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Phenotypic flexibility of a southern African duck *Alopochen aegyptiaca* during moult: do northern hemisphere paradigms apply?

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Phenotypic flexibility during moult has never been explored in austral nomadic ducks. We investigated whether the body condition, organ (pectoral muscle, gizzard, liver and heart) mass and flight-feather growth Egyptian geese *Alopochen aegyptiaca* in southern Africa show phenotypic flexibility over their 53-day period of flightless moult. Changes in body mass and condition were examined in Egyptian geese caught at Barberspan and Strandfontein in South Africa. Mean daily change in primary feather length was calculated for moulting geese and birds were dissected for pectoral muscle and internal organ assessment. Mean body mass and condition varied significantly during moult. Body mass and condition started to decrease soon after flight feathers were dropped and continued to do so until the new feathers were at least two-thirds grown, after which birds started to regain body mass and condition. Non-moulting geese had large pectoral muscles, accounting for at least 26% of total body mass. Once moult started, pectoral muscle mass decreased and continued to do so until the flight feathers were at least one-third grown, after which pectoral muscle mass started to increase. The regeneration of pectoral muscles during moult started before birds started to gain overall body mass. Gizzard mass started to increase soon after the onset of moult, reaching a maximum when the flight feathers were two-thirds grown, after which gizzard mass again decreased. Liver mass increased significantly as moult progressed, but heart mass remained constant throughout moult. Flight feather growth was initially rapid, but slowed towards the completion of moult. Our results show that Egyptian geese exhibit a significant level of phenotypic flexibility when they moult. We interpret the phenotypic changes that we observed as an adaptive strategy to minimize the duration of the flightless period. Moulting Egyptian geese in South Africa undergo more substantial phenotypic changes than those reported for ducks in the northern hemisphere.

Much of what we know about waterbirds comes from north-temperate latitudes where the availability of water is seasonally predictable and where water is seldom a limiting resource (Baldassarre and Bolen 2006). High predictability in resource availability has allowed north-temperate birds to fine-tune their life histories, dispersal strategies and physiological responses in a variety of ways to exploit this predictability to the fullest (Wingfield et al. 1992, Svensson 1995, Piersma and Drent. 2003, Bêty et al. 2004).

In areas where resource availability is less predictable, we may expect to find different responses by waterbirds to environmental fluctuations. In this context, southern African waterbirds offer an interesting case study. Much of southern Africa is arid and the region as a whole is considered "water scarce" (Harsch 1992). In addition to its aridity, the timing of rainfall events can be highly unpredictable (Tyson and Preston-Whyte 2000). Local variations in rainfall present a challenge for waterbirds, particularly ducks and geese (Anatidae) that need standing water of sufficient depth for foraging, predator avoidance and flight feather moult.

Ducks undergo a three- to five-week period of flightless moult, during which they replace all of their primary feathers. During this period, grazing ducks and geese generally have to remain close to water and occasionally venture onto land to feed on adjacent, low-quality forage (Halse and Skead 1983, Panek and Majewski 1990). Some of the physiological changes observed in north-temperate ducks and geese during moult have been associated with reductions in mass (Hanson 1962, Folk et al. 1966, Hohman et al. 1992, Fox and Kahlert 2005). Early studies attributed mass loss to nutritional stress caused by a scarcity of food (Hanson 1962, Folk et al. 1966). By contrast, Pehrsson (1987) proposed that mass reduction was an adaptive strategy to reduce wing loading and thereby shorten the flightless period. Recent studies of two north-temperate species, greylag goose *Anser anser* (Fox and Kahlert 2005) and common scoter *Melanitta nigra* (Fox et al. 2008) suggest that the reduction during moult in the mass of body organs associated with flight is an evolutionary adaptation consistent with a trade-off between the importance of their function and cost of their maintenance. It is also interesting to note that most studies of waterfowl (e.g. mottled duck *Anas fulvigula*, Fox et al. 2008; male mallards *Anas platyrhynchos*, Young and Boag 1982) report reductions in pectoral muscle size and yet no concomitant decrease in overall body mass as moult progresses, contradicting the reduced wing-loading hypothesis.

