

Testosterone and Linear Social Dominance Status in Captive Male Dabbling Ducks in Winter

Maud Poisbleau*, Hervé Fritz*, Matthieu Guillemain† & André Lacroix*

**Centre d'Etudes Biologiques de Chizé, CNRS UPR, Beauvoir-sur-Niort, France;*

†*Office National de la Chasse et de la Faune Sauvage, CNERA Avifaune
Migratrice, La Tour du Valat, Le Sambuc, Arles, France*

Abstract

Dominance hierarchies play an important role in avoidance and/or solving conflicts in gregarious species. In dabbling ducks (*Anas* species), dominance allows for feeding-site monopolization in winter quarters where resources are generally limited. In addition, male social rank should theoretically favour access to mates. Dominance rank can be associated with morphological traits, and is often correlated with aggressiveness, a behavioural trait generally related to high testosterone levels. In this study, we investigated the existence of a winter group structure based on dominance relationships and tested for a linear hierarchy, in three species of captive male dabbling ducks (mallard *Anas platyrhynchos*, pintail *A. acuta* and wigeon *A. penelope*). We then analysed the relationship between dominance ranks, morphological parameters and testosterone levels measured in early (Oct.) and mid-winter (Dec./Jan.). We found that the three male groups of the three species exhibited a linear hierarchy. Testosterone levels differed during winter and between species. Morphologic measurements, body mass and body condition were not correlated with individual dominance ranks, whereas dominant males had higher testosterone levels than subordinates. The slopes of the relationships were similar between species and winter period, but the y-intercepts differed between species and between early and mid-winter phases. The linear hierarchy found in the three species indicates that dominance relationships strongly structure dabbling duck groups in winter. Lack of correlation between rank and morphological characters, but correlation of rank with testosterone levels suggests that social rank is more dependent on behavioural traits such as aggressive behaviour. The differences between species and winter periods are discussed in relation to migration and wintering phenology.

Correspondence: Hervé Fritz, Centre d'Etudes Biologiques de Chizé, CNRS UPR 1934, 79360 Beauvoir-sur-Niort, France. E-mail: fritzh@cebc.cnrs.fr

Introduction

Many migratory bird species spend the winter in groups. There are several advantages of group living and of gregarious behaviours in general, mainly because of a reduction of individual vigilance time without an increase in predation risk (e.g. Powell 1974; Bertram 1980; Lima 1995; Roberts 1996). There may even be a decrease in the predation probability because of dilution and confusion effects (e.g. Hamilton 1971; Pulliam & Caraco 1984; Cresswell 1994). However, living in groups also involves costs, such as competition for resources, both in terms of accelerated food depletion (Goss-Custard 1980; Sutherland & Allport 1994) and interference (Appleby 1980; Goss-Custard 1980; Ens & Goss-Custard 1984; Triplet et al. 1999). For most migratory birds, wintering time is a crucial period both to restore fat reserves used during the post-breeding migration and to accumulate fat for the pre-breeding migration and the breeding period (Ebbinge & Spaans 1995; Tamisier et al. 1995). Consequently, minimizing the costs of competition and acquisition of sufficient energetic reserves is of paramount importance to each individual (Pravosudov & Lucas 2000).

Social organization may limit the costs of interactions with conspecifics, through the reduction of aggressive interactions (Rowell 1974; Bernstein 1981; Archer 1988). Indeed, building of a dominance hierarchy decreases fighting in the group as individuals learn to evaluate their chances in conflicts. Therefore, stable dominance–subordination relationships may not only benefit both dominants and subordinates by diminishing the incidence of serious wounds but also by reducing the time devoted to social interactions, thus increasing the time allocated to foraging (Belthoff et al. 1994; Guillemain et al. 2000; MacDonald et al. 2002).

In the Palearctic, wintering dabbling ducks (*Anas* species) gather in large groups during daylight hours, resting, preening and sometimes feeding, and spread in smaller groups at night mainly to feed. Winter quarters are often characterized by non-renewable food supplies and are hence subject to quick depletion. The competition for resources is potentially high (Zwarts 1976; Guillemain & Fritz 2002), in particular, when low temperatures increase energy demands (Frigerio et al. 2004). Consequently, the cost of wintering in groups could be moderated by the existence of a social organization. Few studies have been carried out on the subject, and they do not give consistent conclusions (Hepp 1989; Hoysak & Ankney 1996). Dominance seems to confer better access to food sources in several wildfowl species (Ingold 1991; Kotrschal et al. 1993; Stahl et al. 2001). For dabbling ducks, winter is also the period of pair formation (Heitmeyer 1988; Tamisier et al. 1995; Tamisier & Dehorter 1999). Because of the general male-biased sex ratio in wintering duck populations (Aldrich 1982; Hepp & Hair 1984), competition for mates becomes acute among males in winter, thereby promoting the formation of a social hierarchy. High rank in males improves access to females in several wildfowl species (Brodsky et al. 1988; Holmberg et al. 1989), although this is not always true (Sorenson & Derrickson 1994).

If social rank plays an important role in wintering dabbling ducks it should be associated with individual morphological and/or behavioural traits. Several

correlates of social dominance have been explored in birds (see Piper 1997 for a review). In waterfowl, age, sex, breeding status (paired or single) and body size all have been found to be related to dominance status (Hepp & Hair 1984; Lamprecht 1986; Black & Owen 1987; Hepp 1989). Dominance is often associated with more pronounced aggressive behaviours generally related to high levels of testosterone (Wingfield et al. 1987; Marler & Moore 1988). Consequently, testosterone levels are related to social rank in some species, including birds (Wingfield et al. 1987, 1990; Tremblay et al. 1998; Guillemain et al. 2000). However, although endocrine patterns linked with dominance and reproductive behaviour have been fairly well studied in geese (e.g. Kotrschal et al. 1998; Hirschenhauser et al. 1999, 2000), few studies have been carried out in dabbling ducks (but see Hoysak & Ankney 1996; Davis 2002a,b), particularly in winter.

In this study, we present the results of experiments carried out on captive male mallard *Anas platyrhynchos*, pintail *A. acuta* and wigeon *A. penelope*, for the existence of a linear hierarchy between adult male dabbling ducks and examine the hormonal and morphological correlates of dominance. The experiments were carried out in groups with slightly female-biased sex ratios, hence testing for dominance relationship in a context of potential competition for food and water resources, but not for mates.

