

Changes in body mass and hormone levels between wintering and spring staging areas in dark-bellied brent geese *Branta bernicla bernicla*

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We document seasonal changes in body mass and plasma hormone levels (testosterone and triiodothyronine) between winter and spring quarters in dark-bellied brent geese *Branta bernicla bernicla*. Body mass increased between winter and spring, whereas body size was the same for the birds sampled in winter and those in spring. Adults and males were larger and heavier than juveniles and females. Plasma testosterone levels did not differ significantly between winter and spring, and did not vary with sex, age and morphometry. Plasma triiodothyronine (T_3) levels were significantly higher in spring than in winter, and were higher for males than for females. However, T_3 levels did not vary significantly with age and body measurements. To explain the findings, we discuss potential impacts of social dominance.

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Wintering migratory geese generally replenish protein stores lost during migration before building up their fat stores (Gauthier et al. 1992). Dark-bellied brent geese *Branta bernicla bernicla* winter mainly along the coasts of France, England and the south-western part of the Netherlands, and stage from March till late May mainly in the Wadden Sea, stretching from the northern Netherlands to Denmark (Ebbinge et al. 1999). During spring, geese accumulate body stores needed both for their long-distance migration to the breeding grounds and for reproduction (Spaans et al. 1993, Ebbinge and Spaans 1995). Dark-bellied brent geese, migrating about 5000 km between the wintering and breeding areas (Green et al. 2002), increase their body mass by 25–35% on spring staging areas in April and May prior to migration towards the breeding grounds (Ebbinge and Spaans 1995, Spaans and Postma 2001). In addition,

females that were heavier at spring departure prior to breeding are more likely to return the following autumn with offspring to the wintering grounds than those that did not manage to achieve high body masses in May (Ebbinge et al. 1982, Ebbinge and Spaans 1995). This suggests that deposition of energy stores by females in spring is a major factor influencing breeding success (Ebbinge 1989, Spaans and Postma 2001). Intermediate stop-over sites between the Wadden Sea and the Siberian breeding grounds on the Taimyr peninsula have been discovered lately along the White Sea and the north coast of the European part of Russia (Ebbinge and Spaans 1995, Green et al. 2002). We think, however, that the staging periods on these stop-over sites, though essential for the birds to top up once again, are too short for birds to compensate for a poor start from the Wadden Sea.

Based on earlier studies, we hypothesised that the identification of proximate determinants of body mass changes prior to migration to the breeding grounds is crucial for the identification of key factors influencing population processes and dynamics in Arctic geese. These determinants may have either an endocrinological and/or a behavioural basis. Testosterone influences many aspects of physiology and behaviour in avian species, and thus may affect kinetics of fat stores in a number of different ways (see Wingfield et al. 1987, Ketterson and Nolan 1999, Alonso-Alvarez et al. 2002). At wintering and spring staging areas, for instance, higher plasma testosterone levels may result in a higher social status and increased aggressiveness towards conspecifics perhaps providing advantages during resource acquisition (Stahl et al. 2001, Poisbleau et al. 2005). In particular, males that are more aggressive towards conspecifics protect their mates more efficiently, and allow them to feed without disturbance in better patches (Teunissen et al. 1985, Prop and Deerenberg 1991). This could explain why paired females reached on average a higher body mass than single females (Ebbinge and Spaans 1995) and why female Canada geese *Branta canadensis minima* gained more weight, fat and proteins than did males (Raveling 1979). Hirschenhauser et al. (1999) also found that within-pair testosterone level co-variation influences different reproductive traits, such as clutch and egg size: the higher the within-pair co-variation over the year, the larger the clutches and the heavier the eggs. In addition, avian thyroid hormones like triiodothyronine (T_3) are suggested to be involved in the regulation of metabolic rate, body temperature, and oxygen consumption (reviewed in McNabb 2000; see also Burger and Denver 2002, Jenni-Eiermann et al. 2002, Chastel et al. 2003, Duriez et al. 2004). Fluctuations in these hormone levels could therefore reflect variations in metabolic activity related to season or sex. Studies of variation in plasma levels of both testosterone and T_3 could thus contribute to the identification of proximate causes of seasonal and individual differences in body mass.

Seasonal and sex-related variations in measures of morphometry, and plasma hormone levels that directly or indirectly influence body measurements, could be used as indices of the resource-based environmental, climatic and/or social circumstances experienced by geese on wintering and spring staging areas. Until now, few studies have investigated plasma hormone levels and their potential consequences for body mass in non-breeding migratory geese (Hirschenhauser et al. 1999, 2000, Kotrschal et al. 2000). Here, we present results of a three-year study that quantified fluctuations in body measurements, plasma testosterone, and plasma T_3 in male and female dark-bellied brent geese from different age classes. Based on findings in former goose studies, we expected (1) an overall higher body mass in spring

than in winter, (2) higher plasma testosterone levels for adult males compared to females or juveniles, especially during the mate guarding period, and (3) a higher metabolic activity during the spring fattening period than during the wintering period for both sexes.