If the water body in which a duck is living dries down during the moult period, mortality is likely. It follows that over evolutionary time frames there must have been strong selective pressures for southern African ducks to (1) select permanent (and/or deeper) water bodies for moulting, even if food availability was low; and (2) minimize the duration of the flightless phase of moult.

The extent of phenotypic flexibility that exists in nomadic, south-temperate ducks during moult has never been explored. Indeed, there are few studies globally that address the issue of phenotypic flexibility of moulting waterfowl. black-necked grebes *Podiceps nigricollis* have small pectoral muscles during their flightless moult but during the two weeks prior to departure from the moulting grounds, their pectoral muscles double in size (Gaunt et al. 1990). To date, no such pattern has been documented for (more nomadic) southern African waterfowl. Douthwaite (1976) and Milstein (1993) both reported a decrease in body mass of flightless moulting red-billed teals *Anas erythrorhyncha* and seven captive Egyptian geese *Alopochen aegyptiaca* respectively, but could not link the change to phenotypic flexibility. Rather, they hypothesized that the mass decrease reflected the high energy costs of feather replacement and therefore expected it to continue as moult progressed.

In this paper we analyze physiological changes that occur during moult in Egyptian geese (Anatidae: a true duck, despite its common name *Alopochen aegyptiaca*). Specifically, we investigate whether or to what degree body condition, flight-feather growth, pectoral muscle mass and organ (gizzard, liver and heart) mass of Egyptian geese living in variable environments show phenotypic flexibility over the short period of flightless moult. We tested the hypothesis that moulting Egyptian geese adjust their mass and body condition to minimize the duration of the flightless period (when food availability is low). We expected that moulting ducks would lose weight, body condition, and pectoral muscle mass during moult; and that shortly before they regained the ability to fly, they would increase their pectoral muscle mass but would depart from their moulting grounds in poor overall body condition (Brown and Saunders 1998).

The study also evaluated two alternative hypotheses. The 'feather growth cost hypothesis', proposes that flight-feather moult is energetically costly to Egyptian geese and that this cost will be countered by building up body reserves before commencing moult. Once moult begins, birds are predicted to lose mass (including pectoral muscle mass) and body condition steadily during the moult period (Hanson 1962). The hypothesis does not predict significant change in liver and heart mass, but the gizzard is expected to decrease in mass with limited use (the cost-benefit hypothesis of Piersma and Lindström 1997). The second hypothesis was that remigial moult is not energetically costly to Egyptian geese. This hypothesis predicts that there will be no significant change in weight, body condition, organ (gizzard, liver and heart) mass or pectoral muscle mass during moult (Ankney 1979, Fox et al. 1998)

Materials and methods

Study sites

Adult Egyptian geese were caught at Barberspan Nature Reserve (26°33′S, 25°37′E) in the North West Province and Strandfontein Wastewater Treatment Works (34°05′S, 18°32′E) in the Western Cape Province, South Africa, between March 2007 and February 2008.

Barberspan Nature Reserve is a Ramsar-designated site in a semi-arid, summer rainfall region. It is a perennial pan that is shallow, alkaline and connected to the Hart's River. When full, it covers an area of *ca* 2010 ha, but water levels fall considerably during late winter. Surrounding natural habitats comprise mainly gently undulating and flat, short to very short grassland interspersed with acacia trees. There are also surrounding farmlands used mainly for maize and sunflower cultivation. Large numbers of waterfowl and waders use the pan for foraging, breeding, roosting and moulting. In winter, Egyptian goose numbers regularly exceed 1000 individuals (Taylor et al. 1999).

Strandfontein Wastewater Treatment Works is in a coastal, winter-rainfall area. The site comprises 319 ha of open permanent ponds and canals, some with sandy islands, and 58 ha of terrestrial habitats, much of which is grassy. The woody species found in the area are mainly exotic *Acacia cyclops* (Kaletja-Summers et al. 2001). The hydrology of the site is managed and, depending on the management practice of the moment, some ponds have open mudflats that serve at roosting sites for waterfowl and feeding grounds for waders.

Fieldwork

Five hundred and seventy-two geese were caught during the study, 178 at Barberspan and 532 at Strandfontein, using maize-baited walk-in traps placed near the water's edge. All geese were banded with metal rings and 410 individuals were also marked with a uniquely engraved colour ring. Mass was measured to the nearest gram using a spring balance. Moult, body condition (see below), forewing (to the tip of the longest primary), total head, culmen (to feathering) and tarsus length (from the end of the calcaneal ridge to the base of the complete scale before the toes diverge) were recorded for all birds. Head, tarsus and culmen lengths were measured with Vernier callipers to the nearest 0.1 mm.