While controlling for potential confounding effects on individual testosterone levels such as time of day, order of capture, handling time and body condition, the following predictions were tested: (1) morphologically larger males are more likely to be dominant, (2) males in better body condition have a dominant status, and (3) dominant males are more aggressive, and have higher blood testosterone levels. We assessed dominance once in mid-winter, and postulated that it was stable since early winter because of social inertia (Wingfield & Ramenofsky 1985 in Archawaranon et al. 1991; Sorenson et al. 1997). We then discuss the biological significance of the relationships between testosterone level and social hierarchy in light of migration and mating phenology in the three species.

Methods

Birds and Observations

The experiments were carried out between September 2000 and February 2001 at the Centre d'Etudes Biologiques de Chizé (CEBC), in western France, using adult ducks descended from individuals caught in the wild. This programme was approved by the Ministry of the Environment and satisfied the requirements of the Animal Welfare regulations from the Ministry of Research and Higher Education. The birds were maintained at the CEBC for at least 3 yr before the experiments, and were therefore accustomed to their environment. During the day, mallards were free to move about in the field station's yard (approx. 1000 m²) with food and water provided ad libitum. Pintails and wigeons were kept in separate 110-m² enclosures (50 m² grass, 60 m² concrete) equipped with a

10-m² pool. At night, ducks were caged in three different 200 m² aviaries (100 m² grass, 100 m² concrete), one per species, equipped with a 25-m² pool. Food in aviaries (ad libitum) was composed of a mixture of crushed corn, wheat and commercial duck food.

Mallards were reared together for > 2 mo before the experiments, and 'knew' each other in the larger group (only 30 individuals) for 3 yr. For pintails and wigeons, they were together for 3 yr prior to the experiment. In this context, the hierarchy between individuals would have been well established, and if stable, well conserved. No pairs were identified prior to or during the experiment.

During the experiments, birds were kept apart from late Aug. in three separate 10 m × 10 m grass areas during the day and in 5 m × 10 m concrete aviaries during the night, all equipped with a 10-m² pool. We used all the available wigeon (seven adult males and eight adult females) and pintail (six adult males and 11 adult females); for mallard, we selected individuals randomly from a larger (i.e. 30 individuals) flock to obtain an even sex ratio (eight males and eight females). Food was provided ad libitum. Only the males, and their ranks, were considered in the analyses and experiments.

The birds were marked individually with plastic badges glued to their backs with non-toxic glue (3 cm × 6 cm, with black and white codes). The ducks were observed in the morning (45 min) and in the afternoon (45 min) for five consecutive days, from 18 to 22 December for mallards, 15 to 19 January for pintails and 29 January to 2 February for wigeons. During each 45-min session, the group of birds was placed in a 2 m × 4 m arena and videotaped using a digital video camera recorder (Sony Digital Handycam; Sony, Tokyo, Japan) positioned 2 m from the enclosure and 2 m from the ground level to facilitate reading of the badge codes. No observer was visible to the ducks after the camera was positioned. In the morning session, the camera field (2 m × 2 m) included a bowl of 400 g of wheat and a bowl with a surface of 700 cm² of water. In the afternoon, the bowl of water was replaced with a 1-m² pool of clear water and two cameras covered the complete area of the enclosure. All interactions, close to the resources or elsewhere in the enclosure were noted in the videotapes, in order to record all agonistic encounters. For each aggressive encounter, we determined the winner and the loser, and the type of interaction: threat, chase, fight and/or avoidance. The birds were deprived of food the night (10 h) before each day of observation to increase competition for resources so as to obtain a sufficient number of interactions during each observation session. This treatment engendered no injuries or abnormal body mass variations ($\bar{x} \pm \text{SD}$: +0.18 ± 0.018%).

Blood Sampling

Blood samples were first collected on 29 Sep. 2000 for mallards, 2 Oct. 2000 for pintails and 3 Oct. for wigeons (early winter). A second sample was collected in mid-winter on 14 and 15 Dec. 2000 for mallards, 11 and 12 Jan. for pintails, and 25 and 26 Jan. for wigeons, 3 d before the start of observation sessions for

each species. Birds were individually captured with a net, one after the other. Immediately after capture, we drew 600 μ l of blood from the brachial vein into a 1-ml heparinized syringe using a 25-gauge needle. We completed the entire capture and handling process as quickly as possible to minimize the effects of handling stress on circulating hormones. The handling time, i.e. time between capture and completed blood sampling, never exceeded 350 s ($\bar{x} \pm$ SD: 160 \pm 74). Collection of blood samples in all males was carried out within the same time of day (9:30 to 10:30 hours) to minimize the effect of diurnal fluctuations in testosterone levels (Balthazart 1976). Testosterone levels were not correlated with the time of day (regression analysis of testosterone level vs. time of day: early winter for mallards: $n = 8$, $r = 0.05$, $p = 0.915$; pintails: $n = 6$, $r = 0.14$, $p = 0.768$; wigeons: $n = 7$, $r = 0.09$, $p = 0.855$; mid-winter for mallards: $n = 8$, $r = 0.10$, $p = 0.811$; pintails: $n = 6$, $r = 0.32$, $p = 0.554$; wigeons: $n = 7$, $r = 0.27$, $p = 0.565$), which suggests that our protocol was effective in minimizing these sources of variation. Samples were centrifuged (5 min at 1800 *g*) immediately after collection. The plasma was decanted and frozen at -20°C until radioimmunoassay analysis.

Radioimmunoassays

Plasma testosterone levels were determined at the CEBC laboratory by radioimmunoassay using a specific antibody for testosterone (Lormée et al. 2000). Testosterone antiserum was provided by Dr Gérard Picaper (Medecine nucléaire, CHU la Source, Orléans, France). Testosterone was extracted from a 50- μ l plasma sample with diethyl-ether with a recovery rate $> 95\%$. The extracts were re-dissolved in 0.01 M phosphate-buffered saline (pH 7.4) containing 0.1% phosphate-buffered saline-bovine serum albumin (PBS-BSA) and incubated overnight at 4°C with approx. 9000 cpm (counts per minute [= DPM (disintegrations per minute) \times efficiency of the spectrometer (env. 85%) of the appropriate ^3H -testosterone (F-91898 ORSAY; Amersham Pharmacia Biotech, Orsay, France) and antiserum. The bound testosterone fraction was separated by addition of dextran-coated charcoal and counted in a Packard scintillation spectrometer (Packard Instruments Co., Meriden, CT 06450, USA). 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. Two of the seven wigeon samples from early winter fell below the detectable limit of the assay and were assigned the lowest detectable value for testosterone (0.10 ng/ml).

