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Short report

# DHEA levels and social dominance relationships in wintering brent geese (*Branta bernicla bernicla*)

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ABSTRACT

After testosterone, dehydroepiandrosterone (DHEA) is the main hormone involved in aggressive behaviour in birds. While the role of DHEA has been verified for wintering territorial passerines, it has not been shown for gregarious species. In wintering geese species, both sexes present very low testosterone levels and aggression in a non-sexual context is not testosterone-related. Therefore, testosterone does not seem to be responsible for aggressive behaviour by geese during winter and the role of DHEA must be explored. We used brent geese (*Branta bernicla bernicla*) to examine the roles of testosterone and DHEA in dominance relationships. For the first time, we highlighted the presence of plasma DHEA in free-living geese. As the level of DHEA was lower than that of testosterone, and there was no obvious impact of DHEA level on dominance status, our results failed to confirm the role of plasma DHEA in the social hierarchies of this species during winter. Nevertheless, because DHEA levels were greater in singletons than in paired birds, we discuss the need to explore hormonal and/or behavioural mechanisms implicated within dominance status acquisition and maintenance within each reproductive status class, to underline the role of the presence of relatives as a signal of dominance abilities. We also acknowledge and discuss the possibility that the long handling time may have affected DHEA levels and masked subtle differences between individuals.

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## 1. Introduction

Most studies have demonstrated that testosterone is the main hormone involved in aggressive behaviour during both breeding and non-breeding periods, animals with higher testosterone levels being more aggressive (see for example Wingfield and Ramenofsky, 1985; Smith et al., 2005). Nevertheless, recent studies in some bird species, on territorial aggression during the non-breeding season, have shown that there may be exceptions to this rule (Wingfield, 1994; Soma and Wingfield, 1999; Wingfield et al., 2001b) and that another hormone, dehydroepiandrosterone (DHEA), could be involved in aggressive behaviour during the non-breeding season (Soma and Wingfield, 1999, 2001; Soma et al., 2000; Hau et al., 2004). This precursor of testosterone is mainly produced by suprarenal glands and subsequently converted into testosterone in the brain, where it is active (Labrie et al., 1995; Soma and Wingfield, 1999, 2001). This alternative mechanism could avoid most of the costs associated with a continuously high testosterone level (body mass loss, alteration of immune functions, survival costs, altered parental behaviour; Dufty, 1989; Ketterson and Nolan, 1992; Duffy et al., 2000).

These arguments were initially developed to explain the low testosterone levels found in wintering song sparrows (*Melospiza melodia morphna*) despite extreme territorial aggression during this period (Soma and Wingfield, 1999; Soma et al., 2000), but could be applied to social dominance relationships within wintering groups because most of the implicated behaviours are the same (Soma and Wingfield, 1999). Male and female song sparrows and spotted antbirds (*Hylophylax n. naevioides*) have several times more DHEA than testosterone during the non-breeding season and these DHEA levels are positively correlated to aggressive behaviour (Soma and Wingfield, 2001; Soma et al., 2002; Hau et al., 2004). The presence of DHEA and its role in aggressive behaviour has thus been verified for some wintering territorial passerines but, to our knowledge, its presence (but not its role in aggressive behaviour) has only been validated for one gregarious species (domestic goose; *Anser anser*; Thi Dong Xuan et al., 2005).

In goose species, (1) both sexes present very low testosterone levels during the wintering period (Akesson and Raveling, 1981; Dittami and Reyer, 1984; Hirschenhauser et al., 1999; Poisbleau et al., 2006a,b), (2) aggression in a non-sexual context does not have to be testosterone-related (Wingfield et al., 1990; Frigerio et

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al., 2004; Poisbleau et al., 2006c), and (3) plasma levels of DHEA show peaks at the onset of autumn and spring in both sexes (Thi Dong Xuan et al., 2005). These observations suggest that testosterone is not responsible for aggressive behaviour by geese during winter (Poisbleau et al., 2006c) and that DHEA provides a plausible alternative.