Moult scores were recorded following de Beer et al. (2000). For each of the ten primary feathers moult was scored using a six point scale: 0 = fully grown old (worn) feather, 1 = feather missing or in pin, 2 = feather emerging from sheath up to 33% grown, 3 = new feather 33–67% grown, 4 = new feather from 67% to fully grown with remains of the sheath still visible, 5 = new, fully grown feather with no remaining traces of a sheath. Scores for each feather were summed, giving a total moult score. Because ducks undergo synchronous moult of the remiges, six distinct moult stages (i.e. 0, 10, 20, 30, 40 and 50) are recognizable.

A measure of body condition was derived from a body condition index (BCI) modified from Pehrsson (1987). The BCI was calculated by dividing body mass (g) by the product of two reliable structural measurements, *viz* tarsus and head length. Forewing length was not deemed a reliable structural measure because a) it may vary irrespective of body size (Pehrsson 1987), and b) most of the birds handled in this study were in moult. The BCI thus corrected mass for structural size.

Feather growth of captive birds

Forty adult moulting Egyptian geese (21 in June 2008 and 19 in March 2009) were caught at Barberspan Nature Reserve and housed for 5 days in a walk-in aviary (20 × 3 × 2.5 m). The geese were fed *ad lib.* on poultry grain (a mix of wheat, sorghum and crushed corn) and were free to graze the grass inside the aviary. Clean drinking water was provided daily.

The length (mm) of the right ninth primary flight feather (P9) was measured (from the point where the feather quill emerges out of the forewing to the tip of the feather) on the second day the geese were in captivity and again on the fifth day before they were released. P9 length measurements from 221 non-moulting Egyptian geese previously captured at Barberspan and Strandfontein during 2007 and 2008 were used to calculate the mean P9 length of non-moulting Egyptian geese. Assuming constant rates of change in the length of P9 (e.g van de Wetering and Cooke 2000) the average flightless duration and moult duration were established by dividing the mean P9 length of non-molting birds by the mean average P9 growth per day of flightless birds and the mean average P9 growth per day of all moulting birds respectively.

Muscles and organs

Fifteen birds, including three from each of the five moult categories, were collected from different areas around Cape Town. The birds were caught using walk-in traps and then euthanased in carbon monoxide chambers in compliance with Cape Nature permits and University of Cape Town animal ethics regulations. Pectoral muscles (*pectoralis major* and *supracoracoideus*) on both sides of the keel were cut from the sternum and at the underside of the humerus, excised and rinsed in distilled water. The gizzards were removed, emptied, and washed in distilled water. Organs were weighed (wet mass) using a laboratory scale with a 0.01 g precision.

Abdominal and mesenteric fat deposits were extracted and weighed. Subcutaneous fat was scored using Fox et al.'s (2008) six-point scale, where 0 = none; 1 = thin layer patchily distributed; 2 = thin layer evenly distributed, no blood vessels; 3 = medium layer, continuous over much of the body, obvious blood supply; 4 = thick layer continuous over body; and 5 = extensive thick deposits throughout, extending down the abdomen and around the neck.

Statistical analysis

A Student's unpaired *t*-test was used to test for significant differences in means of morphometric measurements from the two study sites. The Student's unpaired *t*-test was also used to test for differences in P9 growth rate between flightless and flight-capable moulting Egyptian geese. We calculated the mean P9 length of non-moulting geese and the mean P9 growth per day of moulting geese. We then fitted a linear regression model on all average P9 increments per day (mm) against initial P9 lengths and estimated the duration of moult and that of the flightless period. A correlation matrix was used to test for interaction terms between body mass, moult, pectoral muscle mass, organ mass and the body condition index. Regression models were fitted that best described changes in body mass, pectoral muscles mass, organ mass and body condition as a function of the moult stage. MANOVA was used to test for the effects of moult stage on weights of pectoral muscle, gizzard, liver and heart. Hypotheses were tested at the 5% level of significance and all analyses were carried out using the package SPSS 17 (2008).

