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Body mass loss amongst moulting Pochard *Aythya ferina* and Tufted Duck *A. fuligula* at Abberton Reservoir, South-east England

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Body mass loss amongst moulting Pochard *Aythya ferina* and Tufted Duck *A*. *fuligula* at Abberton Reservoir, South-east England

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Abstract We assessed the contribution of endogenous fat stores to meeting energetic needs during the flightless moult period in Pochard and Tufted Duck, by regressing mass on the progression of wing moult, measured by primary length. Pochard lost between 22.1% (males) and 24.2% (females) of body mass and female Tufted Duck 12.2% during wing moult at Abberton Reservoir, Essex. Based on a 27 day flightless period, Pochard lost on average 8.3-8.4 g per day and Tufted Duck 3.2-3.4 g per day, assumed to be the result of fat expenditure. Assuming daily energy expenditure (DEE) to be 1.7x basal metabolic rate (BMR), the contribution from burning endogenous fat equated to 37-40% of Pochard and 19-20% of Tufted Duck DEE during remiges moult. One frequently re-trapped female Pochard expended fat stores that almost fulfilled her entire energetic requirements during moult if she rested and did not feed for most of the moult. These results confirm that Pochard and Tufted Duck accumulated fat stores that helped meet energetic needs during the flightless wing moult period. This endogenous source of energy may free them to exploit habitats that are safe from predation but which may not fully supply the energetic needs of moulting ducks from exogenous sources.

Key words wing moult; moult migration; phenotypic plasticity; fat stores; energy budget

Zusammenfassung

Verlust von Körpermasse bei mausernden Tafel- (*Aythya ferina*) und Reiherenten (*Aythya fuligula*) im Abberton Reservoir im Südosten Englands

Wir erfassten den Anteil endogener Fettreserven an der Bewältigung energetischer Anforderungen während der mauserbedingten Flugunfähigkeit bei Tafel- und Reiherenten durch Regression der Masse gegen das Fortschreiten der Flügelmauser, gemessen an der Länge der Handschwingen. Am Abberton Reservoir in Essex verloren Tafelenten zwischen 22,1% (Männchen) and 24,2% (Weibchen) Körpermasse, während Reiherentenweibchen 12,2% Körpermasse verloren. Gemessen an einer flugunfähigen Periode von 27 Tagen verloren Tafelenten durchschnittlich 8,3 - 8,4 g pro Tag und Reiherenten 3,2 - 3,4 g pro Tag, was vermutlich auf die Nutzung von Fettdepots zurückzuführen ist. Unter der Annahme eines täglichen Energiebedarfs (DEE) von 1,7x Grundstoffwechselrate (BMR) beträgt der Verbrauch von endogenen Fettreserven während der Mauser der Flugfedern 37-40 % des DEE bei Tafelenten und 19-20 % bei Reiherenten. Eine mehrfach wieder gefangene weibliche Tafelente verbrauchte Fettreserven, die allein nahezu ihren gesamten Energiebedarf während der Mauser decken könnten, sofern sie rastet und nicht nach Futter sucht. Diese Ergebnisse bestätigen, dass Tafel- und Reiherenten Fettreserven anlegen, die ihnen helfen, die flugunfähige Zeit der Mauser zu überbrücken. Diese endogenen Energiereserven erlauben es ihnen Habitate aufzusuchen, die sicher vor Fressfeinden sind, aber nicht ausreichend Futterquellen bieten, um den Energiebedarf während der Mauser zu decken.

