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ORIGINAL ARTICLE

Do captive waterfowl alter their behaviour patterns during their flightless period of moult?

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Abstract Many different behavioural changes have been observed in wild waterfowl during the flightless stage of wing moult with birds frequently becoming inactive and reducing time spent foraging. Increased predation risk, elevated energetic demands of feather re-growth and restriction of foraging opportunities are thought to underlie these changes. By studying captive populations of both a dabbling and a diving duck species at the same site, we determined whether captive birds would reflect the behavioural responses of wild waterfowl to moult. The time-budgets of 42 Common Eiders, *Somateria mollissima*, (a diving duck) and 18 Garganeys, *Anas querquedula*, (a dabbling duck) were recorded during wing moult (July–August) and non-moult (January) with behaviour recorded under six categories. Despite captivity providing a low predation risk and constant access to food, birds altered their behaviour during the flightless period of wing moult. Time allocated to foraging and locomotion decreased significantly during moult compared to non-moult periods, while resting time increased significantly. Moulting Eiders underwent a greater reduction in time spent foraging and in locomotion compared with Garganeys, which is likely to be in response to a higher energetic cost of foraging in Eiders. It is possible that increased resting in both diving and dabbling ducks reduces their likelihood of detection by predators, while allowing them to remain vigilant. We demonstrate that there is much potential for using captive animals in studies that can augment our knowledge of behaviours of free-living conspecifics, the former being a hitherto under-exploited resource.

Keywords Behaviour · Captivity · Common Eider · Dabbling duck · Diving duck · Garganey · Moult

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Introduction

Most waterfowl species undergo a complete moult of their flight feathers after breeding, rendering them flightless for approximately 3–4 weeks (Hohman et al. 1992). Many display marked changes in their behavioural time-budgets during this flightless period (e.g. Adams et al. 2000; van de Wetering and Cooke 2000). For example, birds will often become inactive and devote less time to foraging and maintenance such as preening (e.g. Canvasbacks, *Aythya valisineria,* Thompson 1992; Harlequin Ducks, *Histrionicus histrionicus*, Adams et al. 2000). In addition, some species switch from diurnal to nocturnal foraging (e.g. Kahlert et al. 1996), increase vigilance bouts (e.g. Kahlert 2003) and/or reduce vocalisations to avoid detection by predators (e.g. Bailey 1981). An increase in predation risk as a result of being flightless, increased energy demands through feather re-growth and restriction of foraging opportunities are commonly cited reasons for these behavioural changes (Owen and Ogilvie 1979; Kahlert 2006).

Recent work by Portugal et al. (2007, 2009) on captive Barnacle Geese, *Branta leucopsis*, provided the first evidence that captive waterfowl respond behaviourally to wing moult in the same manner as free-living conspecifics by increasing time resting and decreasing time engaged in locomotion and foraging, despite the absence of predators and despite access to ad libitum food in captivity. The captive geese showed other traits characteristic of wild moulting waterfowl such as body mass loss (Portugal et al. 2007), increases in metabolic rate (Portugal 2008) and changes in the leg and flight muscle morphology (Portugal et al. 2009; see also Douthwaite 1976; Guozhen and Hongfa 1986; Fox et al. 1998 for studies on wild waterfowl). Therefore, it appears that by housing geese in captive conditions with constant access to food and in the absence of predators, they still respond behaviourally to moult in the same manner as moulting wild waterfowl. This phenomenon in captive waterfowl has, however, only been studied in depth in Barnacle Geese. Therefore, to gain a better perspective on whether similarities in the behavioural responses to moult between wild and captive waterfowl are commonplace, further species need to be examined. Working with captive moulting waterfowl presents an opportunity to study moult behaviour and ecology in a far more detailed manner than would be possible on wild moulting waterfowl, while also providing evidence of the endogenous nature of behavioural responses. Here, we present preliminary evidence that duck species also respond behaviourally to moult in a manner consistent with what would be expected in moulting free-living waterfowl. We tested the hypotheses that during moult the captive ducks would (1) decrease time dedicated to foraging and locomotion, and (2) increase time spent resting. Furthermore, we predicted that (3) diving ducks would reduce time spent foraging and in general locomotion to a greater extent during moult than dabbling ducks.