Results

Mean head, culmen and tarsus lengths did not differ between Egyptian geese at Barberspan and Strandfontein. Non-moulting birds from Strandfontein were slightly, but not significantly heavier than those from Barberspan, with means of 2342 ± 49 g and 2166 ± 55 g respectively. Because there were no significant differences in the metrics of the birds from the two study sites, data were pooled for subsequent analysis.

Two hundred and forty-eight Egyptian geese with old feathers were caught at Strandfontein. Of these, 62 were moulting body feathers, mainly in the neck and back regions. No body-feather moult was observed on ducks in flight feather moult or on those that had just completed moult. No body moult was observed in all non-moulting Egyptian geese from Barberspan with both old and new flight feathers.

Mean body mass varied significantly ($F = 45.99$, $p < 0.001$) over the flightless moult period. Mass started to decrease as soon as the flight feathers were dropped and continued to do so until these flight feathers were at least two-thirds grown, after which mass started to increase (Fig. 1a). Mean BCI followed a similar trend to that of mass (Fig. 1b; $F = 71.17$, $p < 0.001$).

Feather growth of captive birds

Of the 40 birds held in captivity, 22 were flightless and 18 were capable of flight. The latter had a P9 length of at least 158 mm (two-thirds grown). The mean P9 growth rate for all the moulting geese was $4.59 \pm 0.32\ \mathrm{mm.d^{-1}}$. P9 growth rate decreased ($r = -0.56$; $p < 0.001$) as feathers elongated (Fig. 2). Mean feather growth rate of flightless birds was $5.54 \pm 0.32\ \mathrm{mm.d^{-1}}$ and for birds capable of flight the equivalent growth rate was $3.52 \pm 0.46\ \mathrm{mm.d^{-1}}$. Therefore moulting geese are likely to be flightless for

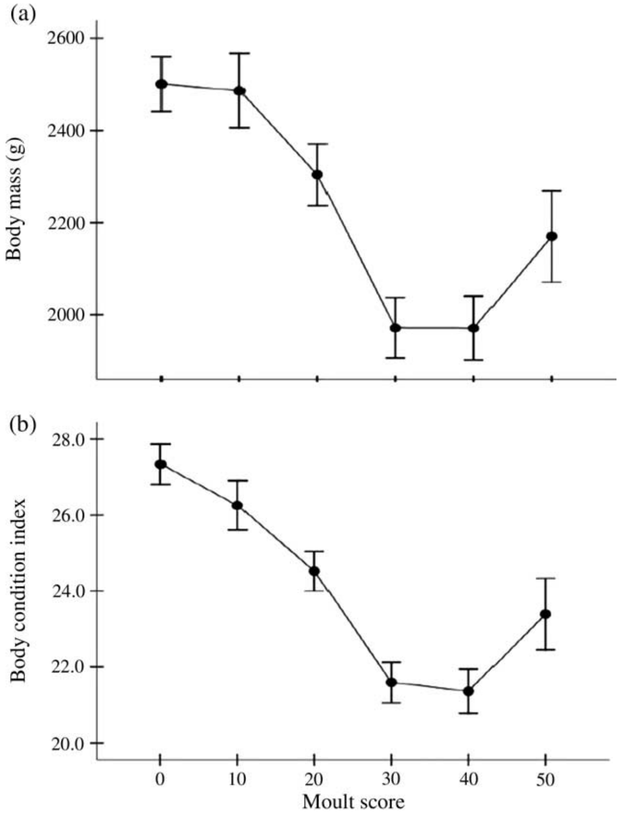

Figure 1. Mean mass (a) and body condition index (b) [± 95% C.L] as a function of moult score for Egyptian geese at Barberspan and Strandfontein.

at least 28.5 days. The mean P9 length of 221 non-moulting Egyptian geese was 247.22±1.31 mm. Therefore the average duration of moult based on the mean P9 growth rate for all moulting geese was 53.83 days, almost double the period of flightless moult.

Muscles and organs

Fat reserves with a score of 1 were recorded in three non-moulting geese and in one goose with new feathers. All other birds at all moult stages had no fat layer (score 0) and fat scores were not considered in subsequent analysis. The multivariate analysis suggests that masses of all organs measured, except the heart, varied significantly during moult (Table 1).