Our own previous investigations in wintering dark-bellied brent geese (*Branta bernicla bernicla*) have shown that families with offspring were dominant over pairs, pairs were dominant over singletons and males were dominant over females. These relationships were independent of individual testosterone levels, these birds having low plasma testosterone levels (<0.8 ng/ml) with little inter-individual variation (Poisbleau et al., 2006b,c). This result underlined the need to explore the DHEA hypothesis for this species. Therefore, in the present study, we first tested for potential confounding effects (handling time, age, sex, body condition and reproductive status) on testosterone and DHEA levels. We then examined the role of each hormone in social dominance relationships, taking account of the effect of other important parameters such as age, sex, body condition and reproductive status. If the DHEA hypothesis was to be verified in winter social dominance relationships of this gregarious species, as has been done for the territorial behaviour of passerines, we expected to find (1) a higher plasma level of DHEA than of testosterone and (2) a positive correlation between the dominance status of birds and their DHEA level.

## 2. Materials and methods

### 2.1. Birds and study site

On the 22nd and 24th of January 2002, we captured respectively 16 and 43 dark-bellied brent geese in their wintering area on Oléron Island (45°56′N, 1°21′W, France) using a cannon net (Bub, 1991). Geese were captured at a watering place where they came in small flocks. Care was taken to avoid injuring the geese.

We determined sex by cloacal examination and distinguished juveniles (first-year) from birds in adult plumage (second-year and older) by the white edges of wing coverts, producing a "chevron" (Lambeck, 1990a). We marked each bird individually with coded Darvic coloured leg-rings that could be identified from a distance of up to 250 m with a 20 × 60 telescope. This resulted in about 2% of birds in the wintering population being individually marked. Darvic rings are those used for the past 14 years in the European Brent network, and no significant negative effect has been reported.

### 2.2. Morphometric measurements and body condition

We weighed birds to the nearest gram using a spring balance and measured tarsus and culmen lengths to the nearest 0.01 mm using an electronic calliper. Wing length was measured to the nearest millimetre with a ruler. One observer (M.P.) carried out all measurements to minimise observer bias.

We used the ratio of body mass (g) to (wing + culmen + tarsus lengths) (mm) as an index of body condition (Poisbleau et al., 2005a,b). High values represent individuals who were relatively heavy for their body size and low values represent those who were especially lean for their size. After measurement, birds were kept in individual holding boxes before blood sampling (Bub, 1991). As the cannon-net procedure leads to long and variable handling times (time elapsed between capture and blood sampling: 2:18 ± 1:25 h), we tested the effect of handling time on hormone levels.

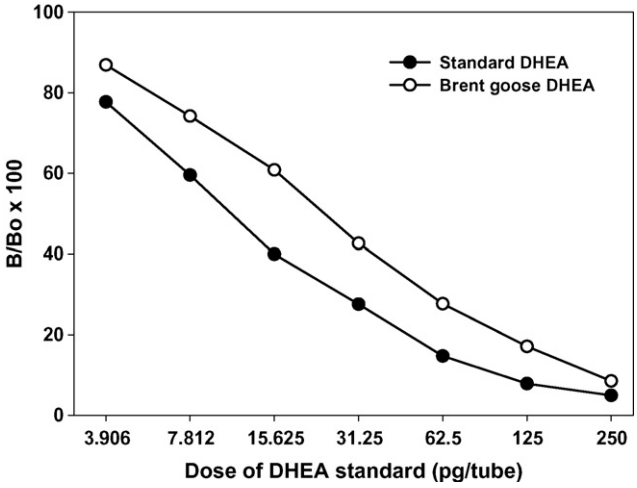


**Fig. 1.** Dilution curve for standard and brent goose DHEA.

### 2.3. Blood sampling and radio immunoassays

All birds were bled using a 1 ml heparinized syringe with a 25 gauge needle and around 800 μl of blood was collected from the brachial vein. Blood samples were put onto ice and centrifuged within one hour. Plasma was subsequently stored at −20 °C. Blood sampling had no adverse effect in the short term (immediate flying after release) or in the long term (no behavioural difference from non-handled birds during the following weeks).