Methods

Birds and maintenance

Captive ducks were studied at the Wildfowl and Wetlands Trust (WWT) headquarters at Slimbridge, Gloucestershire, UK (51°43′N, 3°37′W). Forty-two Common Eiders, *Somateria mollissima* (hereafter referred to as 'Eiders'), and 18 Garganeys, *Anas querquedula,* were observed for a total of 39 days. Both species have had self-sustaining populations at Slimbridge since ca. 1980 (R. Cromie, personal communication). Eiders (1.9–2.1 kg) were selected as a representative diving duck species since they obtain their food exclusively through diving (Guillemette et al. 2007). Garganeys (0.2–0.3 kg) were selected as a representative dabbling duck species because they forage exclusively from the surface of the water, by so-called 'up-ending' (Guillemain et al. 2004). Both species had the largest number of individuals in a self-contained area at WWT where observations of all individuals could be made at all times. Birds were not able to fly as their flight feathers were cut annually or they were pinioned. It was not possible to identify individual ducks since they were not all ringed nor did they have distinguishing morphological markings.

Birds were fed with a 1:1 diet (Lilico, Surrey, UK; Charnwood Milling, Suffolk, UK) of mixed poultry corn (4% fat, 12% protein and 71% carbohydrate) and poultry grower's pellets (3% fat, 16% protein and 61% carbohydrate) with the food provided daily at approximately 1000 hours GMT. Food was thrown on the ground, in the water and placed in feeding trays. Consequently, food was available ad libitum throughout the day.

Eiders were housed in a large outdoor enclosure approximately 0.4 ha (1 acre) in size comprising a lake with a maximum depth of approximately 3 m, a number of small islands, and areas of open grass and concrete. The Eider's enclosure also included the following other waterfowl species: Hawaiian Geese, *Branta sandvicensis*, Tufted Ducks, *Aythya fuligula*, Greylag Geese, *Anser anser*, Mute Swans, *Cygnus olor*, Bar-headed Geese, *Anser indicus*, and Barnacle Geese. Garganeys were housed in an enclosure 15 × 8 m with a shallow, reed-fringed lake, and open areas of grass and hedgerow. The Garganeys' enclosure also included the following other waterfowl species: African Pochard, *Netta erythrophthalma*, and White-headed Duck, *Oxyura leucocephala*. For both Eiders and Garganeys, all birds were adults. The male:female sex ratio was approximately 1:2 and 2:1 for Eiders and Garganeys, respectively. None of the individuals had bred in the year of the study.

Time-budgets

Time-budgets of ducks were recorded at two points during the annual cycle: 17 July–14 August 2007 and 2–12 January 2008. In total, birds were observed for approximately 36 h during July–August, and 26 h during January. Moult was defined according to Ankney (1984), Bridge (2004) and Portugal et al. (2007). The July–August period was considered the 'wing moult' sampling session (hereafter referred to as 'moult'), and the January period the 'non-wing moult' sampling session (hereafter referred to as 'non-moult'). Birds were checked daily to assess moult stage and all birds were in wing moult during the summer sampling period. Males and females moulted synchronously. Behaviours were recorded in notebooks at two different times of day: morning (summer and winter: 0800–1200 hours GMT) and afternoon (summer: 1300–1800 hours GMT; winter: 1300–1630 hours GMT). Observations were made from vantage points a short distance (ca. 6 m) away from the birds during periods when it was not raining heavily. An individual bird was selected and observed for a total period of 5 min with behaviours recorded every 15 s. A focal bird was selected by choosing an individual that had not knowingly just been sampled, and all birds were visible throughout the duration of the sampling. If there was any disturbance (e.g. raptor flying over or members of the public approaching birds at close range) during the observation period, data were discarded. So as to provide an approximate equal number of each sex, different sexes were observed alternately (Mayhew 1987). Both species are sexually dimorphic during moult and non-moult (Kear 2005). For both species, approximately 432 five-min sampling sessions were conducted during moult, and 312 five-min sampling sessions during non-moult. Overall, sampling sessions were comprised of a 50:50 ratio of afternoon and morning sessions, and of male and female birds.