Introduction

Most ducks replace wing feathers simultaneously, rendering them temporarily flightless; males and nonbreeding females (sub-adult, other non- or failed breeders) often do so remote from breeding areas (the "moult migration" of Salomonsen 1968). Protein synthesis is energetically costly (Portugal et al. 2007) and feather protein, keratin, is characterized by its high sulphur-containing amino-acid content, making wing moult a period of potential nutrient and energetic stress (Hanson 1962; Hohman et al 1992). Recent studies suggest that waterfowl show remarkable phenotypic plasticity to meet the needs of the flightless wingmoult period, notably resorbing and reconstructing organs and muscle blocks in anticipation of need (rather than a result of training, Fox and Kahlert 2005; Portugal et al. 2009), synthesising flight feathers from protein stores accumulated in the body prior to moult (Fox et al. 2009) and using stored fat reserves, also accumulated pre-moult, to meet energetic needs during flight feather re-growth (Fox and Kahlert 2005; Kahlert 2006). Most adaptations are shown by waterbirds exposed to high predation risk, so plasticity responses to flightlessness can be interpreted as mechanisms to enable rapid re-growth of feathers in an environment which enables the birds to avoid predation, without complete reliance on exogenous sources of energy and/or nutrients to balance their daily needs. In other words, where predation risk is high (as, for instance, on land for normally terrestrial grazing geese), waterbirds can potentially reduce mortality rates whilst flightless by restricting feeding time, maximising food retention time and using body stores to help meet energy and nutrient needs during flightless moult (Fox and Kahlert 1999).

It might therefore be expected that waterbirds exploiting very extensive aquatic habitats, characterised by abundant food resources and low predation risk, would exhibit reduced reliance upon endogenous stores, particularly to meet the energetic costs of moult. In moulting seaducks, a combination of an abundant and unrestricted benthic food supply and lack of predators in the open sea would predict no loss of body mass and particularly of fat stores during moult; as is the case for moulting Common Scoter *Melanitta nigra* in Danish waters (Fox et al. 2008). Similar patterns seems likely in freshwater diving ducks that moult remiges on very large water bodies, especially those that undertake long moult migrations from the breeding areas to moult sites at or near their ultimate winter quarters (e.g. the *Aythya* ducks of eastern Europe that come to western Europe to moult and winter, Salomonsen 1968; Fox and Salmon 1988;

Wernham et al. 2002). Thus, Tufted Duck *A. fuligula* and Pochard *A. ferina* might arrive at moult sites after long migration that would deplete fat stores, making it unlikely that they could invest endogenous energy stores in meeting the needs of feather replacement. However, evidence suggests that at least some *Aythya* duck species do lose body mass during the wing moult, with 31% depletion of lipid stores in Redheads *A. americana* (Bailey 1981) and 45% in female Ring-necked Ducks *A. collaris* (Hohman et al. 1988), whilst others do not (male Ring-necked Ducks Hohman et al. 1988, female Lesser Scaup *A. affinis* Hohman et al. 1992 and Canvasbacks *A. valisineria* Thompson and Drobney 1996, 1997).

So, do moult migrant Tufted Duck and Pochard in western Europe lose mass due to depletion of fat stores during moult to assist with meeting energy requirements? In situations with abundant food supply and limited predation risk (such as large lakes which form the winter quarters of far higher densities of the same species later in the season), there should be no need to accumulate fat stores for exploitation during the flightless period. Here we test this hypothesis by reporting changes in body mass amongst these two species from birds caught during flightless moult at the large (>500 ha) Abberton Reservoir (51° 49' N, 00° 52' E) an important wintering site for both species in Essex, south east England, which lacks aerial or aquatic predators of ducks.

METHODS

Measurements from live-trapped free-living ducks

Tufted Duck and Pochard were caught opportunistically in baited traps at Abberton during the late summer of 1979. Data are presented here from 27 female (21 flightless, 6 completed moult and able to fly) and 18 males (13 flightless 5 flying) Pochard and 46 female (36 flightless and 10 flying) and 8 flightless male Tufted Ducks. Birds were aged and sexed, fitted with BTO metal rings, the flattened and straighten wing length measured to the nearest mm and body mass determined to the nearest 5 g using a balance by RK. Notes were taken of the state of moult, especially to differentiate old full grown from new feathers. We reasoned that although the rate of wing feather regrowth may not be linear with time, the length of the longest growing primary gave the best measure of the moult stage of an individual. One female Pochard GK65638, was caught and recaptured 18 times, enabling assessment of feather growth rate and mass change in a single individual throughout the flightless period. We assessed the rate of mass change during wing moult in these two species using linear and quadratic regression.