Pectoral muscle mass varied significantly during the moulting period. Non-moulting Egyptian geese with very old flight feathers (i.e. about to moult) had high pectoral muscle mass, accounting for at least 26% of total body mass. Once moult started, pectoral muscle mass decreased and continued to do so until the flight feathers were at least one-third grown, after which pectoral muscle mass started to increase (Fig. 3a). In other words, the regeneration of pectoral muscles during moult began before birds started to gain overall body mass.

Gizzard mass started to increase soon after the onset of moult, peaking when the flight feather were two-thirds grown, after which gizzard mass again decreased. Liver mass increased significantly ($p < 0.001$) as moult progressed, while heart mass remained unchanged (Fig. 4).

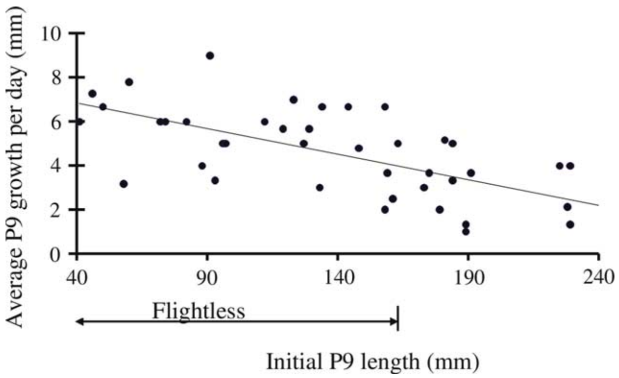

Figure 2. Average P9 increment per day (mm) as a function of initial P9 length for Egyptian geese in captivity. $Y = -0.023x + 7.778$; $r = -0.65$; $F = 28.75$; $p < 0.001$.

Discussion

Egyptian geese exhibit substantial phenotypic flexibility during moult. These changes in both muscle and organ mass can be interpreted as strategies to balance energy and nutrient demands with the costs associated with reduced food availability during the flightless moult period.

The overall loss of body condition and mass (Fig. 1) that occurs from the onset of moult until birds are once again able to fly, albeit not well, is interpreted as a response to a combination of lost foraging opportunity (reduced foraging time and low-quality food) and the cost of feather growth (Murphy 1996). At face value, these findings support the conclusions of Hanson (1962) and Folk et al. (1966) that moulting ducks are nutrient stressed and lose body mass and condition as a result. However, a logical extension of this interpretation is that geese will, periodically, starve to death during moult: there is apparently no such instance of this having been recorded (Halse 1984, Milstein 1993). An equally sound interpretation of this pattern is that geese reduce body condition and mass to a safe minimum level and then maintain this. Once flight feathers are more than two-thirds grown and the birds are able to fly, they can venture farther from water to higher quality foraging areas, allowing them to increase body mass and improve overall body condition towards the end of the moult period. Similar patterns of changing body mass during moult have been documented for north-temperate waterfowl (e.g. Ankney 1984, Jehl 1997). The most parsimonious explanation for changes in body mass and condition appears to be that they represent strategic responses which simultaneously reduce metabolic demand (through reduction in flight

Table 1. MANOVA of organ weights during moult

Organ Mass (g)	DF	F	p
Heart	5	0.266	0.923
Gizzard	5	127.957	<0.001
Liver	5	58.932	<0.001
Pectoral muscles	5	10.616	<0.001