For both species, the following behaviours were recorded and pooled into six general categories (after Goudie 1986; Austin 1987; Klaassen et al. 1994; Adams et al. 2000; Portugal et al. 2007): *foraging* (feeding and pausing during foraging bouts); *resting* (loafing and sleeping); *maintenance* (preening, scratching, stretching and splash bathing); *locomotion* (tail-wagging, walking, swimming, wing-flapping and scooting); *social* (agonistic, antagonistic and courtship); and *alert* (head-raising and scanning the immediate area). For Eiders, diving was also added as a foraging category.

Statistical analysis

Following non-significant statistical testing between the sexes, data from the time-budgets were pooled across the sexes for both species (Eiders, ANOVA, $F_{(1,38)} = 1.4$, $P = 0.17$; Garganeys, ANOVA, $F_{(1,38)} = 1.7$, $P = 0.1$). For within-species comparisons, time spent in each behavioural category from each sampling session was expressed as a proportion of the observation period, which was arcsin square-root transformed to normalise data. Two-way ANOVA revealed no difference in time-budgeting between morning and afternoon observations within each sampling period for either Eiders (ANOVA, $F_{(1,38)} = 3.1$, $P = 0.07$) or Garganeys (ANOVA, $F_{(1,38)} = 3.6$, $P = 0.08$) so sessions were pooled. A one-way ANOVA (moult/non-moult as factors) with post hoc Tukey HSD tests ($\alpha < 0.01$) was performed to test for differences in the mean proportion of time dedicated to each category of behaviour between the moult and non-moult periods. To determine how the time-budgets differed between species, a two-way ANOVA with post hoc Tukey's tests ($\alpha < 0.01$) was used, with each species and sampling period as a category (i.e. Eider moult, Eider non-moult, Garganey moult, Garganey non-moult). As the ducks were not individually identifiable, it was not possible to guarantee independence of data. As such, all results are considered at the $\alpha = 0.01$ level of significance (sensu Grant and Grant 2002).

Results

Within-species comparisons

When flightless, Garganeys spent 41% of their time resting, a significant increase compared with 12% of time during non-moult (Fig. 1a, b, respectively, ANOVA, $F_{(1,38)} = 52.17$,