Modelling mass loss

Previous studies of flightless Greylag Geese Anser anser showed that mass in late moult was almost entirely explained by loos of fat accumulated prior to moult (Fox and Kahlert 2005). For the purposes of this analysis, we assumed that mass loss during moult related to fat used to help meet the energetic demands during moult (Kahlert 2006). We have assessed the relative contribution of fat to the overall energy expenditure of the two species during their flightless periods (here considered to be 27 days based on observations). The daily energy contribution of fat during the flightless period was calculated by dividing the mass lost (known precisely in the case of GK65638, modelled by regression for other birds) by 27 days and converted to daily energy by multiplying by 38.9, the energy density of fat in kJ g^{-1} (Pennycuick 2008). Daily energy expenditure (DEE measured in kJ d⁻¹) in Anatidae has been widely estimated as 2.6x basal metabolic rate (BMR) during other parts of the annual cycle (Drent et al. 1981). This conversion factor incorporates periods of flight, an activity which is energetically costly relative to other activities (10-12x BMR, e.g. Mooij 1992) but which self-evidently forms no part of the flightless moult period of the ducks. Thus, DEE should be lower than 2.6x BMR this during moult. Bevan et al. (1995) and de Leeuw et al. (1999) experimentally found that DEE of Tufted Ducks amounted to between 1.7 and 2.5x BMR in summer (based on tank experiments indoors and outdoors respectively), which included diving activity, which is also energetically costly. Kahlert (2006) suggested 1.7x BMR was more realistic based on observations of free-living flightless moulting Greylag Geese travelling up to 6 km per day to feed. Portugal et al. (2010) have shown that Common Eiders Somateria mollissima (a maritime diving duck) and Garganey Anas querquedula show significant reductions in feeding and locomotion and increases in resting during moult, therefore it seems likely that these two Aythya ducks may also further reduce energy expenditure by resting more and diving less during the flightless period, although this will be offset by the additional energetic costs of feather synthesis (Portugal et al. 2007). We compare the calculated DEE of the two species during moult based on 2.6x, 1.7x and 1.0x BMR to assess the degree to

which Tufted Duck and Pochard could meet their DEE under the differing scenarios, varying from normal energy consumption and to highly elevated levels of resting, to no feeding (i.e. no diving).

RESULTS

Body mass (M) significantly declined with wing length (w) amongst female and male Pochard caught while flightless (Fig. 1). The best fit regression was M = 1164.8 - 2.53w ($F_{1,20} = 12.4$, r = 0.63, P = 0.002) for females and M = 1236.70 - 2.55w ($F_{1,11} = 7.3$, r = 0.65, P = 0.02) for males. Taking the moult period as being that between the shortest and longest wing measurements on flightless birds and substituting these values in the regression models equates to losses of 227 g and 224 g in females and males respectively, or 24.2% and 22.1% of the original weights at the start of moult. In the case of GK56538, the regression model had the formula M = 1198.9 - 3.06w ($F_{1,18} = 7.3$, r = 0.97, P << 0.0001).

There was a significant decline in body mass with increasing wing length in female Tufted Ducks caught during flightless moult (M = 798.1 - 0.97w $F_{1,36}$ = 6.6, r = 0.40, P = 0.014) and a similar rate of decline among males, although the male regression was not significant due to low sample size (M = 815.1 - 0.93w ($F_{1,7}$ = 2.2, r = 0.52, P = 0.184, Fig. 1). Using the same approach as for Pochard, this equates to losses of 86.9 g in females and 92.9 g in males, 12.2% and 12.6% of the original weights at the start of moult.

If all mass loss in moulting Pochard reflects fat use, the amount of energy available to both sexes from fat stores during moult amounted to c.25% of their total daily requirements at normal levels of DEE, and rises to c.38% if energy costs were 1.7x those of BMR (Table 1). If female GK65638 had ceased foraging and simply subsisted at normal BMR for the duration of the flightless period, her fat stores could have met 92% of her energy needs during her flightless period (Table 1).

Based on the same assumptions as for Pochard, moulting Tufted Duck of both sexes were able to meet only c.12% of their total daily requirements based on 2.6x BMR, raising to c.19% if energy costs were 1.7x those of BMR and just under one third of DEE if energetic costs were those of resting metabolism (Table 1).

DISCUSSION

Do Pochard and Tufted Duck lose mass during moult?

