

## Body measurements and hormonal within-pair covariation in wintering and spring staging Dark-bellied Brent Geese *Branta bernicla bernicla*

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For long-term monogamous species, it may be important to have demographic, morphological, physiological and/or behavioural compatibility within pairs. We used field data on wild populations of Dark-bellied Brent Geese, a species showing extreme mate fidelity, to test for (1) within-pair covariations of body measurements (body mass and size) and hormone levels (testosterone and  $T_3$ ) during winter and spring and (2) the impact of male seasonal hormone levels on the accumulation of body reserves by the female during the spring staging period. Here, we used testosterone as a proxy of aggressiveness and dominance and  $T_3$  as a proxy of male metabolism and activity. We observed a covariation of body mass within pairs, at least on the wintering grounds. Body sizes and plasma hormone levels of mates did not covary, neither in winter nor spring. We did not observe an association of female body mass with male hormonal levels.

Key words: hormones, assortative pairing, body size

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### Introduction

Some authors have argued that monogamous animals may pair assortatively to favour within-pair compatibility (Johnston & Johnson 1989), whereas others have shown that increased compatibility between mates arrives only after pairing as a 'mate familiarity effect' (see Black 1996). Pair member compatibility could exist through within-pair covariations for demographic (e.g. age, Potti

2000), morphological (Choudhury *et al.* 1996), physiological (Hirschenhauser *et al.* 1999) and/or behavioural (Spoon *et al.* 2006) traits. This within-pair covariation should be more important for species maintaining long-term pair relationships. For example, Black (2001) showed that Barnacle Geese *Branta leucopsis* maintaining long-lasting pair bonds during their lifetime produce more offspring than those with shorter pair duration.

Choudhury *et al.* (1992) suggested that, in this latter species, there was no assortative mating for body size and mass, but that members of a pair build up similar amounts of body reserves after pairing. Similarly, when two geese form a pair, they acquire the same social dominance rank (Lamprecht 1986b, Black & Owen 1989). Moreover, pairs of Greylag Geese *Anser anser* in which individuals show higher degrees of seasonal testosterone correlation have a better long-term reproductive output even if this high correlation is not the result of long-term monogamy (Hirschenhauser *et al.* 1999). In addition to gonadal steroids, avian thyroid hormones like triiodothyronine ( $T_3$ ) are suggested to be involved in the regulation of metabolic rate, body temperature, and oxygen consumption (McNabb 2000). Within-pair covariation in both these hormone levels could therefore reflect covariation in metabolic activity.

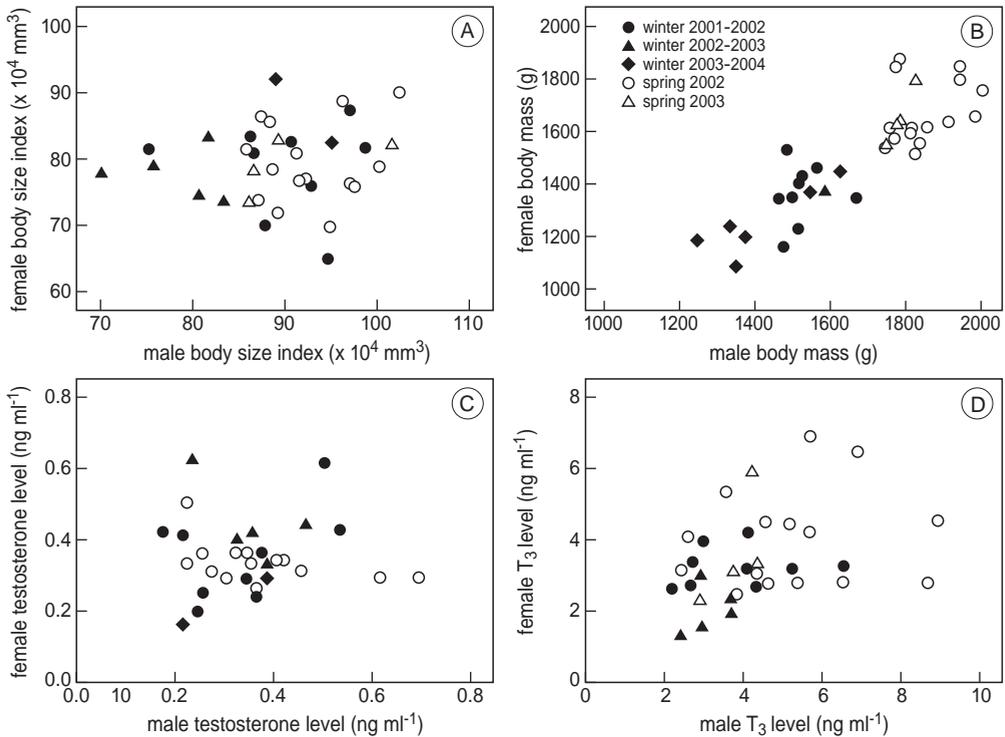
Wintering and spring staging are two important periods influencing reproductive success for Brent Geese *Branta bernicla* (see for example Ebbs & Spaans 1995, Poisbleau *et al.* in press): those birds that return to their wintering grounds in autumn with offspring were the heaviest adults during the previous winter and/or the heaviest females during spring. Brent Geese leave their wintering areas on the Atlantic coasts of Britain and France during March–early April, and travel to Russia. They breed mainly along the coasts of the Taimyr Peninsula where they arrive around the second week of June and leave between mid August and the first week of September (Ward 2004). Spring staging stops in the Wadden Sea (The Netherlands, Germany, and Denmark) and the White Sea (North-west Russia) are required to accumulate reserves in preparation for reproduction (Ebbs & Spaans 1995). During the winter, partners have nearly the same activities and are exposed to similar environments. During spring staging, by contrast, females feed a lot while a role of males is to protect the space around their mate. Therefore, we could expect that traits showing seasonal variation covary within pairs, and that females with more active and aggressive males have better body condition than others.

