset allows for less time foraging and more time resting out of the reach of potential predators.

In the present study there was variation between individuals in their moult strategies. None of the Geese spent 100% of their time resting, suggesting that supplementation from exogenous sources was always required for every individual. Simple energy balance calculations can illustrate how those Geese that lose the most mass during wing moult are able to supply the majority of their energy requirements from their nutrient stores. If we assume that protein requirements of wing moult are met entirely from food intake and that each gram of body mass loss consists of 30% water and 70% lipid (Hohman *et al.* 1992), then 1 g of mass would provide 27.5 kJ. Multiplying this by the total mass lost gives the range among the Geese of energy provided from stores (5089–22 558 kJ). If we assume that the Geese are relatively inactive during the 42-day wing moult, then based on measurements of metabolic rate in the laboratory at this time (Portugal *et al.* 2007, 2009a, 2009b, 2010, in press) the Geese would have an average energetic requirement of 36 776 kJ (95% confidence intervals: 32 573–40 980 kJ) for self-maintenance and the demands for growing new feathers. Accordingly, the mass lost during the wing moult would have provided between 14% (95% CI: 12–16) and 61% (95% CI: 55–69) of the total energy required. As a result, there was a negative relationship between percentage energy supplied from mass loss and time spent foraging ($P = 0.03$). These values are maximal estimates, as none of the Geese rested for 100% of the time (Fig. 2), but for individual geese that have relatively low energy stores energy requirements for foraging will be relatively high as the act of foraging will itself increase metabolic rate above resting levels (Piersma *et al.* 2003).

The structural size of the Geese had a significant effect on time spent resting during wing moult. Size is known to influence many aspects of life for adult geese, primarily status within the flock (e.g. Black & Owen 1989). Larger birds are generally more dominant, and dominance status can enhance individual fitness in various ways, such as privileged access to food resources (e.g. Poisbleau *et al.* 2006). In wing-moulting geese, the prime foraging area is the immediate strip of land adjacent to water, which the geese can return to rapidly should there be a threat of danger (Owen & Ogilvie 1979, Kahlert 2006a, 2006b). It is likely that this area is also ideal for resting, and resting on land is preferable to resting on water, as contact with water increases thermal conductance by a factor of approximately 2.2 (de Vries & Eerden 1995). Therefore, a larger structural size helps to achieve a more dominant status within the flock and allows an individual bird to rest in the safest locations during the vulnerable flightless stage.

There are risks associated with having a body mass that is either too high or too low, and this balance is more pertinent during the flightless phase of wing moult, when the birds are restricted to one foraging area. If body mass is too low and all food resources are exhausted, there is risk of starvation. Moreover, if body mass is too high, it will impair flight manoeuvrability (Witter & Cuthill 1993, Witter *et al.* 1994, Dietz *et al.* 2007) and increase wing loading once flight is regained on the completion of wing moult. Moulting geese with large fat stores, therefore, may use these stores to increase feather regrowth, while ensuring they return to a suitable mass at the end of wing moult, ready for flight (Owen & Ogilvie 1979, Zimmer *et al.* 2010). This balance of having sufficient stores to reduce foraging but without having excessive mass that would cause problems when flight is regained has been suggested as the reason that no species of waterfowl studied to date spend 100% of their time resting during wing moult (Pehrsson 1987, Panek & Majewski 1990, Moorman 1993). It is thought to be adaptive to not be totally dependent on body stores and risk being too heavy at the point at which flight is regained. Our data support this idea, as none of the individuals gained sufficient mass prior to wing moult to eliminate foraging during wing moult, even in the presence of *ad libitum* food and no apparent barrier to energy storage. On the other hand, availability of protein rather than energy (fat) stores might be the more limiting factor for birds in order to decrease feeding time and thereby increase resting time throughout moult. Most proteins have no special storage form but serve specific body functions. While catabolism of muscle proteins can be the major source of amino acids for feather synthesis in fasting moulting birds like penguins (Cherel *et al.* 1994a, 1994b), it will result in some functional loss. Gaining flight soon with the end of feather growth is arguably vital for volant birds but will be hampered with atrophied breast muscles. Indeed, although Barnacle Geese undergo compensating changes in breast and leg muscles during moult, total muscle mass remains stable (Portugal *et al.* 2009a, 2009b), which can only be achieved by devoting some time to foraging.