Morphometric Measurements

Both in early and mid-winter, the ducks were weighed to the nearest gram after blood collection. In mid-winter, tarsus and bill lengths were measured to the nearest 0.01 mm using an electronic calliper. Wing length was measured to the nearest millimetre with a ruler. All measurements were made by the same observer (M. Poisbleau) to minimize observer biases.

Body mass to wing length, bill and tarsus ratios are commonly used to assess body conditions in birds (Chastel et al. 1995). However, as often happens in captive conditions, we found the ducks to wear out their wings more rapidly than in natural conditions, hence this parameter may not be representative of structural size. Bill and tarsus length did not change seasonally. To estimate body condition, a ratio of body mass (g) to (bill + tarsus length) (mm) was therefore calculated (Kitaysky et al. 1999). High values represented individuals that were relatively heavy for their respective body size and low values represented those individuals that were especially lean for their size.

Statistical Analysis

Interactions between birds were organized in sociometric matrices from which we calculated Kendall's coefficient of linearity (K), Landau's index and the index of linearity (h') (De Vries 1995), using MatMan 1.0 (MatMan, 1998; De Vries et al. 1993). Each index varies from 0 (absence of linearity) to 1 (complete linearity). h' is based on h and takes into account the existence of unknown relationships, when two members of a dyad were not observed to perform any agonistic interaction. Statistical significance of K is provided by a chi-square test. For the h' index, a sampling process using 10 000 randomizations is performed (De Vries 1995). When the dominance hierarchy was significantly linear, individuals were reordered by a two-step iterative procedure (10 000 sequential trials), finding the rank order most consistent with a linear hierarchy by minimizing the number of inconsistencies and then minimizing the total strength of the inconsistencies (De Vries 1998). The birds were ranked from 1 (most dominant) to 6, 7 or 8 (most subordinate).

In the statistical analysis, initial data were tested for assumptions required by a parametric statistical test, and testosterone levels were log₁₀-transformed (Sokal & Rohlf 1981). In addition to time of day, other parameters can affect individual testosterone levels: order of capture, handling time and body condition indexes. We first tested for these effects before constructing the statistical models testing for dominance correlates. For that, factors (periods of winter, species and order of capture) and covariates (handling time and body condition) affecting testosterone levels were examined with an ANCOVA. First, we tested a complete model with all biologically sensible interactions. Higher order interactions were then removed one by one from the model when non-significant ($p > 0.05$). The parameters values for all statistical relationships were those estimated from the final model, i.e. with all variables being significant. As body condition was calculated from body mass and body size, they could not be included in the same statistical model. Thus, secondly, we built two models: one considering body mass and body size parameters (tarsus and bill lengths), and one considering body condition, to test for their possible effects on dominance rank. Winter periods, species and log-transformed testosterone levels were also included in the model. All statistical analyses were performed using SYSTAT 7.0 (release 9 for Windows; SPSS Inc., Chicago, IL, USA; Wilkinson 1997). Values are presented as mean \pm SE.

Results

Determination of Dominance Status

Mallards

The analysis of the males' sociometric matrix comprised 455 interactions and revealed a clear linear hierarchy (Kendall's linearity index $K = 0.9375$, $\chi^2 = 47.5$, $df = 21$, $p < 0.001$). The values of Landau's index and the corrected index were particularly high ($h = 0.94$, $h' = 0.95$, improved linearity test using h' , $p < 0.001$) and clearly indicated that male ranking was linear. The matrix contained 1.25 circular triads, or 6.25% of the maximum possible number of circular triads (Fig. 1a).

Pintails

The matrix of males comprised 88 interactions and clearly revealed a significant linear hierarchy ($K = 0.906$, $\chi^2 = 49$, $df = 30$, $p < 0.05$; $h = 0.91$, $h' = 0.97$, improved linearity test using h' , $p < 0.05$). The matrix contained 0.75 circular triads, or 9.375% of the maximum possible number of circular triads, and still indicated linearity (Fig. 1b).

Wigeons

The matrix of males comprised 303 interactions and showed a significant linear hierarchy ($K = 0.714$, $\chi^2 = 37.3$, $df = 23$, $p < 0.05$; $h = 0.714$). As there were no unknown interactions, we did not calculate any h' . This matrix contained four circular triads, or 28.571% of the maximum possible number of circular triads and two effective circular triads (e.g. $A > B$, $B > C$ but $C > A$, under the diagonal in the matrix) (Fig. 1c).

Confounding Effects on Testosterone Levels

Order of capture, handling time and body condition indexes did not have a significant effect on testosterone levels (Table 1). Conversely, testosterone levels differed between winter periods, with birds having higher testosterone concentration in mid-winter than in early winter (Table 1, Fig. 2). In addition, there was a species effect on testosterone levels, with values in pintail being systematically lower than those of wigeon and mallard (Table 1, Fig. 2). Both species and winter periods were therefore included in the analysis of dominance correlates, as potential confounding factors for testosterone levels in the analysis.