Plasma testosterone levels were determined at the Centre d'Etudes Biologiques de Chizé (CEBC) by radioimmunoassay using a specific antibody for testosterone according to the procedure previously described by Chastel et al. (2003). Only one assay was performed and the intra-assay coefficient of variation was 6.5% ($n = 3$ duplicates). The lowest concentration detectable was 0.10 ng/ml (lowest measurement: 0.20 ng/ml).

DHEA levels were measured by radioimmunoassays at the CEBC of 50 μl plasma samples. After diethyl-ether extraction, duplicate aliquots of 140 μl (46.6% of the whole extraction volume) were incubated overnight at 4 °C with 2500 cpm of tritiated DHEA (PerkinElmer Life Sci., Courtaboeuf, France) and a commercial antiserum (raised in rabbits against $^{15}$alpha$CH_2$CO-BSA-DHEA, P.A.R.I.S., Compiègne, France). Bound and free DHEA were separated by adding cold dextran-coated charcoal. After centrifugation, the bound fraction was counted in a liquid scintillation counter (Packard). The extraction efficiency, tested by adding tritiated DHEA (ca. 500 cpm) to 12 plasma samples, was above 90%. The cross-reactivity of the antiserum, expressed as the concentration necessary to inhibit the binding of the antibody to tritiated DHEA by 50%, was less than 0.1% with various other steroids (testosterone, dihydrotestosterone and androstenedione). The reliability of the radioimmunoassay procedure of DHEA, tested by adding 3 aliquots of goose plasma mixed with 7.81, 15.625 and 31.25 pg of standard DHEA and assayed for hormone recovery, was from 86 to 112%. Furthermore, to validate the use of this assay for brent geese, plasma from this species was mixed with 350 pg of DHEA and serially diluted before assaying for a parallelism test with the standard curve. Pooled plasma of brent geese produced a dose–response curve that paralleled the DHEA standard curve (Fig. 1). All samples were run in a single assay and the coefficient of intra-assay variation was 13.1% ($n = 6$ duplicates). Minimal detectable DHEA levels were 0.04 ng/ml.

### 2.4. Behavioural observations

From capture until the departure of the geese in spring, we determined the dominance hierarchy of the flock by observing interactions according to the procedure previously described by Poisbleau et al. (2006c). An individual dominance score was defined as the percentage of interactions won by a focal bird divided by the total number of interactions in which this bird participated, whatever its opponent. We recorded enough interactions to calculate individual dominance scores for 23 different ringed brent geese (see figures for the sample size within each category of sex, age and reproductive status). Each of the following analyses included all these 23 birds.

Because parents and their offspring normally stay together until spring (Lambeck, 1990b), we determined reproductive status (singletons, paired birds without offspring, paired birds with offspring) using behavioural observations. Family members coordinate their behaviour and stay in proximity. For example, the family moves as a unit, and conspecifics that come too close are pecked at or chased away (Gregoire and Ankney, 1990).

### 2.5. Statistical analysis

As we found no difference in morphological or hormonal parameters between the two dates of capture (Mann–Whitney *U*-test, all $P > 0.05$), we combined all data for subsequent analyses. All measured parameters followed a normal distribution without transformation, and dominance scores expressed as percentages were arcsine-transformed, allowing parametric testing (Sokal and Rohlf, 1995).

To explore dominance score correlates, we used analyses of covariance on arcsine-transformed dominance scores in adult birds. We first tested for confounding effects of handling time, sex, age, reproductive status and body condition on testosterone and DHEA levels. Sex, age, reproductive status, body condition, testosterone and DHEA levels were afterwards considered as factors and covariates to explain the variation in dominance score.

All statistical analyses were performed using SAS software (SAS Institute, 1997). Values are presented as means ± standard error.