We are grateful to Alan Gardner, Phil Archer, Ben Heanue and Pete Jones for looking after the Geese. Thanks also to Graham Martin and Craig White for useful discussions. We very much appreciate the constructive and useful comments provided by two reviewers, Rene Groscolas and Lewis Halsey, and to the Editor and Associate Editor, Ruedi Nager and Lorien Pichegru. This work was undertaken while S.J.P. was on a BBSRC studentship.

REFERENCES

Adams, P.A., Roberson, G.J. & Jones, I.L. 2000. Time–activity budgets of Harlequin Ducks molting in the Gannet Islands, Labrador. *Condor* **102**: 703–708.

Ankney, C.D. 1984. Nutrient reserve dynamics of breeding and moulting Brant. *Auk* **101**: 361–370.

Austin, J.E. 1987. Activities of postbreeding Lesser Scaup in southwestern Manitoba. *Wilson Bull.* **99**: 448–456.

Bailey, R.O. 1981. *The postbreeding ecology of the Redhead Duck (Anas americana) on Long Island Bay, Lake Winnipegosis, Manitoba*. PhD Dissertation, McGill University, Montreal.

Beauchamp, G. 2009. Sleeping gulls monitor the vigilance behaviour of their neighbours. *Biol. Lett.* **5**: 9–11.

Black, J.M. & Owen, M. 1989. Agonistic behaviour in Barnacle Goose flocks: assessment, investment and reproductive success. *Anim. Behav.* **37**: 199–209.

Cherel, Y., Gilles, J., Handrich, Y. & Le Maho, Y. 1994a. Nutrient reserve dynamics and energetics during long-term fasting in the King Penguin (*Aptenodytes patagonicus*). *J. Zool.* **234**: 1–12.

Cherel, Y., Charrasson, J.B. & Challet, E. 1994b. Energy and protein requirements for moult in the King Penguin (*Aptenodytes patagonicus*). *Am. J. Physiol.* **266**: R1182–R1188.

Dietz, M.W., Piersma, T., Hedenström, A. & Brugge, M. 2007. Intraspecific variation in avian pectoral muscle mass: constraints on maintaining manoeuvrability with increasing body mass. *Funct. Ecol.* **21**: 317–326.

Döpfner, M., Quillfeldt, P. & Bauer, H.G. 2009. Changes in behavioural time allocation of Waterbirds in wing-moult at Lake Constance. *Waterbirds* **32**: 559–571.

Ettinger, A.O. & King, J.R. 1979. Time and energy budgets of the Willow Flycatcher *Empidonax traillii* during the breeding season. *Auk* **97**: 535–546.

Fox, A.D. & King, R. 2011. Body mass loss amongst moulting Pochard, *Aytha farina* and Tufted Duck *A. fuligula* at Abberton Reservoir, South East England. *J. Ornithol.* **152**: 727–732.

Gauthier-Clerc, M. & Tamisier, A. 2000. Sleep–vigilance trade-off in Gadwall during the winter period. *Condor* **102**: 307–313.

Gauthier-Clerc, M., Tamisier, A. & Cézilly, F. 1994. Sleeping and vigilance in the White-faced Whistling-duck. *Wilson Bull.* **106**: 759–762.

Gauthier-Clerc, M., Tamisier, A. & Cézilly, F. 2002. Vigilance while sleeping in the breeding Pochard *Aythya ferina* according to sex and age. *Bird Study* **49**: 300–303.

Geldenhuys, J.N. 1983. Morphological variation in wing-moulting South African Shelduck. *Ostrich* **54**: 19–25.

Guillemain, M., Martin, G.R. & Fritz, H. 2002. Feeding methods, visual fields and vigilance in dabbling ducks (Anatidae). *Funct. Ecol.* **16**: 522–529.

Guillemette, M. & Ouellet, J.F. 2005. Temporary flightlessness as a potential cost of reproduction in pre-laying Common Eiders *Somateria mollissima*. *Ibis* **147**: 301–306.

Guozhen, Q. & Hongfa, X. 1986. Molt and resting metabolic rate in the Common Teal *Anas crecca* and the Shoveller *Anas clypeata*. *Acta Zool. Sin.* **32**: 73–84.