Dominance Correlates

Body size parameters, body mass and body condition were not significantly related to rank (Table 2a,b). Conversely, testosterone levels (\log_{10} -transformed)

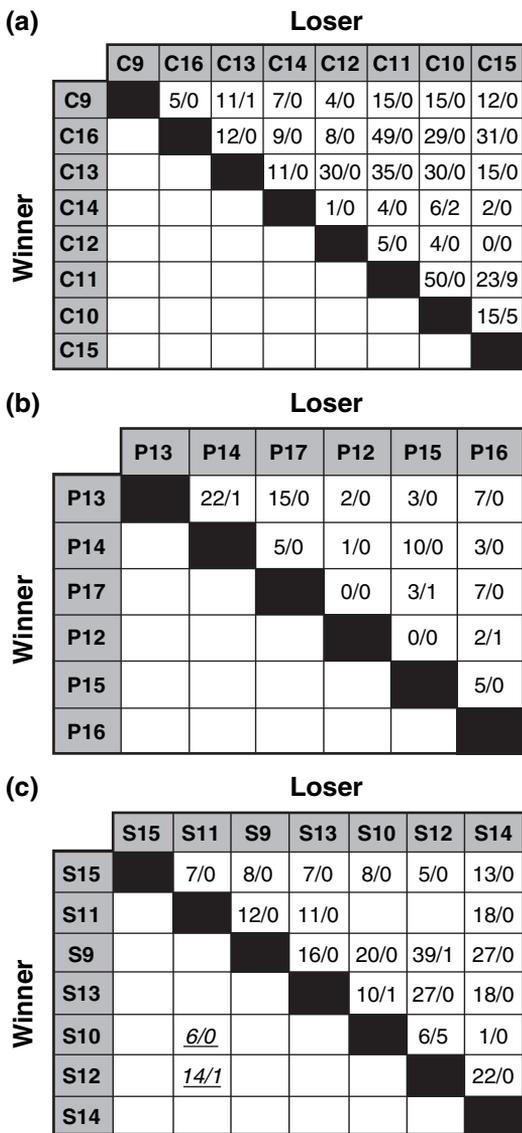


Fig. 1: Dominance matrices for male (a) mallards (N total = 88 interactions), (b) pintails (N total = 455 interactions) and (c) wigeons (N total = 303 interactions). The birds are ranked according to dominance; their scores decrease from left to right and from the bottom to the top. Each cell in the matrix shows the number of encounters won by the bird in that row over the bird in the column. Where a bird won a majority of the encounters, the proportion won by each is entered as a proportion in the winner’s row. Inconsistencies are below the diagonal

were significantly related to rank ($p = 0.001$; Tables 2b and 3, Fig. 3), with the dominant individual having a higher testosterone level than the subordinates ($F_{1,37} = 17.775, p < 0.001$ in the final model with only significant variables). As

Table 1: Results of ANCOVA on log₁₀-testosterone levels with winter period and species as factors, and order of capture, handling time and body condition as covariates (n = 42, r² = 0.425)

Source	SS	df	MS	F-ratio	P-value
Species	0.356	2	0.178	5.738	0.007
Period	0.345	1	0.345	11.129	0.002
Order	0.011	1	0.011	0.356	0.554
Handling	0.064	1	0.064	2.060	0.160
BC	0.037	1	0.037	1.196	0.282
Error	1.086	35	0.031		

All interactions were non-significant and therefore removed from the model during the backwards stepwise procedure. Only period and species eventually had a significant effect (see text).

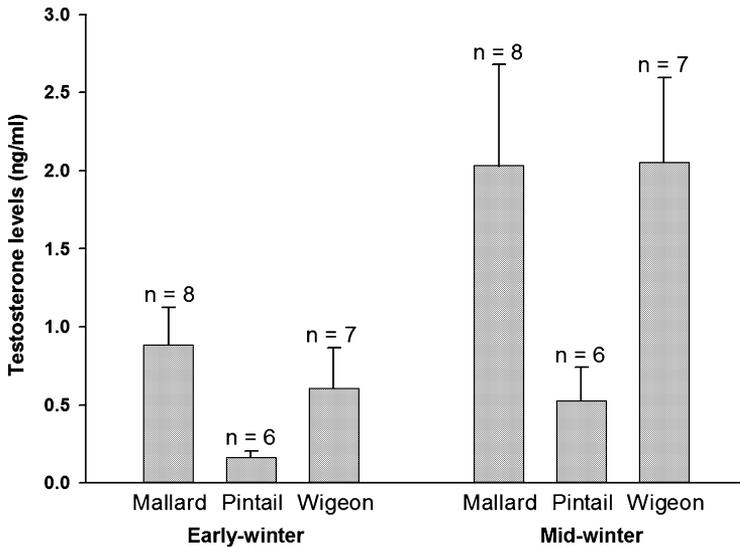


Fig. 2: Variation in testosterone levels between species and between winter periods (mean ± SE)

expected from the analysis on testosterone levels, in the final ANCOVA model both period of winter ($F_{1,37} = 4.881, p = 0.034$) and species ($F_{2,37} = 6.513, p = 0.004$) affected the relationship between testosterone and dominance. This can be through their effect of testosterone levels, but probably primarily because of the fact that the average value of rank per species differed initially as the numbers of birds differed. The slope of the relationship did not differ between periods and species as neither period–testosterone interaction nor species–testosterone interactions were significant ($F_{[1,33]} = 0.572, p = 0.57$ and $F_{[2,34]} = 1.721, p = 0.20$, respectively, when excluded from the model). The estimated relationships are summarized in Table 3.

Table 2: Results of ANCOVA on dominance rank with winter period and species as factors for (a) body mass, tarsus length, bill length and \log_{10} testosterone as covariates ($n = 42$, $r^2 = 0.418$), and (b) body condition and \log_{10} testosterone as covariates ($n = 42$, $r^2 = 0.354$)

Source	SS	df	MS	F-ratio	P
(a)					
Species	21.318	2	10.659	3.460	0.043
Period	12.536	1	12.536	4.069	0.052
T (log)	53.663	1	53.663	17.419	0.001
Tarsus	11.811	1	11.811	3.834	0.058
Mass	1.234	1	1.234	0.401	0.531
Bill	4.798	1	4.798	1.558	0.221
Error	104.745	34	3.081		
(b)					
Species	28.448	2	14.224	4.359	0.020
Period	13.140	1	13.140	4.026	0.052
T (log)	57.198	1	57.198	17.527	0.001
BC	1.009	1	1.009	0.309	0.582
Error	117.484	36	3.263		

All interactions were non-significant and therefore removed from the model during the backwards stepwise procedure. Only \log_{10} testosterone, period and species remain in the final model (see text).