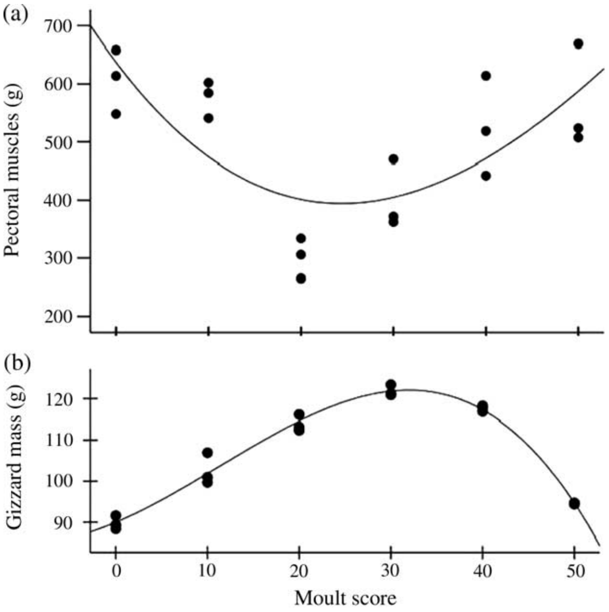

Figure 3. Changes in (a) wet pectoral muscle mass and (b) wet gizzard mass of Egyptian geese at Strandfontein as a function of moult score. Fitted polynomial curves: (a) $y = 0.3488x^2 - 18.165x + 630.63$; $r = 0.729$; $p = 0.003$, (b) $y = -0.001x^3 + 0.035x^2 + 0.94x + 89.98$; $r = 0.99$; $p < 0.001$

muscle mass – Fig. 3a) and wing loading (by reducing mass). The combined effect of this is to reduce the period of flightless moult (heavier birds would have to wait for longer before the feathers had grown sufficiently to enable them to fly). The advantage of shortening the flightless moult period is that it speeds up birds' access to higher quality foraging areas which in turn enables them to be in better condition at the end of moult than would be the case had they been flightless for longer. Predation pressure could be an alternative explanation for adopting a strategy to reduce body mass and shorten the flightless period (Owen and Ogilvie 1979, Sjöberg 1986). We were unable to test this hypothesis explicitly in our study. However, Egyptian geese probably have few natural predators in their southern African range: they are aggressive and are able to drive away large carnivores (Errington 1967, Howcroft 1968, Milstein 1993). In addition, they are only infrequently hunted for sport. This lack of extrinsic sources of mortality may contribute to explaining the species' major range expansion in southern Africa in the last 50–100 years (Okes et al. 2008).

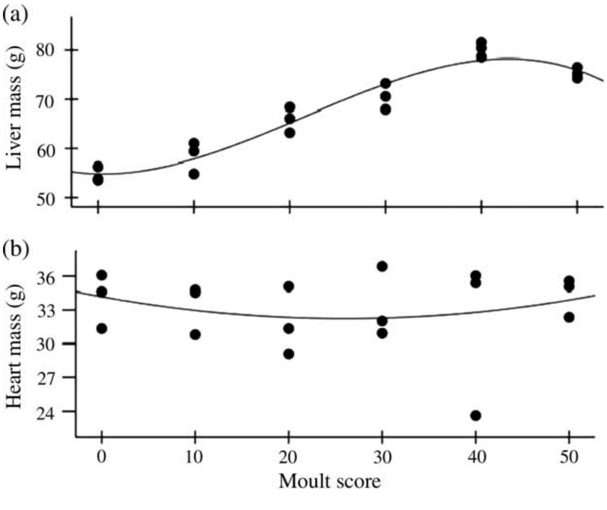

Figure 4. Changes in (a) wet liver mass and (b) wet heart mass of Egyptian geese at Strandfontein as a function of moult score. Fitted polynomial curves: (a) $y = -0.0063x^2 + 0.8102x + 53.013$ and $r = 0.9412$; $p < 0.0001$, (b) $y = 0.003x^2 - 0.15x + 34.188$ and $r = 0.229$; $p = 0.667$

The overall average daily primary feather growth rate of 4.59 ± 0.315 mm.day^{-1} for Egyptian geese in this study is less than that reported for most northern hemisphere ducks and geese (there are no southern African studies with which to compare these findings), although similar primary growth rates of 4.04 mm.d^{-1} have been reported for barrow's goldeneye *Bucephala islandica* (van de Wetering and Cooke 2000). The much larger mute swans *Cygnus olor* have an average primary growth rate of 6.5 mm.d^{-1} and barnacle geese *Branta leucopsis*, similar in size to Egyptian geese, have a primary growth rate of 7.5 mm.d^{-1} (Owen and Ogilvie 1979). Therefore Egyptian geese seem to take longer to complete their moult as compared to northern hemisphere waterfowl of equivalent size. However, the duration of the flightless period (*ca* 28–29 days) is relatively short compared to most northern hemisphere ducks (32–36 days; e.g Owen and Ogilvie 1979, Pehrsson 1987, van de Wetering and Cooke 2000). Despite their long moult duration, Egyptian geese are able to minimize the flightless period by reducing wing loading. They are able to fly with primaries that are only 67% grown as compared to northern hemisphere ducks (which maintain mass during moult) that can only fly once their primaries are at least 80% grown (Pehrsson 1987).