Thompson and Drobney (1996) showed that Nearctic male Canvasbacks gradually catabolised somatic lipids from arrival on moulting sites through their mid-remigial moult. They argued that if Canvasbacks relied on lipid stores to meet the energy requirements of moult, they should have stored fat after their arrival at moulting sites and prior to the flightless period; however, there was no evidence for this fattening schedule (Thompson and Drobney 1995). Instead, lipogenesis began during mid-remigial growth, suggesting that male Canvasbacks primarily rely on their diet to meet energetic needs during moult. In contrast, the results presented here suggest more dramatic and consistent mass loss amongst two Palearctic Aythya species throughout the period of flightlessness. Pochard lost about 23% of their initial biomass during the moult period and Tufted Duck lost 12%. We infer that this mass loss reflects use of stored fat for energy, because changes in breast and leg muscles in Canvasbacks could not explain such mass loss (Thompson 1992). Evidence from other moulting waterfowl suggests such rapid changes in mass are not linked to changes in protein, water or other body components (e.g. Young and Boag 1982; Thompson and Drobney 1996) but are related to fat metabolism (Fox et al. 2005) despite the caution of Piersma (1990). The mass of both Pochard and Tufted Duck immediately after completion of remiges moult showed some signs of stabilisation and even increased, suggesting that the mass loss we observed was specifically associated with the flightless period (see Fig. 1). Although we lack large samples of birds caught in the prelude to moult, mass in both species was higher in the pre-moult period than in mid summer or early autumn suggesting a pre-moult acquisition of fat that Thompson and Drobney (1996) failed to find in the Canvasback. In this respect, Pochard and Tufted Duck show similarities to dabbling ducks (Folk et al. 1966; Hay 1974; Young and Boag 1982; Pehrsson 1987; Sjöberg 1988; Panek and Majewski 1990) and southern moulting geese (Fox et al. 2005; Portugal et al. 2007).

Contribution of fat stores to total energy needs during moult

Table 1 suggests that Tufted Duck could fulfil c.19% of their DEE during moult from fat stores, assuming some energy expenditure for feeding and enhanced energetic consumption to meet the demands of feather

synthesis (1.7x BMR). In this species, endogenous fat stores could supplement, but not completely meet, energy demands during flightless moult. In contrast, the "trap happy" Pochard GK65638 was potentially able to meet over 90% of her energy requirements at resting metabolism from fat storage alone. We should be extremely cautious in the interpretation of patterns shown by this one individual, because her frequent recapture could suggest poor body condition or otherwise aberrant behaviour. Although she benefited from bait at the trap, her case suggests that ducks could meet their DEE for flight feather replacement without feeding. Our data likely under represent the extent of body mass loss during the flightless period, since few birds (not even GK65638) were caught immediately after shedding flight feathers, when body mass is likely to be at its highest point during the moult. Furthermore, the flightless period may be shorter than the 27 days we used to calculate DEE (3-4 weeks reported in Cramp and Simmons 1977, but Mallard *Anas platyrhynchos* can vary between 22 and 29 days, Panek and Majewski 1990). If the flightless period was as short as 22 days, GK65638 could have met all her energy needs at DEE of 1x BMR with substantial unused fat stores, and the "average" Pochard could have met c.80% of their DEE from endogenous fat stores.

Species and sex differences in mass loss

There was no evidence of differences in mass loss between the sexes within the two species considered here at the same moulting site, although the small sample size amongst Tufted Duck restricts our ability to make firm conclusions for this species. Pochard consumed a quarter and Tufted Duck one eighth of their pre-moult body mass, suggesting consistent between-species differences at Abberton Reservoir. Why the difference? Typically, both of these bird species take advantage of feeding by night on areas that are often subject to disturbance by day, for example, waters subject to fishing (Bell and Austin 1985), intensive water sports (Fox et al. 1994), shooting disturbance (Evans and Day 2001) or building and redevelopment (Marsden 2001). Hence, in western Europe these species may exploit risky, but food-rich habitats outside of the breeding season that are generally subject to human disturbance or sources of high predation risk, and use safer, geographically separated habitats for roosting and resting at other times during the 24 hour cycle (Fox et al. 1994). This may mean that, in order to exploit such habitats during the vulnerable flightless moult period, evolution has favoured a strategy in these species that energetically buffers birds against the costs of flight feather replacement and enables them to exploit habitats which may not fulfil all