## 3. Results

### 3.1. Confounding effects on testosterone levels

None of the two-way interactions was significant (all $P > 0.05$). In the analysis of covariance, testosterone levels were not significantly related to handling time ($F_{1,17} = 0.636$, $P = 0.436$). Moreover, testosterone levels were not influenced by age ($n = 6$, $0.337 \pm 0.046$ ng/ml for juveniles and $n = 17$, $0.338 \pm 0.022$ ng/ml for adults, $F_{1,16} = 0.250$, $P = 0.624$), sex ($n = 15$, $0.360 \pm 0.025$ ng/ml for males and $n = 8$, $0.296 \pm 0.028$ ng/ml for females, $F_{1,21} = 2.474$, $P = 0.131$) or body condition ($F_{1,18} = 1.103$, $P = 0.352$). Finally, reproductive status had no impact on plasma testosterone level ($F_{2,19} = 1.103$, $P = 0.352$; singletons versus paired birds: $F_{1,16} = 0.151$, $P = 0.703$ and without against with offspring: $F_{1,21} = 0.834$, $P = 0.371$, Fig. 2).

### 3.2. Confounding effects on DHEA levels

None of the two-way interactions was significant (all $P > 0.05$). In the analysis of covariance, DHEA levels were not significantly related to handling time ($F_{1,20} = 1.554$, $P = 0.227$). Moreover, DHEA levels were not influenced by age ($n = 6$, $0.148 \pm 0.020$ ng/ml for juveniles and $n = 17$, $0.121 \pm 0.006$ ng/ml for adults, $F_{1,17} = 0.345$, $P = 0.565$), sex ($n = 15$, $0.136 \pm 0.009$ ng/ml for males and $n = 8$, $0.114 \pm 0.012$ ng/ml for females, $F_{1,19} = 3.189$, $P = 0.090$) or body condition ($F_{1,16} = 0.366$, $P = 0.554$). Finally, although reproductive status did not have a significant overall impact on individual plasma DHEA level ($F_{2,18} = 2.041$, $P = 0.159$ and birds without against birds with offspring $F_{1,18} = 0.603$, $P = 0.447$), singletons had higher plasma DHEA levels than paired birds ($F_{1,21} = 5.553$, $P = 0.028$, Fig. 2).

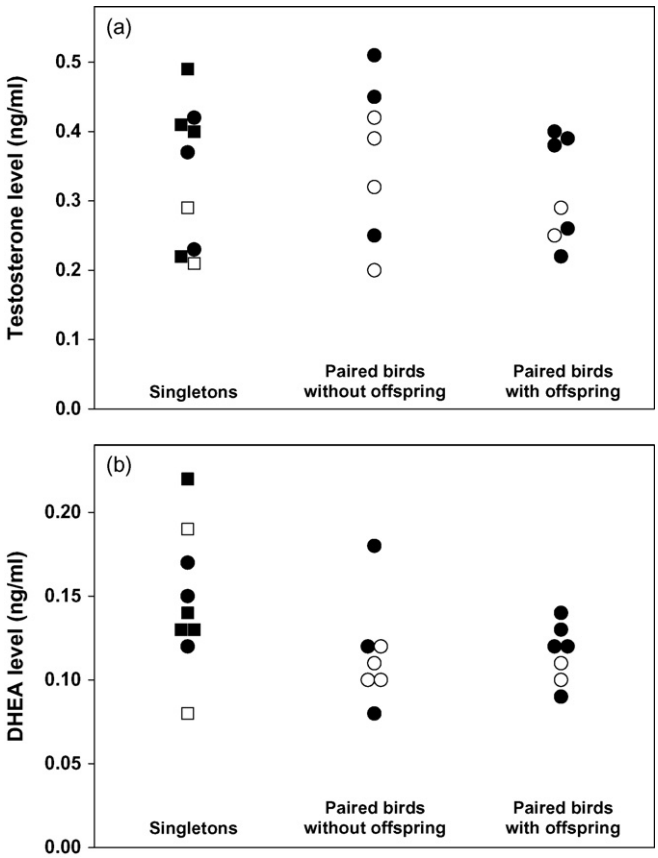


**Fig. 2.** Differences in plasma (a) testosterone and (b) DHEA levels (ng/ml) according to reproductive status, age and sex in dark-bellied brent geese. Closed symbols: males ($n = 15$); open symbols: females ($n = 8$); circles: adult birds ($n = 17$); squares: juvenile birds ($n = 6$). See text for statistics.