Hayes, J.P. & Shonkwiler, J.S. 2001. Morphological indicators of body condition: useful or wishful thinking? In Speakman, J. (ed.) *Body Composition Analysis of Animals*: 8–38. Cambridge: Cambridge University Press.

Hohman, W.L., Ankney, C.D. & Gordon, D.H. 1992. Ecology and management of postbreeding 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*: 128–189. Minneapolis: University of Minnesota Press.

Houston, D.C., Donnan, D. & Jones, P.J. 1995. The source of the nutrients required for egg production in Zebra Finches (*Pophila guttata*). *J. Zool.* **235**: 469–483.

Jehl, J.R. Jr 1990. Aspects of moult migration. In Gwinner, E. (ed.) *Bird Migration*: 102–113. Berlin: Springer-Verlag.

van der Jeugd, H.P., Gurtovaya, E., Eichhorn, G., Litvin, K.Y., Minneev, O.Y. & van Eerden, M. 2003. Breeding Barnacle Geese in Kolokova Bay: number of breeding pairs, reproductive success and morphology. *Polar Biol.* **26**: 700–706.

Kahlert, J. 2003. The constraint on habitat use in wing-moulting Greylag Geese *Anser anser* caused by anti-predator displacements. *Ibis* **145**: E45–E52.

Kahlert, J. 2006a. Factors affecting escape behaviour in moulting Greylag Geese, *Anser anser*. *J. Ornithol.* **147**: 569–577.

Kahlert, J. 2006b. Effects of feeding patterns on body mass loss in moulting Greylag Geese *Anser anser*. *Bird Study* **53**: 20–31.

Kahlert, J., Fox, A.D. & Ettrup, H. 1996. Nocturnal feeding in moulting Greylag Geese *Anser anser* – an anti-predator response? *Ardea* **84**: 15–22.

Lendrem, D.W. 1984. Sleeping and vigilance in birds, II. An experimental study of the Barbary Dove (*Streptopelia risoria*). *Anim. Behav.* **32**: 243–248.

Mayhew, P. & Houston, D. 1989. Feeding site selection by Wigeon, *Anas Penelope*, in relation to water. *Ibis* **131**: 1–8.

McNamara, J.M. & Houston, A.I. 1990. The value of fat reserves and the trade-off between starvation and predation. *A. Biotheor.* **38**: 37–61.

van der Meer, J. & Piersma, T. 1994. Physiologically inspired regression models for estimating and predicting nutrient stores and their composition in birds. *Physiol. Zool.* **67**: 305–329.

Moore, P.G. 2001. Concerning grey seals killing Eider Ducks in the Clyde area. *J. Mar. Biol. Assoc.* **81**: 1067–1068.

Moorman, T.E. 1993. Carcass mass and nutrient dynamics of mottled ducks during remigial moult. *J. Wildl. Manage.* **57**: 224–228.

Owen, M. & Ogilvie, M.A. 1979. Wing moult and weights of Barnacle Geese in Spitsbergen. *Condor* **81**: 42–52.

Panek, M. & Majewski, P. 1990. Remex growth and body mass of Mallards during wing moult. *Auk* **107**: 255–259.

Pehrsson, O. 1987. Effects of body condition on moulting Mallards. *Condor* **89**: 329–339.

Piersma, T. 1988a. The annual moult cycle of Great Crested Grebes. *Ardea* **76**: 82–95.

Piersma, T. 1988b. Breast muscle atrophy and constraints on foraging during the flightless period of wing moulting Great Crested Grebes. *Ardea* **76**: 96–106.

Piersma, T. & Davidson, N.C. 1991. Confusions of size and mass. *Auk* **108**: 441–443.

Piersma, T., Lindeboom, R. & van Eerden, M.R. 1988. Foraging rhythm of Great Crested Grebes *Podiceps cristatus* adjusted to diel variations in the vertical distribution of their prey *Osmerus eperlanus* in a shallow eutrophic lake in The Netherlands. *Oecologia* **76**: 481–486.

Piersma, T., Dekinga, A., van Gils, J.A., Achterkamp, B. & Visser, G.H. 2003. Cost–benefit analysis of mollusk-eating in a shorebird. Foraging and processing costs estimated by the doubly labelled water method. *J. Exp. Biol.* **206**: 3361–3368.