of their energy requirements but which do offer safety from predation. But why the difference between these two species and other *Aythya* species, such as the Canvasback? Perhaps the explanation is diet, because Tufted Duck consume more animal prey with higher fat and protein content than the more omnivorous Pochard. Pochard tend to occur in larger groups than Tufted Ducks during the non-breeding period and that these aggregations more often feed and roost on different water bodies than Tufted Duck. If Tufted Ducks are subject to less predation when flightless than are Pochard, then the interspecific differences may reflect the ability of their moulting sites to provide adequate energy and protein to sustain moulting ducks without risk of predation. Whatever the explanation, these Anatid species show remarkable plasticity in their ability to renew flight feathers simultaneously without being forced to use feeding habitats that may expose them to high predation risk, but we still need to better understand the ecophysiology of Anatids during the critical wing moult period.

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TABLE

	Total imputed fat mass consumption (g)	Imputed daily fat mass consumption based on a flightless period of 27 days	Energy supplied by this amount of fat (kJ per day)	Initial body mass (g)	Predicted daily energy consumption based on initial body mass estimated by different levels of energy consumption relative to BMR (percent of total energy needs)		
		(g per day)			2.6 x BMR	1.7 x BMR	1.0 x BMR
Pochard Female GK65638	310	11.5	446.7	940	1261.3 (35.4%)	824.7 (54.2%)	485.1 (92.1%)
Average Pochard Female	228	8.4	327.6	945	1266.2 (25.9%)	827.9 (39.6%)	487.0 (67.3%)
Average Pochard Male	224	8.3	322.2	1014	1333.6 (24.2%)	872.0 (37.0%)	512.9 (62.8%)
Average Tufted Duck Female	87	3.2	125.2	711	1026.1 (12.2%)	670.9 (18.7%)	394.6 (31.7%)
Average Tufted Duck Male	93	3.4	133.9	737	1053.6 (12.7%)	688.9 (19.5%)	405.2 (33.0%)

Table 1. Estimates of daily energy consumption of moulting Pochard at Abberton Reservoir, Essex, southeast England. Body mass changes are shown for a single female GK65638 which was re-trapped almost daily throughout the flightless moult period, as well as for "average" females and males based on the regression models described in the text. It is assumed that the body mass loss equates entirely to fat consumption and that 1 g fat provides 38.9 kJ energy. Predicted Basal Metabolic Rate (measured in kJ per day) is based on the equation BMR = $3.06 \times \text{mass}^{0.74}$ and daily energy expenditure is based on different multiples of BMR as indicated, expressing the potential daily source of energy from fat stores as a percentage of daily energy needs.

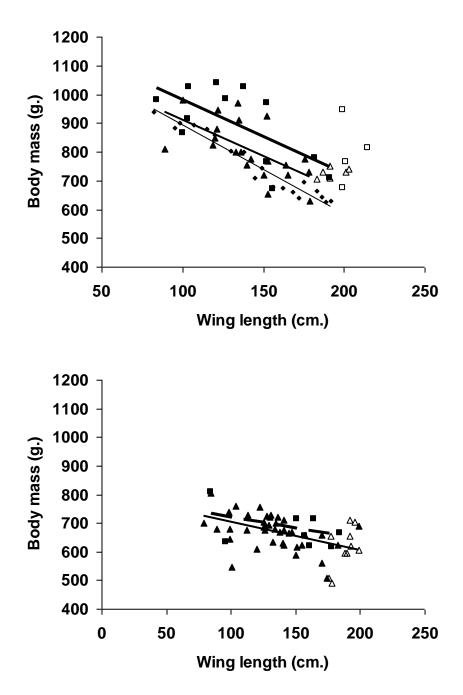


Figure 1. Relationship between body mass and the wing length based on the measurement of the longest primary feather of Pochard (upper) and Tufted Duck (lower) captured at Abberton Reservoir, Essex, southeast England. Filled symbols indicate individuals unwilling or unable to fly, open symbols those which could fly on release. Squares and bold regression line indicate males, triangles and medium thickness regression line females. Fitted lines indicate best least squares regression models to the data from flightless birds only (see text for details). Small diamond symbols and thin regression line in the upper graph show the repeated trapping and sequential measurements from female Pochard with metal ring GK65638. The regression model for Tufted Duck males (pecked solid line lower) failed to reach significance at P = 0.05 (see text for details).