When flight feathers of Egyptian geese were half grown, and before flight was possible, the pectoral muscles gradually increased in size, allowing sustained flight once the flight feathers were over two-thirds grown. Similar atrophy and hypertrophy of pectoral muscles has been recorded for moulting greylag geese (Fox and Kahlert 2005) and black-necked grebes (Gaunt et al. 1990) in the northern hemisphere. These findings also concur with Piersma and Lindström (1997) who predict that peak flight performance is sustained by enlarged pectoral muscles whilst temporary flightlessness will cause the pectoral muscles to shrink. Ankney (1979) further suggests that the proteins and nutrients released as pectoral muscle atrophies may be used to supplement the growth of new flight feathers and the enlarged digestive organs.

The significant increase in the mass of the gizzard (which happens before the increase in pectoral muscle mass - Figs 3a, b) is interpreted as an adaptation to low diet quality during moult (i.e. below the point at which birds can maintain good body condition). Similar changes in gizzard size in response to diet have been demonstrated in domesticated Japanese quail *Coturnix japonica* (Starck 1999, Starck and Rahmaan 2003) and in red knots *Calidris canutus* (Dekinga et al. 2001). In both cases, gizzard mass increased within a week in response to hard-textured, low-protein forage and these changes reversed when birds were fed soft, high-quality food. The growth of the gizzard is a response to an increase in the work load involved in processing low-quality food (Starck 1999), as Egyptian geese are forced to do early in the moult period. In the case of Egyptian geese, gizzard mass started to decrease once birds were able to fly to higher quality foraging areas. This phenomenon has yet to be investigated for ducks in the northern hemisphere.

Our findings cannot fully discount the alternative hypothesis that the observed patterns are driven purely by the high energetic costs of feather growth. If the patterns were driven exclusively by stress (i.e. exogenously), it is possible to explain the pattern of increasing then decreasing gizzard mass as nothing more than a physiological response to forage quality (and one which has been demonstrated experimentally; see Starck 1999, Dekinga et al. 2001, Starck and Rahmaan 2003). It is also possible to explain why overall body mass decreases up to the time that birds are able to exploit high-quality food, because a combination of a poor nutritional environment coupled with the energetic demands of feather growth results in a negative energy balance (Murphy 1996). What cannot be explained by the 'feather growth cost' hypothesis is the allocation of increasingly scarce resources to pectoral muscles (i.e. increasing flight muscle mass while overall body mass continues to fall) before birds have access to high-quality food. This strongly implies an anticipation of need (i.e., a strategy) rather than an inevitable response to stress. Indeed, based on low-quality foraging conditions until the time the birds are able to fly, it is very difficult to understand how this pattern could be explained by the feather growth cost hypothesis. The findings of the study are consistent with the hypothesis that moulting Egyptian geese adjust their mass and body condition to minimize the flightless period; i.e. the phenotypic changes observed represent an adaptive strategy, *sensu stricto*.

The problem of reducing the flightless period is fundamental to all ducks that moult on water but graze on land. Grazing ducks in the northern hemisphere have an accelerated feather growth rate that they maintain by using stored fat reserves (e.g. Ankney and MacInnes 1978, Fox and Kahlert 2005). Unlike northern hemisphere ducks, Egyptian geese do not deposit fat reserves prior to moult and they have a slower feather growth rate. However, they trade off body mass, condition and muscle size for a reduction in wing loading that in turn shortens the flightless period.

In summary, unlike north-temperate ducks, moulting Egyptian geese in South Africa undergo substantial phenotypic changes during moult, including asynchronous changes (e.g. flight muscle mass increasing while body mass decreases). This phenotypic plasticity appears to have evolved to allow moult to be completed as rapidly as possible in environments characterized by stochasticity rather than predictability (which prevails at boreal latitudes). Specifically, the moult strategy of Egyptian geese is geared towards minimizing the duration of the flightless period and could not have been predicted based on prevailing northern hemisphere paradigms. These findings offer new insights into duck life history strategies in different environments, especially stochastic environments.

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