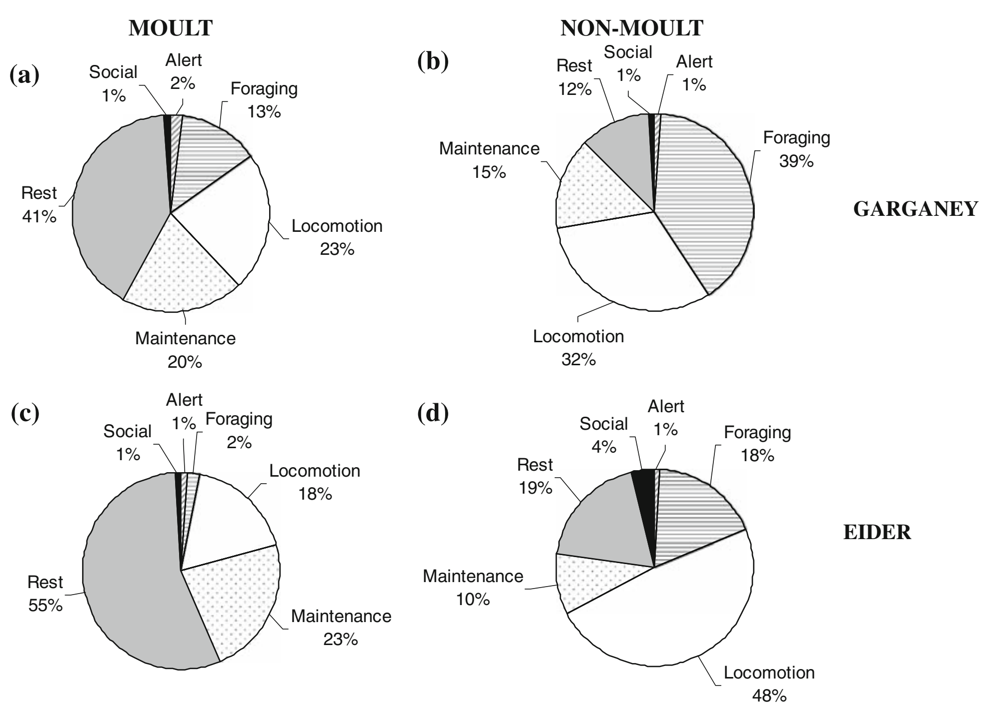

Fig. 1 Time activity budgets of 18 captive Garganeys, *Anas querquedula*, (**a**, **b**) and 42 captive Common Eiders, *Somateria mollissima*, (**c**, **d**) between moult and non-moult periods, respectively

$P < 0.001$). Time spent foraging during wing moult was 13%, a significant decrease compared with 39% during non-moult (Fig. 1a, b, respectively, ANOVA, $F_{(1,38)} = 51.72$, $P < 0.001$). Maintenance took significantly more time (20%) during moult than when not moulting (15%; Fig. 1a, b, respectively, ANOVA, $F_{(1,38)} = 4.32$, $P < 0.01$). Locomotion decreased significantly during moult to 23%, compared to 32% during the non-moult period (Fig. 1a, b, respectively, ANOVA, $F_{(1,38)} = 11.31$, $P < 0.01$). There were no significant changes in time spent in social or alert behaviour between moult and non-moult periods (Fig. 1a, b, respectively).

Eiders during wing moult spent 55% of their time resting compared with 19% during non-moult, a significant increase (Fig. 1c, d, respectively, ANOVA, $F_{(1,38)} = 38.23$, $P < 0.001$). Foraging decreased during wing moult, dropping significantly to 2 from 18% during non-moult (Fig. 1c, d, respectively, ANOVA, $F_{(1,38)} = 57.24$, $P < 0.001$). Maintenance behaviour increased significantly during wing moult (ANOVA, $F_{(1,38)} = 53.96$, $P < 0.001$) from 10% (Fig. 1d) in non-moult to 23% (Fig. 1c) during moult. During moult, Eiders spent 18% of their time engaged in locomotory behaviour, a significant decrease compared to 48% of their time when not moulting (Fig. 1c, d, respectively, ANOVA, $F_{(1,38)} = 78.60$, $P < 0.001$). As in Garganeys, there was no significant change in time spent in social or alert behaviour between moult and non-moult periods.

Between-species comparisons

During wing moult, Eiders underwent a greater reduction in combined time spent engaged in locomotory and foraging activities, compared to that recorded in Garganeys. During non-moult, Eiders spent 66% of time engaged in locomotion and foraging (Fig. 1d) compared with 71% in Garganeys (Fig. 1b). In total, Eiders spent 20% of time engaged in foraging and locomotory activities during moult (Fig. 1c) compared to 36% in Garganeys (Fig. 1a). ANOVA post hoc Tukey's tests showed that Garganeys were more alert than Eiders in both moult ($P < 0.001$) and non-moult ($P < 0.01$) periods, and spent more time foraging ($P < 0.001$) than the Eiders when not moulting. When not moulting, Eiders spent significantly more time engaged in both locomotory ($P < 0.001$) and social ($P < 0.05$) activities than Garganeys. During moult, Eiders spent significantly more time in maintenance ($P < 0.001$) and resting ($P < 0.001$) behaviours.