Methods

Birds and study site

We caught dark-bellied brent geese with a cannon-net (Bub 1991) in two important European brent goose staging sites. In January–March (2001–2004) 112 wintering birds in France on Ile d' Oléron, and in May (2003–2004) 126 spring staging birds on the Dutch island of Terschelling. The French wintering site hosts up to 6.5% of the entire world wintering population (Czajkowski and Schricke 1999), and Terschelling in the Dutch Wadden Sea (The Netherlands) is a preferred traditional staging area for this species hosting 5–10% the entire world wintering population in spring (Ebbinge 1992).

We measured, sexed, aged and ringed birds immediately after capture, and released them as soon as possible. Sex was determined using cloacal examination. We classified birds as either yearling (with pale bars on wing-coverts) or adult. Each bird was marked individually with coded Darvic coloured leg-rings identifiable from up to 250 m with a telescope.

Body measurements

To minimise observer biases, only one observer (MP) carried out the body measurements. She weighed birds with an electronic balance to the nearest gram, measured tarsus and culmen lengths to the nearest 0.01 mm using electronic callipers, and wing length to the nearest mm with a ruler. A body size index was calculated as the multiplication of the three size measures to give a volumetric estimate. After measurements, birds were kept in keeping cages before blood sampling (Bub 1991). In this way we tried to keep the time elapsing between catching and blood sampling as similar as possible for all individuals.

Blood sampling and radio immunoassays

In order to minimise inter-individual hormonal variations due to handling, all birds were bled as quickly as possible following the same standardized technique (Wingfield 1994): a blood sample (around 800 μ l) was collected from the brachial vein with a 1 ml heparinized syringe. Blood samples were stored in ice and centrifuged as soon as possible (within 3 hours). Plasma was

subsequently stored at -20°C . Plasma testosterone levels were determined at the CEBC laboratory by radioimmunoassay (for methods see Poisbleau et al. 2005). The lowest concentration detectable was 0.10 ng ml^{-1} . For each plasma sample, we performed three assays. Intra-assay coefficients of variation were 3.7%, 9.2% and 10.5% with 3 duplicates for each assay. The inter-assay coefficient of variation was 10.9% ($n=9$ duplicates). Total plasma T_3 was also determined at the CEBC (see method in Chastel et al. 2003). The lowest concentration detectable was 0.04 ng ml^{-1} . Intra-assay coefficients of variation were 1.6%, 2.3% and 11.0% with 3 duplicates for each assay. The inter-assay coefficient of variation was 9.4% ($n=3$ duplicates). Because of lack of plasma, T_3 levels were not determined for birds captured during winter 2003–2004.

Statistical analyses

At the within-season level for a given year, body measurements and hormonal levels did not fluctuate significantly with capture dates. We therefore combined measurements from the same season for a given year in statistical analyses. As the cannon-net procedure leads to long waiting times for individual birds (time elapsed between capture and blood sampling: 3.46 ± 2.02 hours), and considerable differences in waiting time before blood was taken across individuals, we included waiting time as a factor in all statistical analyses. We tested initial data for assumptions required for parametric statistical tests (Sokal and Rohlf 1995). Data violating assumptions were transformed, and examined again. Plasma testosterone levels values were not normally distributed even after \log_{10} or square-root transformations. Therefore, in order to assess the separate effects of several variables on plasma testosterone concentrations, we ranked the testosterone values and used the ranked values (Montgomery 2001) in parametric analyses. T_3 , morphological measurements and body mass indexes followed a normal distribution without transformation.

We tested the effects of season (winter vs. spring), year, waiting time, age (yearling vs. adult) and sex (male vs. female), and their interactions, on body measurements (size or mass) and hormonal levels (testosterone or T_3) using two-way ANCOVA. We initially tested a complete model with all biologically sensible interactions. Subsequently, higher order interactions were removed from the model one by one when statistically non-significant ($P > 0.05$). Parameter values for all statistical relationships were those estimated when parameters were removed from the model, if their relationships were not significant, or from the final model, i.e. with all variables being significant if their relationships were significant.

All statistical analyses were performed using SYSTAT 7.0 (release 9 for Windows; SPSS Inc., Chicago, USA, Wilkinson 1997). We presented values as means \pm SD.