Poisbleau, M., Fritz, H., Valeix, M., Perroi, P-Y., Dalloyau, S. & Lambrecht, M.M. 2006. Social dominance correlates and family status in wintering Dark-bellied Brent Geese, *Branta bernicla bernicla*. *Anim. Behav.* **71**: 1351–1358.

Portugal, S.J. & Guillemain, M. 2011. Vigilance patterns of wintering Eurasian Wigeon: female benefits from male low-cost behaviour. *J. Ornithol.* **152**: 661–668.

Portugal, S.J., Green, J.A. & Butler, P.J. 2007. Annual changes in body mass and resting metabolism in captive Barnacle Geese (*Branta leucopsis*). *J. Exp. Biol.* **210**: 1391–1397.

Portugal, S.J., Thorpe, S.K.S., Green, J.A., Myatt, J.P. & Butler, P.J. 2009a. Testing the use/disuse hypothesis: pectoral and leg muscle changes in captive Barnacle Geese *Branta leucopsis* during wing moult. *J. Exp. Biol.* **212**: 2403–2410.

Portugal, S.J., Green, J.A., Cassey, P., Frappell, P.B. & Butler, P.J. 2009b. Predicting the rate of oxygen consumption from heart rate in Barnacle Geese, *Branta leucopsis*: effects of captivity and annual changes in body condition. *J. Exp. Biol.* **212**: 2941–2948.

Portugal, S.J., Isaac, R., Quinton, K. & Reynolds, S.J. 2010. Do captive waterfowl alter their behaviour patterns during the flightless period of moult? *J. Ornithol.* **151**: 443–448.

Portugal, S.J., Butler, P.J., Green, J.A. & Cassey, P. In press. Indications of phenotypic plasticity in moulting birds: captive geese reveal adaptive changes in mineralisation of their long bones during wing moult. *J. Ornithol*. doi: 10.1007/s10336-011-0699-9.

Proctor, N.S. 1993. *Manual of Ornithology: Avian Structure and Function*. New Haven: Patri.

Schifferli, L. 1976. *Factors affecting weight and condition in the House Sparrow, Passer domesticus, particularly when breeding*. D.Phil. thesis, Oxford University.

Schmidt, L. & Loonen, M.J.J.E. 2006. Changing environmental conditions cause variability in individual fitness in arctic-breeding Barnacle Geese, *Branta leucopsis*. *J. Ornithol.* **147**: 247.

Sjöberg, K. 1986. The flightless period of free-living male Teal *Anas crecca* in northern Sweden. *Ibis* **130**: 164–171.

Thompson, J.E. 1992. *The nutritional ecology of molting male Canvasbacks (Aythya valisineria) in central-Alberta*. MSc thesis, University of Missouri, Columbia, MO.

Thompson, J.E. & Drobney, R.D. 1997. Diet and nutrition of male Canvasbacks during post-breeding moults. *J. Wildl. Manage.* **61**: 426–434.

de Vries, J. & van Eerden, M.R. 1995. Thermal conductance in aquatic birds in relation to the degree of water contact, body mass and body fat: energetic implications of living in a strong cooling environment. *Physiol. Zool.* **68**: 1143–1163.

van de Wetering, D. & Cooke, F. 2000. Body weight and feather growth of male Barrow's Goldeneye during wing moult. *Condor* **102**: 228–231.

Wiklund, C.G. 1996. Body length and wing length provide univariate estimates of overall body size in the Merlin. *Condor* **98**: 581–588.

Witter, M.S. & Cuthill, I.C. 1993. The ecological costs of avian fat storage. *Philos. Trans. R. Soc. Biol. Sci.* **340**: 73–92.

Witter, M.S., Cuthill, I.C. & Bonser, R.H.C. 1994. Experimental investigations of mass-dependent predation risk in the European starling, *Sturnus vulgaris*. *Anim. Behav.* **48**: 201–222.

Zimmer, C., Boos, M., Petit, O. & Robin, J.P. 2010. Did body mass variations in disturbed Mallards fit to the mass-dependent starvation–predation risk trade-off? *J. Avian Biol.* **41**: 637–644.

Received 6 April 2011;
revision accepted 29 July 2011.
Associate Editor: Lorien Pichegru.