Here we use field data on wild populations of Dark-bellied Brent Geese to test (1) for within-pair covariations of body measurements (body mass and size) and hormone levels (testosterone and  $T_3$ ) during winter and spring and (2) for the impact of male seasonal hormone levels on the accumulation of body reserves by the female during the spring staging period. We use testosterone as a proxy of aggressiveness and dominance and  $T_3$  as a proxy of male metabolism and activity. Based on earlier goose studies, we expected (1) no within-pair covariation in body size but a within-pair covariation in body mass and hormonal levels, with higher within-pair covariations in winter than in spring, and (2) an increase of female mass with male hormonal levels in spring.

## Methods

We caught Brent Geese with a cannon-net at two important Brent Goose sites. We captured 112 geese in the wintering area of Oléron Island (France) during three consecutive winters (Fig. 1). In mid-May 2002 and 2003, we captured 126 geese during spring staging on the island of Terschelling, The Netherlands (detailed in Poisbleau *et al.* 2006). From each captured bird, we took biometric measurements (body mass, culmen, tarsus and wing lengths), determined the sex and age (juvenile versus adult). To minimise observer bias, one observer (Maud Poisbleau) carried out all measurements. Each bird was marked individually with coded Darvic coloured leg-rings that can be identified from up to 250 m with a telescope (see Poisbleau *et al.* in press).

We conducted visual observations to determine pair-bond composition up to seven days after the date of capture. In Anatids, the best criterion is sustained proximity to a member of the opposite sex (Guillemain *et al.* 2003). In contrast, unpaired birds do not tolerate the approach of other individuals. Because family members walk a similar pathway within the flock and coordinate vigilance bouts, aggressive encounters with neighbours, and social displays (Black 2001), we also used the coordination of activities as indicative of paired birds.



**Figure 1.** Comparison of morphological and hormonal measurements within pairs for (A) body size index, (B) body mass, (C) testosterone level, and (D)  $T_3$  level. We present the non-standardised values. Statistical tests were based on standardised data.

Poisbleau *et al.* (2006) described in detail all procedures for blood sampling and hormone analyses used. Because of lack of plasma,  $T_3$  levels were not determined for birds captured during winter 2003–2004.

We calculated a body size index as the multiplication of our three size-related parameters to give a volumetric estimate, following Piersma & Davidson (1991). We only analysed data from pairs known to exist immediately after ringing. Data fulfilled the requirements for parametric statistics (Sokal & Rohlf 1995). To exclude potential effects of season and year which might mask the existence of short-term within-pair covariations in phenotypic traits due to habitat selection or behavioural activities, we standardised the data following Choudhury *et al.* (1992). For each individual measure, we subtracted the year- and season-spe-

cific mean and then divided by the year- and season-specific standard deviation. We used Pearson correlations on the entire standardised data set to examine within-pair covariations for the phenotypic traits considered. Effects of male hormonal levels on female body mass were explored using regression analysis. We performed all statistical analyses with SYSTAT 7.0 (release 9 for Windows; SPSS Inc., Chicago, USA; Wilkinson 1997).