Results

Body size

Adults were larger than juveniles ($R^2=0.508$, $F_{1,233}=51.095$, $P<0.001$), and males were larger than females ($F_{1,233}=85.547$, $P<0.001$). The age effect was more pronounced in males than in females ($F_{1,233}=6.390$, $P=0.012$ for the interaction sex \times age, Fig. 1a). Body size indices did not vary significantly with season ($R^2=0.514$, $F_{1,229}=0.196$, $P=0.658$, Fig. 1a), year ($R^2=0.513$, $F_{2,231}=1.189$, $P=0.306$), or waiting time ($R^2=0.513$, $F_{1,230}=0.182$, $P=0.670$).

Body mass

As expected, brent geese were heavier at the spring staging area than on the wintering grounds (1669 ± 175 g, $n=126$ vs. 1359 ± 145 g, $n=112$, $R^2=0.649$, $F_{1,234}=278.174$, $P<0.001$, Fig. 1b). Adults were heavier than yearlings (1563 ± 218 g, $n=188$ vs. 1373 ± 176 g, $n=50$, $F_{1,234}=47.819$, $P<0.001$), and males were heavier than females (1593 ± 218 g, $n=133$ vs. 1434 ± 198 g, $n=105$, $F_{1,234}=58.666$, $P<0.001$ Fig. 1b). However, body mass did not change significantly with year ($R^2=0.658$, $F_{2,231}=2.416$, $P=0.092$), or waiting time ($R^2=0.650$, $F_{1,233}=0.928$, $P=0.336$).

Plasma testosterone

Contrary to our expectations, adults did not have higher testosterone levels than juveniles ($0.372 \pm 0.241\text{ ng ml}^{-1}$, $n=188$ vs. $0.366 \pm 0.285\text{ ng ml}^{-1}$, $n=50$, $R^2=0.086$, $F_{1,232}=0.888$, $P=0.347$), and males did not have higher testosterone levels than females ($0.382 \pm 0.282\text{ ng ml}^{-1}$, $n=133$ vs. $0.358 \pm 0.203\text{ ng ml}^{-1}$, $n=105$, $R^2=0.087$, $F_{1,231}=0.188$, $P=0.665$, Fig. 1c). Plasma testosterone levels were somewhat higher in spring than in winter, but the seasonal effect was statistically not significant ($0.336 \pm 0.117\text{ ng ml}^{-1}$, $n=112$ vs. $0.402 \pm 0.323\text{ ng ml}^{-1}$, $n=126$, $R^2=0.082$, $F_{1,233}=3.294$, $P=0.071$, Fig. 1c). However, testosterone levels fluctuated significantly across years ($R^2=0.064$, $F_{2,235}=8.022$, $P<0.001$), with generally more testosterone during the period winter 2001–2002/spring 2002 (2001–2002 and 2003–2004: $R^2=0.089$, $F_{1,170}=16.593$, $P<0.001$, 2002–2003 and 2003–2004, $R^2=0.012$, $F_{1,107}=1.293$, $P=0.258$, 2001–2002 and 2002–2003, $R^2=0.033$, $F_{1,193}=6.623$, $P=0.011$). Waiting time did not significantly change testosterone levels ($R^2=0.069$, $F_{1,234}=$

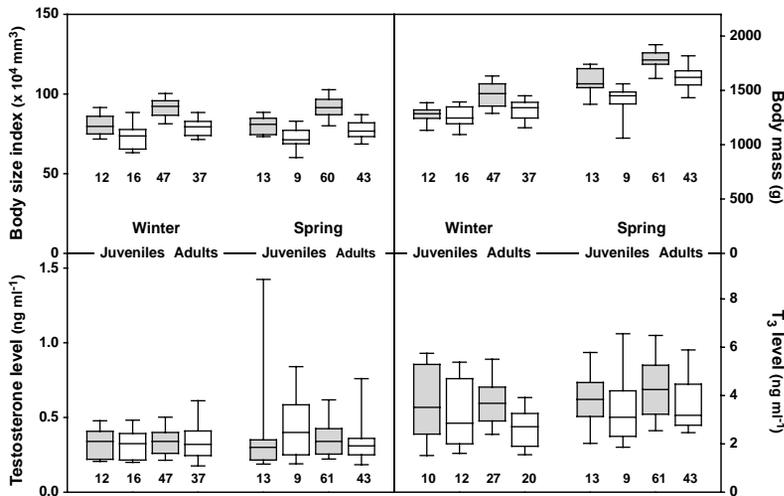


Fig. 1. Comparison of morphological and hormonal parameters between seasons, ages and sexes in dark-bellied brent geese. Grey boxes for males, white boxes for females. Means \pm SD. Sample sizes were given under respective box-plot. See text for statistics.

1.385, $P=0.240$). Also, the correlations between plasma testosterone levels and body measurements were statistically not significant (Body size: $R^2=0.076$, $F_{1,232}=0.835$, $P=0.362$; Body mass: $R^2=0.072$, $F_{1,234}=2.120$, $P=0.147$).