Discussion

Captive ducks showed a marked change in behaviour between wing moult when they were flightless and the period of non-moult. Both species showed a significant increase in resting and maintenance behaviours while simultaneously reducing time spent foraging and in locomotion. These behavioural changes occurred despite the captive birds never having flown. Increased resting allows energy savings that can, in turn, be allocated to the growth of new feathers. This would result in an increase in moult intensity and in a potential shortening of the flightless period (Hohman et al. 1992). As birds have a lower survival probability during periods of flightlessness than during volant ones (Pomeroy 1990), a shortening of the flightless period would be beneficial. In wild Eiders, for example, flightless birds are more likely to be predated by seals (Guillemette and Ouellet 2005). A recent study by Guillemette et al. (2007) noted that moulting Eiders in the wild do not reduce the duration or depth of dives during moult compared to non-moulting periods of the annual cycle, although the number of dives was not reported. These findings suggest, therefore, that it is not the increased cost of diving during moult per se that is responsible for the reduction in foraging, but rather that diving is itself a costly activity regardless of moult status, as has been demonstrated in Eiders (Butler and Jones 1997; Hawkins et al. 2000). Piersma (1988) suggested that diving birds will also reduce foraging during wing moult to minimise the risk of breaking newly growing flight feathers through the opening of the wings underwater during a dive. This, combined with the energetic cost of diving, may explain why Eiders do not increase foraging rate and food intake during moult to compensate for the nutritional demands of feather replacement.

No behavioural time-budget studies exist for Garganeys or Eiders. Studies conducted on other moulting wild waterfowl have shown varying changes in time spent resting and foraging during the flightless period. Redhead Ducks, *Aythya americana*, and Red-crested Pochards, *Netta rufina*, both of which are diving ducks, fed primarily at night during wing moult (Bailey 1981; van Impe 1985), which may be related to predator avoidance rather than to energetic savings as the colder water temperature at night would increase thermoregulatory costs. Austin (1987) studied the response of diving ducks to moult and reported a 10% increase in time spent resting during the flightless period in Lesser Scaup, *Aythya affinis*, while Mottled Ducks, *Anas fulvigula*, spent only 9% of their time feeding during wing moult compared with 65% of their time before and after (Paulus 1984). The same is true in Black Ducks, *Anas rubripes*, and Canvasbacks (Bowman 1987; Thompson 1992). The time spent foraging by Mottled Ducks (65%) reported by Paulus (1984) during non-moult periods is markedly higher than the 18% we found in captive Eiders. However, Eiders were on a nutrient-rich diet, which may have resulted in reduced foraging effort compared with free-living conspecifics.

There was a notable difference in the degree of change in behaviours between the two species. Compared with the dabbling duck species, the diving duck demonstrated a greater reduction in time spent in foraging and locomotory behaviours during wing moult compared to non-moult. These foraging observations agree with those of Goudie and Ankney (1976) who established that smaller species of ducks tended to spend proportionately more time feeding during wing moult than larger species. It is possible that, in our study, larger Eiders (both in body mass and structural size; Kear 2005) were able to deposit proportionately more fat prior to wing moult (Biebach 1996) than smaller Garganeys, enabling them to reduce foraging to a greater extent because of a greater ability to mobilise endogenous fat stores during moult. The larger Eiders will also have a proportionately lower metabolic rate than the Garganeys, so will need less food on a per kg basis. It is unlikely that any species of waterfowl is able to cease foraging altogether during moult (i.e. rely entirely on fat stores) unlike penguins, for example, which fast for the duration of moult (e.g. Green et al. 2004). The present study is limited by our inability to explore fully how feeding ecology influences behavioural responses to moult in ducks as we compared only two species. Behavioural data from additional moulting waterfowl species would be required to explore this in greater detail.