Discussion

Linearity of the Hierarchy

This is the first study on behavioural dominance in waterfowl using matrix-ranking procedures (MatMan; De Vries 1995), which takes into account and combines all the different principles developed in recent research on social hierarchies. All three species show a high index of linearity, although in mallards ($h = 0.94$) and pintails ($h = 0.91$) the hierarchies seemed to be more stable and linear than in wigeons ($h = 0.71$). Only two effective circular triads (e.g. $A > B$, $B > C$ but $C > A$) were observed, both in wigeons. Our observations, therefore, confirm that dominance in male dabbling ducks is organized according to a defined social hierarchy, which is in agreement with other studies on geese and ducks (*Branta leucopsis* Black & Owen 1987; *Chen caerulescens caerulescens* Gregoire & Ankney 1990; six species of dabbling ducks Hepp & Hair 1984; *Anser indicus* Lamprecht 1986; *Branta canadensis* Raveling 1970). In addition, our experiments show that this social hierarchy is extremely linear, an aspect of dominance that has been poorly investigated in dabbling ducks (but see Hepp 1989; Hoysak & Ankney 1996), although it has already been demonstrated for many other bird species (e.g. Harris' sparrows *Zonotrichia querulea*; Chase & Rohwer 1987; Oystercatcher *Haematopus ostralegus*; Ens & Goss-Custard 1984). Our values of the coefficients of

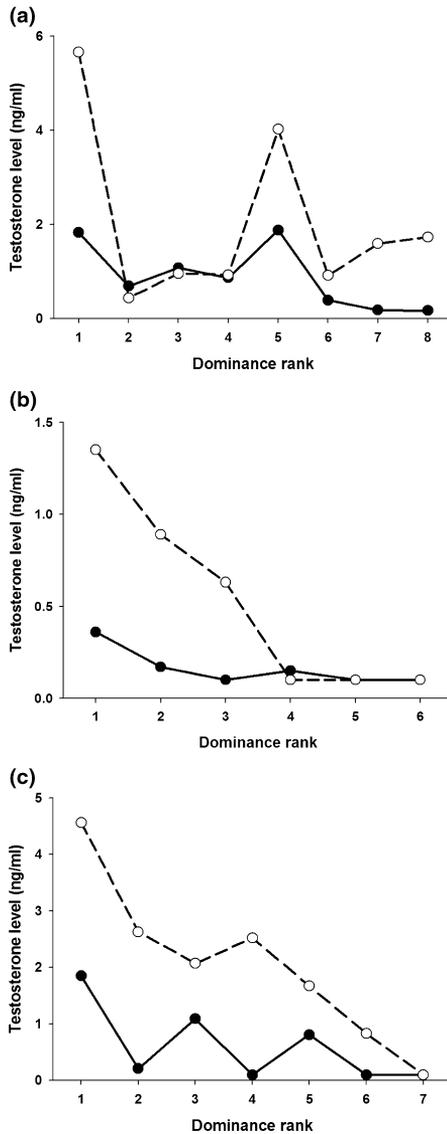


Fig. 3: Relationship between plasma levels of testosterone and rank order. Black circles and solid line: early winter. Open circles and dashed line: mid-winter; (a) mallards, (b) pintails and (c) wigeons

linearity (K and h) are consistent with the few published ones found for captive American black ducks *Anas rubripes* (K between 0.78 and 0.99; Hepp 1989) and in the upper range of values found by Hoysak & Ankney (1996) for American black ducks and Mallards (h between 0.44 and 0.83).

Table 3: Estimated equation from the ANCOVA models relating dominance rank to \log_{10} testosterone, with species and period as factors ($n = 42$, $r^2 = 0.374$)

Species	Period	Estimate
Mallard	Early winter	Rank = $-2.819 \times \log \text{Testosterone} + 3.793$
Mallard	Mid-winter	Rank = $-2.819 \times \log \text{Testosterone} + 4.461$
Pintail	Early winter	Rank = $-2.819 \times \log \text{Testosterone} + 0.916$
Pintail	Mid-winter	Rank = $-2.819 \times \log \text{Testosterone} + 1.584$
Wigeon	Early winter	Rank = $-2.819 \times \log \text{Testosterone} + 2.463$
Wigeon	Mid-winter	Rank = $-2.819 \times \log \text{Testosterone} + 3.131$

Confounding Effects on Testosterone Levels

We acknowledge the fact that the protocol was not ideal, because blood samples were collected sequentially from each species rather than simultaneously, as in most similar studies (Hoysak & Ankney 1996). However, this did not affect dominance ranks, as the correlation between dominance rank and sampling order was not significant. The testosterone levels were not influenced by order of capture even if birds had seen their conspecifics being manipulated before. Similarly, handling time was not related to individual testosterone levels. Previous studies have shown that circulating levels of testosterone decrease within few minutes after capture during the non-breeding winter phase of white-crowned sparrows *Zonotrichia leucophrys gambelii* and *Z. l. pugetensis* (Wingfield et al. 1982); hence our levels of testosterone are not likely to result from the stress linked to handling. Another possible source of bias would be if our dabbling ducks perceived captures as aggressive interactions, and increased their levels of testosterone: testosterone levels may increase as soon as 10 min after aggressive male interactions (Wingfield & Wada 1989 in Sorenson et al. 1997). In our case, the total manipulation was always <6 min (approx. 2 min on average); hence our recorded levels of testosterone are not likely to be related to capture and handling.

Persistently high plasma testosterone levels are believed to be costly to males because of their negative effects on body condition in gregarious species (Ros et al. 1997). Our results did not support this hypothesis, as in male yellow-legged gulls *Larus cachinnans* (Alonso-Alvarez et al. 2002).

In mid-winter, testosterone levels were higher for all species. This most probably has to be linked with mating behaviours, which start to be intense in all three species at this period of the year (Guillemain et al. 2003). The testosterone levels we recorded therefore may have been a combination of aggressive and reproductive testosterone production. In each of the two periods, pintails have significantly less testosterone. Personal observations also revealed that pintail was the species in which aggressive behaviours were the least intense during the experiments.