Plasma triiodothyronine (T_3)

As expected, brent geese had more plasma T_3 on the spring staging area than on the wintering grounds (4.089 ± 1.493 ng ml $^{-1}$, $n=126$ vs. 3.376 ± 1.344 ng ml $^{-1}$, $n=69$, $R^2=0.136$, $F_{1,191}=15.313$, $P<0.001$, Fig. 1d), and males had significantly higher T_3 levels than females (4.139 ± 1.467 ng ml $^{-1}$, $n=111$ vs. 3.436 ± 1.404 ng ml $^{-1}$, $n=84$, $F_{1,191}=11.099$, $P=0.001$, Fig. 1d). T_3 levels also showed between-year fluctuations, with significantly more T_3 during the winter 2001–2002/spring 2002 ($F_{1,191}=6.961$, $P=0.009$). However, waiting time ($R^2=0.144$, $F_{1,190}=1.795$, $P=0.182$), age ($R^2=0.148$, $F_{1,189}=0.840$, $P=0.361$), and body measurements (Body size: $R^2=0.139$, $F_{1,188}=0.043$, $P=0.836$; Body mass: $R^2=0.141$, $F_{1,190}=1.091$, $P=0.297$) did not significantly affect the observed T_3 levels.

Discussion

Dark-bellied brent geese are significantly heavier and expressed higher metabolic activity at the spring staging area than on the wintering grounds. The average seasonal increase in body mass and plasma T_3 levels was 23% and 21%, respectively. However, in contrast to our initial expectations, the factors season, sex, and age, did not significantly influence the plasma testosterone levels measured. This could be because of biological or methodological reasons.

According to the challenge hypothesis (Wingfield et al. 1987, 1990), social agonistic interactions should stimulate the production of high plasma testosterone levels, for instance when males establish social hierarchies, defend territories or guard mates. During these periods with intense social interactions, testosterone levels are also expected to vary with the individual dominance status, with dominant males expressing higher plasma testosterone levels than subordinates (Wingfield and Farner 1978, Wingfield 1984). The same hypothesis also predicts low testosterone levels, not correlated with social status, once territory boundaries and/or stable relationships have been established (Ramenofsky 1984, Wingfield 1984), probably to reduce the physiological costs of having a high testosterone level. Earlier goose studies, showed that plasma testosterone levels are maximal during the early mating and pre-laying stages, and decrease significantly during incubation (Hirschenhauser et al. 2000). However, we observed low average plasma testosterone levels in males and females, whatever the age, season and year. Hirschenhauser et al. (1999, 2000) reported similar results in semi-captive wintering greylag geese *Anser anser*. Our findings are thus inconsistent with the hypothesis that males maintain high plasma testosterone levels to protect the family or the female during spring fattening (Teunissen et al. 1985, Prop and Deerenberg 1991). Both the group composition and site-fidelity of dark-bellied brent geese in both the wintering and spring staging areas were relatively stable (authors' unpubl. data and, Spaans and Postma 2001). Stable social dominance relationships may probably be established and maintained through individual recognition and social inertia (Guhl 1968, Wiley et al. 1999). Perhaps the stable social relationships may have minimised aggressive interactions, and therefore may have reduced the fluctuations in plasma testosterone across seasons, also explaining why testosterone levels did not

vary significantly with sex, age, and year. The lack of significant relationships between plasma testosterone concentrations and body measurements observed in this brent goose study were also reported in other Anatidae (e.g. Poisbleau et al. 2005).

Although the seasonal effect on average plasma testosterone concentrations was statistically not significant, there was a tendency for an increase in testosterone levels between the winter and spring period ($P=0.071$), also the expression of higher inter-individual variations in testosterone levels later in the season. We therefore do not fully exclude the possibility that plasma testosterone levels may have increased somewhat in some individuals, perhaps those involved in social agonistic interactions at the spring staging areas. Also, hormones other than plasma testosterone may be involved in the expression of resource-based aggressive behaviour outside the breeding season. One potential candidate could be a precursor of testosterone, dehydroepiandrosterone (DHEA), which may be potentially involved in aggressiveness of non-breeding birds (Hau et al. 2004, Ferree et al. 2004). Definitely, additional investigations will be required to (1) increase the sampling efficiency either in free-ranging or captive populations, (2) quantify in more detail causal links between behaviour (agonistic interactions, foraging) and hormone levels, (3) experimentally manipulate social interactions or hormone levels, and (4) analyse endocrine or neuroendocrine measurements other than plasma testosterone or T_3 . These new investigations should contribute to a better understanding of the underlying proximate mechanisms responsible for seasonal fluctuations in body mass in brent geese, and, ultimately to determine the longer term consequences for processes at the population level.

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