Ideally, future research on behavioural responses to moult in waterfowl would also focus on the relationship between relative body fat stores prior to wing moult and time spent foraging and resting during moult, in both within and between-species comparisons. To achieve this, birds would have to be individually marked and handled to quantify fat reserves at the beginning and at the end of moult. This was not possible in the present study as the WWT does not routinely handle birds, and rings on birds are too small to be read at distance or when birds are on water. Where circumstances allow, nasal saddles and neck rings could be used to individually identify birds. An ability to identify individual birds would significantly improve the study design and the statistical approaches, enabling a repeated-measures statistical design to be employed. That said, the present study was conducted as effectively as possible within the constraints of the captive conditions at Slimbridge and it is difficult to foresee how we would obtain access to this number of birds without an organisation's cooperation. Nevertheless, we demonstrate the latent value of such captive studies to unlock research potential.

In conclusion, captive ducks in our study still reduced time spent foraging during the flightless period of wing moult. Eiders, a diving duck, reduced time spent foraging and in locomotion to a greater extent than Garganeys, a dabbling duck. This is likely to be a response to the higher cost of foraging in the former. These behavioural changes occurred despite the birds being flightless year-round in captivity, with constant access to food and no predation. These findings suggest that increased resting during a potentially vulnerable period of the bird's annual cycle is a highly endogenous and necessary behavioural response to moult.

Zusammenfassung

Ändern Wasservögel in Gefangenschaft ihre Verhaltensmuster während ihrer flugunfähigen Mauserperiode?

Bei wildlebenden Wasservögeln sind während des flugunfähigen Stadiums der Flügelmauser viele unterschiedliche Verhaltensänderungen beobachtet worden—Vögel wurden häufig inaktiv und reduzierten die Zeit der Nahrungsaufnahme. Es wird angenommen, dass ein erhöhtes Prädationsrisiko, erhöhte Energieanforderungen durch das Federwachstum und eine Einschränkung der Möglichkeiten zur Nahrungsaufnahme diesen Veränderungen zugrunde liegen. Anhand zweier in Gefangenschaft gehaltener Populationen einer Gründel- sowie einer Tauchente am selben Standort haben wir untersucht, ob in Gefangenschaft gehaltene Vögel dieselben Verhaltensantworten auf die Mauser wie wildlebende Wasservögel zeigen. Die Zeitbudgets von 42 Eiderenten *Somateria mollissima* (Tauchente) und 18 Knäkenten *Anas querquedula* (Gründelente) wurden während der Flügelmauser (Juli-August) und im Januar ohne Mauser erfasst und ihr Verhalten in sechs Kategorien eingeteilt. Obwohl Gefangenschaft ein niedriges Prädationsrisiko und dauernden Zugang zu Futter bedeutet, änderten die Vögel ihr Verhalten während der flugunfähigen Periode der Flügelmauser. Die Zeit, die für Nahrungssuche und Fortbewegung aufgewendet wurde, nahm während der Mauser im Vergleich zu Nicht-Mauser-Perioden signifikant ab, während die Ruhezeit signifikant anstieg. Mausernde Eiderenten erfuhren eine stärkere Reduktion in der Zeit, die für die Nahrungssuche und Fortbewegung aufgewendet wurde als Knäkenten, was wahrscheinlich eine Reaktion auf die höheren Energiekosten der Nahrungssuche bei Eiderenten ist. Es ist möglich, dass erhöhtes Ruhen bei Tauch- und Gründelenten die Wahrscheinlichkeit der Entdeckung durch Fressfeinde reduziert, während es ihnen erlaubt, wachsam zu bleiben. Wir zeigen, dass Potential besteht, in Gefangenschaft gehaltene Tiere für Studien zu benutzen, die unser Wissen über Verhaltensweisen wildlebender Artgenossen erweitern können. In Gefangenschaft gehaltene Tiere sind für solche Studien bislang zu wenig verwendet worden.

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