Correlates of Dominance

Larger body mass and/or structural size could be a physical advantage during fights (e.g. Stahl et al. 2001) but this was not clear during our experiments where no significant correlation was observed between morphological parameters and dominance ranks. Body condition could be the cause of this dominance: by a more efficient foraging, fatter birds could invest more in social behaviour. However, the inverse hypothesis is also possible: high ranking birds may have a better access to food, and therefore a better body condition. All these hypotheses cannot be tested with our data as ducks had food ad libitum, and hence food was not a limiting factor. There was no significant correlation between morphological parameters and dominance ranks. This is consistent with other studies: dominant Anatidae generally appear not be morphologically different (Sorenson & Derrickson 1994; Hoysak & Ankney 1996). Despite our small sample sizes, the lack of correlation between dominance rank and size clearly suggests that the acquisition of rank may have more to do with behavioural traits such as aggressive behaviour. However, we acknowledge the fact that causality in studies such as ours is impossible to ascertain, as it is difficult to know what comes first between dominance and testosterone.

According to the challenge hypothesis (Wingfield et al. 1987, 1990), testosterone levels are correlated with dominance rank during periods of high aggression among males such as hierarchy formation, territory establishment or mate guarding (Wingfield & Farner 1978; Wingfield 1984). Testosterone levels remain low and uncorrelated with dominance rank once territory boundaries and/or stable relationships have been established (Ramenofsky 1984; Wingfield 1984). In our study, carried out during early and mid-winter, mate guarding was an unlikely explanation for the maintenance of high testosterone levels especially because ducks were not paired in the aviaries at the time of the experiment. Although the elevation of testosterone between early and mid-winter may be due to the start of the courtship period, our results are more likely to be related to hierarchy establishment, or hierarchy maintenance during the non-breeding season. Because our groups were formed long before our behavioural observations, we could have expected that stable dominant relationships were established and maintained by individual recognition and social inertia (Wingfield & Ramenofsky 1985 in Sorenson et al. 1997; Archawaranon et al. 1991), hence minimizing aggression and therefore, fluctuations of testosterone levels. The fact that dominance was generally related to testosterone levels during winter suggests that: (1) social hierarchies may be more labile than expected in dabbling ducks and (2) therefore it may be possible for some individuals to improve their social status through aggressive interactions with others.

Adaptive Significance of the Hierarchy Formation during the Wintering Period

Our results on captive birds suggest that natural selection promoted the establishment of aggressive behaviour when the birds arrive on the wintering

grounds. In the wild, migratory ducks arriving at their wintering quarters often experience a period of fairly unstable conditions, having to assess the quality of the resources, but also mixing with a large number of strange individuals. In addition, food is rarely renewable for dabbling ducks in winter and hence, depletion can induce major changes in patch and habitat quality with time (Guillemain et al. 2002). This would therefore be an important period during which social hierarchies need to be defined, and several studies on waterbirds already show that dominance provides real advantages in access to resources (Goss-Custard et al. 1984; Hepp & Hair 1984; Kotrschal et al. 1993; Stahl et al. 2001). We can expect that the relationship between testosterone, i.e. aggression, and dominance may be the strongest when birds arrive in their wintering quarters, in order to acquire a high social rank at the onset of the winter. If this is the case, the intensity of the relationship may vary between species according to their migratory phenology. Our data set was too small to really discriminate seasonal changes in the slopes relating testosterone and dominance between species. The fact that the relationship seemed stronger for pintail and wigeon in mid-winter compared to mallard is consistent with their migratory pattern for western France (Guillemain & Fritz 2002), and certainly calls for further investigation.

Our results show that male dabbling ducks are organized in a linear hierarchy during winter, and spend time interacting to acquire and maintain their social rank. This is presumably associated with a benefit, such as an easier access to mates (Hoysak & Ankney 1996; Sorenson et al. 1997) or access to better food patches (Stahl et al. 2001). Further work is required to test the influence of dominance on individual wintering strategies. This could include the manipulation of hormonal status in the wild, with testosterone implants on arrival in wintering areas.

Acknowledgements

We are grateful to David Lucchini, Sandra Blais, Daphné Durant and more particularly Noël and Nadine Guillon for help with ducks manipulations. We also highly appreciate the skillful assistance in testosterone dosages of Colette Trouvé. The manuscript profited greatly from critical comments by Patrick Duncan, Charles-André Bost, Marcel M. Lambrechts, Francesco Bonadonna and Camille Bonneaud. We thank Bart Kempenaers and two anonymous reviewers who provided constructive criticism to improve the manuscript. The programme was funded by the CNRS and the Office National de la Chasse et de la Faune Sauvage.

Literature Cited

- Aldrich, J. W. 1982: Disparate sex ratios in waterfowl. In: *Waterfowl Ecology and Management: Selected Readings* (Ratti, J. T., Flake, L. D. & Wentz, W. A., eds). Wildlife Society, Bethesda, MD, pp. 620–625.
- Alonso-Alvarez, C., Ferrer, M., Figuerola, J., Veira, J. A. R., Estepa, J. & Torres, L. M. 2002: The effects of testosterone manipulation on the body condition of captive male yellow-legged gulls. *Comp. Biochem. Phys. A* **131**, 293–303.
- Appleby, M. C. 1980: Social rank and food access in red deer stags. *Behaviour* **74**, 294–309.
- Archawaranon, M., Dove, L. & Wiley, R. H. 1991: Social inertia and hormonal control of aggression and dominance in white-throated sparrows. *Behaviour* **118**, 42–65.