## Results

Standardised female body mass was significantly correlated with the standardised body mass of their mate when the data from different seasons were combined ( $r = 0.387$ ,  $n = 35$  pairs,  $P = 0.022$ , Fig. 1B presenting non-standardised values). When seasons were analysed separately, the relationship was statistically significant for the

winter period ( $r = 0.500$ ,  $n = 16$  pairs,  $P = 0.049$ , Fig. 1B), but not for the spring period ( $r = 0.388$ ,  $n = 19$  pairs,  $P = 0.101$ , Fig. 1B). We did not find statistically significant correlations for the standardised values of the other phenotypic traits considered in winter ( $n = 16$ ; Body size index  $r = -0.081$ ,  $P = 0.765$ ; Plasma testosterone  $r = 0.282$ ,  $P = 0.290$ ; Plasma  $T_3$   $r = 0.093$ ,  $P = 0.753$ ), in spring ( $n = 19$ ; Body size index  $r = 0.219$ ,  $P = 0.369$ ; Plasma testosterone  $r = 0.074$ ,  $P = 0.762$ ; Plasma  $T_3$   $r = 0.174$ ,  $P = 0.476$ ) or for both seasons combined ( $n = 35$ ; Body size index  $r = 0.051$ ,  $P = 0.772$ ; Plasma testosterone  $r = -0.024$ ,  $P = 0.892$ ; Plasma  $T_3$   $r = 0.137$ ,  $P = 0.446$ ). Non-standardised values are shown in Fig. 1A, C and D. In contrast to our initial prediction, no correlations were observed between female body mass in spring and plasma hormone levels of their mate (Plasma testosterone:  $t_{17} = -0.388$ ,  $P = 0.183$ ; Plasma  $T_3$ :  $t_{16} = -0.896$ ,  $P = 0.383$ ).

## Discussion

We observed no size-assortative pairing in Dark-bellied Brent Geese for almost all our phenotypic traits investigated. This is consistent with our first prediction and is in accordance with results obtained for Barnacle Geese (Choudhury *et al.* 1992). However, using standardised variables, we observed body mass to covary within pairs, at least on the wintering grounds. Although pairs stay together throughout the year, use the same wintering and spring staging areas and are exposed to similar environmental stresses (e.g. Choudhury *et al.* 1992, Sedinger & Flint 1995), this winter covariation was not conserved in spring. In wintering areas paired males and females have approximately the same activities, and feed at the same time at the same sites, even if male geese in general initiate significantly more frequent aggressive displays than females or juveniles (e.g. Lamprecht 1986a). During spring, however, covariation in body mass within pairs might not be maintained because males needed to be more aggressive to allow their mates to feed quietly and safely in order to increase body mass. This reasoning seems to be consistent with the studies of Teunissen *et al.*

(1985) and Lemmon *et al.* (1997) who showed that females paired with dominant males, when accompanied by their mate, experienced less frequent aggression and maintained a higher feeding rate than other subordinates in the presence of dominant flock members. However, male plasma testosterone and  $T_3$  levels were not related to the body mass of the female at spring staging areas.

Our hormonal observations validate neither our within-pair covariation hypothesis for testosterone and  $T_3$  levels, nor the hypothesis of the impact of male hormonal levels on female body mass. Hirschenhauser *et al.* (1999), using a different approach in which within-pair measures were taken repeatedly in many seasonal phases through the year, showed the importance of partners being 'coordinated'. However, the present study underlines that this covariation is not observable by comparing different pairs within seasons by only taking single male-female 'snapshots' in time. This suggests that it is necessary to quantify and integrate male dominance status or mate-guarding success in further studies interested in linking fluctuations in male hormonal level to female reserve accumulation within pairs.

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## SAMENVATTING

Tussen succesvolle partners moet het 'klikken', bijvoorbeeld doordat ze even oud zijn, even groot, of dezelfde gedragingen vertonen. In dit artikel wordt onderzocht of er sprake is van overeenkomsten tussen man en vrouw binnen paartjes Rotgans *Branta bernicla*. Ganzen kiezen elkaar voor het leven dus een goede match is belangrijk. Vogels werden gevangen in de winter (Frankrijk) en in het voorjaar (Nederland) om ze op te meten en bloed af te nemen voor hormoonbepalingen. De lichaamscondities van partners waren in de winter nauw gecorreleerd. Dat is begrijpelijk want man en vrouw trekken samen op. In het voorjaar verdwenen deze overeenkomst, wat verklaard werd uit de extra inspanningen van mannen om hun vrouw te beschermen. Er bleek geen verband te bestaan tussen de lichaamsmaten van de partners, dus de grootte van de man voorspelde niets over die van de partner. Evenmin bestond verband tussen de testosteronspiegels in het bloed (als maat voor agressie) van beide partners, of tussen gehalten van triiodothyronine ( $T_3$ , maat voor metabolisme en activiteit). Er werd een verband verwacht tussen de testosteronspiegel van het mannetje en het voorjaarsgewicht van hun partner maar dat bleek niet het geval. Dit negatieve resultaat werd herleid tot de gevolgde methodiek: in plaats van een eenmalige bepaling van hormoonspiegels per individu, zoals in deze studie, is het beter frequent door de tijd monsters te nemen. Bij vrijlevende dieren kan dat echter lastig zijn. (JP)

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