Individual testosterone and DHEA levels were not correlated (Pearson correlation: $R = 0.174$, $P = 0.427$).

### 3.3. Dominance score correlates

Age, body condition and testosterone level were not significantly related to dominance score (Table 1). Males were dominant over females, paired birds with offspring were dominant over paired

**Table 1**
Dominance score correlates of dark-bellied brent geese

| Effect | Num DF | Den DF | *F* value | *P* |
|---|---|---|---|---|
| Sex | 1 | 15 | 14.195 | **0.002** |
| Age | 1 | 15 | 3.027 | 0.102 |
| Reproductive status | 2 | 15 | 21.793 | **<0.001** |
| Body condition index | 1 | 15 | 0.027 | 0.872 |
| Testosterone level | 1 | 15 | 2.185 | 0.160 |
| DHEA level | 1 | 15 | 5.654 | **0.031** |

Results of the ANCOVA on arcsine-transformed dominance scores with sex, age and reproductive status as factors and body condition index, testosterone level and DHEA level as covariates ($n = 23$, $R^2 = 0.887$). All interactions were non-significant and therefore removed from the model during the backwards stepwise procedure. Bold font corresponds to significant effects ($P < 0.05$).

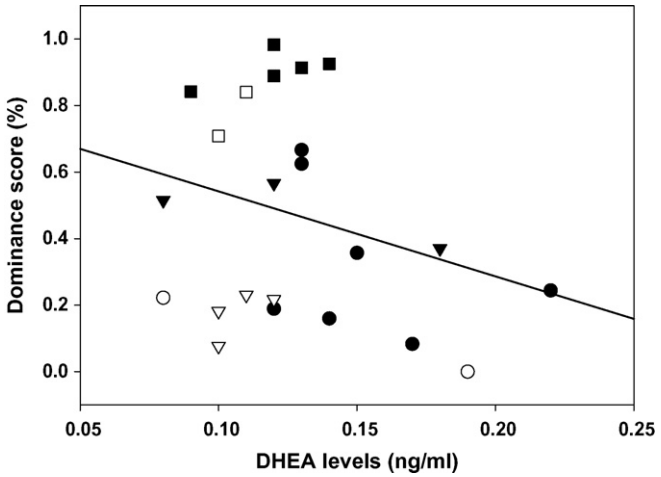


**Fig. 3.** The relationship between the dominance score (percentage) and DHEA level (ng/ml). Closed symbols: males ($n = 15$); open symbols: females ($n = 8$); circles: singleton birds ($n = 9$ including the 6 juveniles); triangles: paired birds without offspring ($n = 7$) and squares: paired birds with offspring ($n = 7$).

birds without offspring, and paired birds without offspring were dominant over singletons (Table 1 and Fig. 3). Moreover, in this model, individual DHEA levels were significantly negatively correlated to dominance scores, dominant geese having lower DHEA levels (Table 1 and Fig. 3).

## 4. Discussion

### 4.1. Plasma levels of DHEA

Brent geese had detectable testosterone and DHEA levels during winter. According to our knowledge, this is the first evidence of the presence of plasma DHEA in a free-living goose. Nevertheless, these winter plasma DHEA levels were extremely low: at less than 0.25 ng/ml, they were on average 2.6 times lower than simultaneous plasma testosterone levels and much lower than previous results obtained in studies of spotted antbirds (0.5 ng/ml, up to 1.5 ng/ml in some individuals; Hau et al., 2004) and song sparrows (0.8 ng/ml, up to 3 ng/ml; Soma and Wingfield, 2001; Soma et al., 2002) in which testosterone was, by contrast, undetectable (<0.1 ng/ml). In this study, it therefore appears difficult to consider the DHEA pool as a supply of testosterone precursor, as was concluded for nazca booby (*Sula granti*) chicks (Ferree et al., 2004).