- Archer, J. 1988: The Behavioural Biology of Aggression. Cambridge Univ. Press, Cambridge.
- Balthazart, J. 1976: Daily variations of behavioural activities and plasma testosterone levels in the domestic duck *Anas platyrhynchos*. *J. Zool. (Lond.)* **180**, 155—173.
- Belthoff, J. R., Dufty, A. M., Jr & Gauthreaux, S. A. 1994: Plumage variation, plasma steroids and social dominance in male house finches. *Condor* **96**, 614—625.
- Bernstein, I. S. 1981: Dominance: the baby and the bathwater. *Behav. Brain Sci.* **4**, 419—458.
- Bertram, B. C. R. 1980: Vigilance and group size in ostriches. *Anim. Behav.* **28**, 278—286.
- Black, J. M. & Owen, M. 1987: Determinants of social rank in goose flocks: acquisition of social rank in young geese. *Behaviour* **102**, 129—146.
- Brodsky, L. M., Ankney, C. D. & Dennis, D. G. 1988: The influence of male dominance on social interactions in black ducks and mallards. *Anim. Behav.* **36**, 1371—1378.
- Chase, I. D. & Rohwer, S. 1987: Two methods for quantifying the development of dominance hierarchies in large groups with applications to Harris' sparrows. *Anim. Behav.* **35**, 1113—1128.
- Chastel, O., Weimerskirch, H. & Jouventin, P. 1995: Body condition and seabird reproductive performance: a study of three petrel species. *Ecology* **76**, 2240—2246.
- Cresswell, W. 1994: Flocking is an effective anti-predation strategy in redshanks, *Tringa totanus*. *Anim. Behav.* **47**, 433—442.
- Davis, E. S. 2002a: Female choice and benefits of mate guarding by male mallards. *Anim. Behav.* **64**, 619—628.
- Davis, E. S. 2002b: Male reproductive tactics in the mallard, *Anas platyrhynchos*: social and hormonal mechanisms. *Behav. Ecol. Sociobiol.* **52**, 224—231.
- De Vries, H. 1995: An improved test of linearity in dominance hierarchies containing unknown or tied relationships. *Anim. Behav.* **50**, 1375—1389.
- De Vries, H. 1998: Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. *Anim. Behav.* **55**, 827—843.
- De Vries, H., Netto, W. J. & Hanegraaf, P. L. H. 1993: MatMan: a program for the analysis of sociometric matrices and behavioural transition matrices. *Behaviour* **125**, 157—175.
- Ebbinge, B. S. & Spaans, B. 1995: The importance of body reserves accumulated in spring staging areas in the temperate zone for breeding in dark-bellied Brent geese *Branta b. bernicla* in the high Arctic. *J. Avian Biol.* **26**, 105—113.
- Ens, B. J. & Goss-Custard, J. D. 1984: Interference among oystercatchers, *Haematopus ostralegus*, feeding on mussels, *Mytilus edulis*, on the Exe Estuary. *J. Anim. Ecol.* **53**, 217—231.
- Frigerio, D., Dittami, J., Möstl, E. & Kotrschal, K. 2004: Excreted corticosterone metabolites co-vary with ambient temperature and air pressure in male Greylag geese (*Anser anser*). *Gen. Comp. Endocrinol.* **137**, 29—36.
- Goss-Custard, J. D. 1980: Competition for food and interference among waders. *Ardea* **68**, 31—52.
- Goss-Custard, J. D., Clarke, R. T. & le V. dit Durell, S. E. A. 1984: Rates of food intake and aggression of oystercatchers *Haematopus ostralegus* on the most and least preferred mussel *Mytilus edulis* beds of the Exe estuary. *J. Anim. Ecol.* **53**, 233—245.
- Gregoire, P. E. & Ankney, C. D. 1990: Agonistic behavior and dominance relationships among lesser snow geese during winter and spring migration. *Auk* **107**, 550—560.
- Guillemain, M. & Fritz, H. 2002: Temporal variation in feeding tactics: exploring the role of competition and predators in wintering dabbling ducks. *Wildl. Biol.* **8**, 81—90.
- Guillemain, M., Fritz, H. & Duncan, P. 2002: The importance of protected areas as nocturnal feeding grounds for dabbling ducks wintering in Western France. *Biol. Conserv.* **103**, 183—198.
- Guillemain, M., Caldow, R. W. G., Hodder, K. H. & Goss-Custard, J. D. 2003: Increased vigilance of paired males in sexually dimorphic species: distinguishing between alternative explanations in wintering Eurasian wigeon. *Behav. Ecol.* **14**, 130—135.
- Guillemain, M.-L., Atramentowicz, M. & Charles-Dominique, P. 2000: Dominance relationships in captive male bare-tailed woolly opossum (*Caluromys philander*, Marsupialia: Didelphidae). *Rev. Ecol. (Terre Vie)* **55**, 337—349.
- Hamilton, W. D. 1971: Geometry for selfish herd. *J. Theor. Biol.* **31**, 295—311.
- Heitmeyer, M. E. 1988: Body composition of female mallards in winter in relation to annual cycle events. *Condor* **90**, 669—680.
- Hepp, G. R. 1989: Benefits, costs, and determinants of dominance in American black ducks. *Behaviour* **109**, 222—234.

- Hepp, G. R. & Hair, J. D. 1984: Dominance in wintering waterfowl (*Anatini*): effects on distribution of sexes. *Condor* **86**, 251–257.
- Hirschenhauser, K., Möstl, E. & Kotschal, K. 1999: Within-pair testosterone covariation and reproductive output in greylag geese *Anser anser*. *Ibis* **141**, 577–586.
- Hirschenhauser, K., Möstl, E., Wallner, B., Dittami, J. & Kotschal, K. 2000: Endocrine and behavioural response of male greylag geese (*Anser anser*) to pairbond challenges during the reproductive season. *Ethology* **106**, 63–77.
- Holmberg, K., Edsman, L. & Klint, T. 1989: Female mate preferences and male attributes in mallard ducks *Anas platyrhynchos*. *Anim. Behav.* **38**, 1–7.
- Hoysak, D. J. & Ankney, C. D. 1996: Correlates of behavioural dominance in mallards and American black ducks. *Anim. Behav.* **51**, 409–419.
- Ingold, P. 1991: Competition for feeding areas and dominance relationships among shelducks *Tadorna tadorna* with broods. *Ornis. Scand.* **22**, 27–32.
- Kitaysky, A. S., Wingfield, J. C. & Piatt, J. F. 1999: Dynamics of food availability, body condition and physiological stress response in breeding black-legged kittiwakes. *Funct. Ecol.* **13**, 577–584.
- Kotschal, K., Hemetsberger, J. & Dittami, J. 1993: Food exploitation by a winter flock of greylag geese: behavioral dynamics, competition and social status. *Behav. Ecol. Sociobiol.* **33**, 289–295.
- Kotschal, K., Hirschenhauser, K. & Möstl, E. 1998: The relationship between social stress and dominance is seasonal in greylag geese. *Anim. Behav.* **55**, 171–176.
- Lamprecht, J. 1986: Structure and causation of the dominance hierarchy in a flock of bar-headed geese (*Anser indicus*). *Behaviour* **96**, 28–48.
- Lima, S. L. 1995: Back to the basics of anti-predatory vigilance: the group-size effect. *Anim. Behav.* **49**, 11–20.
- Lormée, H., Jouventin, P., Lacroix, A., Lallemand, J. & Chastel, O. 2000: Reproductive endocrinology of tropical seabirds: sex-specific patterns in LH, steroids, and prolactin secretion in relation to parental care. *Gen. Comp. Endocrinol.* **117**, 413–426.
- MacDonald, D. W., Stewart, P. D., Johnson, P. J., Porkert, J. & Buesching, C. 2002: No evidence of social hierarchy amongst feeding badgers, *Meles meles*. *Ethology* **108**, 613–628.
- Marler, C. A. & Moore, M. C. 1988: Evolutionary costs of aggression revealed by testosterone manipulations in free-living male lizards. *Behav. Ecol. Sociobiol.* **23**, 21–26.
- MatMan 1998: MatMan Version 1.0 for Windows. Noldus Information Technology, Wageningen, The Netherlands.
- Piper, W. H. 1997: Social dominance in birds. Early findings and new horizons. In: *Current Ornithology* (Nolan, V., Jr, Ketterson, E. D. & Thompson, C. F., eds). Plenum Press, New York, pp. 125–187.
- Powell, G. V. N. 1974: Experimental analysis of the social value of flocking by starlings (*Sturnus vulgaris*) in relation to predation and foraging. *Anim. Behav.* **22**, 501–505.
- Pravosudov, V. V. & Lucas, J. R. 2000: The effect of social dominance on fattening and food-caching behaviour in Carolina chickadees, *Poecile carolinensis*. *Anim. Behav.* **60**, 483–493.
- Pulliam, H. R. & Caraco, T. 1984: Living in groups: is there an optimal group size? In: *Behavioural Ecology: An Evolutionary Approach* (Krebs, J. R. & Davies, N. B., eds). Blackwell Scientific Publication, Oxford, pp. 128–138.
- Ramenofsky, M. 1984: Agonistic behaviour and endogenous plasma hormones in male Japanese quail. *Anim. Behav.* **32**, 698–708.
- Raveling, D. G. 1970: Dominance relationships and agonistic behavior of Canada geese in winter. *Behaviour* **37**, 291–319.
- Roberts, G. 1996: Why individual vigilance declines as group size increases. *Anim. Behav.* **51**, 1077–1086.
- Ros, A. F. H., Groothuis, T. G. G. & Apanius, V. 1997: The relation among gonadal steroids, immunocompetence, body mass, and behavior in young black-headed gulls (*Larus ribibundus*). *Am. Nat.* **150**, 201–219.
- Rowell, T. 1974: The concept of social dominance. *Behav. Biol.* **11**, 131–154.
- Sokal, R. R. & Rohlf, F. J. 1981: *Biometry*. Freeman; W.H. San Francisco, CA.
- Sorenson, L. G. & Derrickson, S. R. 1994: Sexual selection in the northern pintail (*Anas acuta*): the importance of female choice versus male-male competition in the evolution of sexually-selected traits. *Behav. Ecol. Sociobiol.* **35**, 389–400.

- Sorenson, L. G., Nolan, P. M., Brown, A. M., Derrickson, S. R. & Monfort, S. L. 1997: Hormonal dynamics during mate choice in the northern pintail: a test of the "challenge" hypothesis. *Anim. Behav.* **54**, 1117—1133.
- Stahl, J., Tolsma, P. H., Looenen, M. J. J. E. & Drent, R. H. 2001: Subordinates explore but dominants profit: resource competition in high Arctic barnacle goose flocks. *Anim. Behav.* **61**, 257—264.
- Sutherland, W. J. & Allport, G. A. 1994: A spatial depletion model of the interaction between bean geese and wigeon with the consequences for habitat management. *J. Anim. Ecol.* **63**, 51—59.
- Tamisier, A. & Dehorter, O. 1999: Camargue, canards et foulques, 1st edn. Centre Ornithologique du Gard, Nîmes, France.
- Tamisier, A., Allouche, L., Aubry, F. & Dehorter, O. 1995: Wintering strategies and breeding success: hypothesis for a trade-off in some waterfowl species. *Wildfowl* **46**, 76—88.
- Tremblay, R. E., Schaal, B., Boulerice, B., Arseneault, L., Soussignan, R. G., Paquette, D. & Laurent, D. 1998: Testosterone, physical aggression, dominance, and physical development in early adolescence. *Int. J. Behav. Develop.* **22**, 753—777.
- Triplet, P., Stillman, R. A. & Goss-Custard, J. D. 1999: Prey abundance and the strength of interference in a foraging shorebird. *J. Anim. Ecol.* **68**, 254—265.
- Wilkinson, L. 1997: Systat 7.0, New Statistics. SPSS. Inc., Chicago, IL.
- Wingfield, J. C. 1984: Environmental and endocrine control of reproduction in the song sparrow, *Melospiza melodia*. *Gen. Comp. Endocrinol.* **56**, 417—424.
- Wingfield, J. C. & Farner, D. S. 1978: The annual cycle of plasma irLH and steroid hormones in feral populations of white-crowned sparrow, *Zonotrichia leucophrys gambelii*. *Biol. Reprod.* **19**, 1046—1056.
- Wingfield, J. C., Smith, J. P. & Farner, D. S. 1982: Endocrine responses of white-crowned sparrows to environmental stress. *Condor* **84**, 399—409.
- Wingfield, J. C., Ball, G. F., Dufty, A. M., Jr, Hegner, R. E. & Ramenofsky, M. 1987: Testosterone and aggression in birds. *Am. Scient.* **75**, 602—608.
- Wingfield, J. C., Hegner, R. E., Dufty, A. M., Jr & Ball, G. F. 1990: The "challenge hypothesis": theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *Am. Nat.* **136**, 829—846.
- Zwarts, L. 1976: Density-related processes in feeding dispersion and feeding activity of teal (*Anas crecca*). *Ardea* **64**, 192—209.

Received: June 17, 2004

Initial acceptance: September 19, 2004

Final acceptance: November 18, 2004 (B. Kempanaers)