Plasma testosterone levels were not different according to the age, sex, body condition or reproductive status of birds. These results are similar to our previous findings (Poisbleau et al., 2006b). Plasma DHEA levels were not different according to age, sex or body condition. As DHEA is of adrenal origin, the long handling times before blood sampling may have activated the hypothalamic–pituitary–adrenal (HPA) axis to release corticosterone and, as a by-product, to enhance DHEA levels (Sapolsky, 1992; Wingfield and Farner, 1993; Wingfield, 1997). This non-specific activation may have masked potential finer-grained differences between individuals. The HPA axis being generally activated within a few minutes, the lack of a relationship between handling time and DHEA level does not exclude this hypothesis although the generally low DHEA levels argue against it. A solution to investigate this issue would be to bleed some birds within minutes of their capture and to use them as a control. However, in this study we captured brent geese on the shore while the tide was coming in. We did not bleed any birds early, since the priority was to remove them all from the net before the water arrived.

Plasma DHEA levels were greater for singletons compared to paired birds with or without offspring. As plasma DHEA is metabolised to active steroids within the brain, this result may indicate a lower neural metabolism of circulating DHEA among singletons. This result may also be due to a difference in aggressiveness between geese of different reproductive status. Our study using the dominance score (a measure of the dominance status and not of aggressiveness) did not allow further exploration of this hypothesis, although singletons did not seem to be involved in more aggressive encounters (i.e. receive or initiate more attacks) than paired birds (personal observation). The hormonal and/or behavioural mechanisms implicated in the acquisition and maintenance of dominance status may be different according to the presence of a mate. We later discuss this idea in the light of other dominance correlates.

### 4.2. Plasma levels of DHEA and social dominance relationships

Our results confirmed that reproductive status and sex are the most important factors determining the social dominance status of wintering brent geese (Poisbleau et al., 2006c): families socially dominated both pairs and singletons, pairs without offspring dominated singletons and males dominated females. We found no difference in dominance scores between juveniles and adults, probably because juveniles indirectly took advantage of the dominance status of their parents (Siriwardena and Black, 1999). As predicted, testosterone levels were not correlated to dominance scores. However, contrary to our initial prediction and consistent with the fact that singletons had higher DHEA levels and were more dominated than paired birds, plasma DHEA levels were negatively correlated to dominance score, dominant birds having less DHEA. This result may indicate a greater neural metabolism of circulating DHEA in dominant geese but did not suggest a direct influence of plasma DHEA level on dominance status. Alternatively, we could propose that subordinate geese had higher DHEA levels because their HPA axis was more reactive to the stress caused by long handling times.

As wintering brent geese form large flocks with a rotating membership, it is difficult to imagine a social inertia (Guhl, 1968) maintained only by individual recognition (Wiley et al., 1999) after a period of social instability as predicted by the "challenge hypothesis" (Wingfield et al., 1990). In these conditions, Poisbleau et al. (2006c) proposed that, in brent goose populations, the reproductive status of an individual could be an honest signal of its dominance abilities ("status-signalling hypothesis"; Rohwer, 1975). This signal may help to determine individual social dominance status with a minimum of contests. Costly hormones and associated costly behaviours (Wingfield et al., 2001a) generally implicated in the maintenance of social status may not be required between two birds with different reproductive status. In this context, the greater need of singletons than of other individuals to compete aggressively for dominance status could explain why singletons (subordinates) had more plasma DHEA than paired birds (dominants) and/or a more reactive HPA axis. This could also explain the lack of general trends between testosterone and/or DHEA levels and dominance scores.

In conclusion, as (1) DHEA level was not higher than testosterone level in wintering brent geese and (2) there was no obvious impact of DHEA level on the dominance status of these birds, our present results failed to confirm the direct role of plasma DHEA in social dominance within this species during winter. Nevertheless, more work will be necessary to verify our findings within different classes of reproductive status and sex, these being the most important determinants of dominance relationships for wintering brent geese.

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