

Linear social dominance hierarchy and corticosterone responses in male mallards and pintails

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Abstract

In winter, dabbling ducks gather in large flocks and males compete not only for food resources but also for mates. Setting up a social hierarchy is one way to reduce the costs of conflicts, but the position in the hierarchy has implications for individuals, for instance their susceptibility to conflict and interference, hence to social stress. We investigated relationships between linear social dominance and corticosterone levels, baseline levels and induced-stress response, in captive male mallards *Anas platyrhynchos* and pintails *Anas acuta* during the winter period. We hypothesised that corticosterone responses would reflect the costs associated with social stress. From previous work on dominance and corticosterone in wintering birds, we expected that, where the social hierarchy is linear, there would be (1) no relationship between social ranks and baseline corticosterone levels and (2) a significant positive relationship between dominance ranks and responses to acute stress. Our results demonstrated the existence of a linear hierarchy in both species ($h' = 0.95$ for mallards and $h' = 0.97$ for pintails), and we found that pintails had on average more corticosterone than mallards. The relationship between dominance and corticosterone responses followed the predictions, with no differences for baseline levels and an attenuated response to induced-stress for subordinates. We discuss these results in the perspective of the cost–benefits of dominance and wintering strategies of waterbirds.

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Introduction

Relationships between social status and stress are particularly crucial in gregarious vertebrate species because one potential stressor both in the wild and in captivity is the presence of numerous individuals in a confined space (Nephew, 2003). Moreover, living in groups also involves costs, such as competition for resources, both in terms of accelerated food depletion (Goss-Custard, 1980; Sutherland and Allport, 1994) and interference (Appleby, 1980; Ens and Goss-Custard, 1984; Goss-Custard, 1980; Triplet et al., 1999). Thus, individuals are more subject to social stress by direct or indirect interactions and conflicts in gregarious species (Goymann et al., 2003).

Plasma levels of the hormone corticosterone rapidly rise in response to acute stressful conditions (Wingfield and Farner, 1993). The study of the adrenocortical response to stress can therefore shed some light on the mechanisms mediating social stress. Plasma corticosterone levels (baseline as well as increased) can be influenced by a series of intrinsic and extrinsic factors (e.g., O'Reilly and Wingfield, 2001; Sockman and Schwabl, 2001; Wingfield et al., 1995). These factors may express daily and/or seasonal fluctuations linked to changes in energy requirements varying in time and space (Breuner and Wingfield, 2000; Breuner et al., 1999; Romero and Remage-Healey, 2000; Tarlow et al., 2003; Wada and Shimizu, 2004). For instance, corticosterone levels are strongly influenced by sudden environmental changes (Breuner and Wingfield, 2000; Breuner et al., 2003; Frigerio et al., 2004; Wada and Shimizu, 2004; Wingfield et al., 1995), such as storms, food shortage, loss of mate or an

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increase in density. High corticosterone levels mobilise energy and lead to rapid behavioural adjustments in birds (Kitaysky et al., 1999a,b, 2001a; Nephew, 2003). However, the same disturbance can have different effects on corticosterone levels depending on the stage of the life-history cycle of the individuals concerned. For instance, male bush warblers *Cettia diphone* suppress their stress response in the early stages of breeding and just after the breeding season (Wada and Shimizu, 2004). Both baseline and stress-induced corticosterone levels are also influenced by individual characteristics, such as body condition (Kitaysky et al., 1999a, 2001a; Perfito et al., 2002). However, these effects are variable (Lormée et al., 2003), and corticosterone levels can vary with sex and age (Kitaysky et al., 2001b; Lormée et al., 2003; Reeder et al., 2004; Silverin and Wingfield, 1982; Sockman and Schwabl, 2001).

Adrenocortical responses and their behavioural and fitness consequences have been extensively studied in the context of reproduction (see Wingfield and Sapolsky, 2003 for a review). There are, however, few studies that have examined relationships between social dominance and corticosterone responses to stressful events, and the pattern is not clear. In some studies, subordinates have higher baseline levels and/or more increase of plasma corticosterone in response to stressful circumstances than dominant individuals (birds: Rohwer and Wingfield, 1981; Schwabl et al., 1988, fishes: Sloman et al., 2001, 2002; Øverli et al., 2004). Conversely, dominant wintering mountain chickadees *Poecile gambeli* reach significantly higher levels of corticosterone during their response to acute stress compared to subordinates, while no significant difference in baseline corticosterone levels were observed in relation to social dominance status (Pravosudov et al., 2003). In one study, no correlation between corticosterone responses and social status was found at all (e.g. Schoech et al., 1997).

Here, we investigate relationships between linear social dominance and corticosterone responses to stress (see above) in male mallards *Anas platyrhynchos* and pintails *Anas acuta* during the winter period. 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 characterised by non-renewable food supplies which undergo strong depletion. Competition for resources is therefore potentially high (Guillemain and Fritz, 2002; Zwarts, 1976), in particular when low temperatures increase energy demands (Frigerio et al., 2004).

Social stress in winter is particularly important in males because this is when pair formation occurs in dabbling ducks (Heitmeyer, 1988; Tamisier and Dehorter, 1999; Tamisier et al., 1995) and the general male-biased sex-ratio in wintering duck populations (Aldrich, 1982; Hepp and Hair, 1984) increases competition for mates. High ranking males have been reported to have better access to females in several wildfowl species (Brodsky et al., 1988; Holm-

berg et al., 1989), although this is not always true (Sorenson and Derrickson, 1994).

The study of the relationship between corticosterone responses and social dominance status in male dabbling ducks is therefore very relevant to understand the underlying potential physiological costs of their interactions on wintering grounds. In this paper, we examine the influence of social dominance status on baseline and stress-induced corticosterone levels.

We measured acute changes in the adrenocortical response to a standardised environmental stressor (Wingfield, 1994). Dominance hierarchies were determined from interactions between birds and organised in sociometric matrices (De Vries, 1995), hence allowing testing for a linear organisation and giving a more accurate estimate of individual social rank.

A stressed animal might suffer deleterious effects of chronic elevation of corticosterone (Kitaysky et al., 2001a). To avoid detrimental effects of chronic elevation of corticosterone, subordinate individuals might suppress adrenocortical activity in response to all negative events and aggressions (Kitaysky et al., 2001a). The only study on birds in winter suggests that this suppression phenomenon, in an extreme climatic context, may lead to an absence of differences in baseline corticosterone levels between dominants and subordinates, as well as an attenuated response to stress from subordinates compared to dominants (Pravosudov et al., 2003). In the event of a linear social hierarchy, we expected no relationship between social ranks and baseline corticosterone levels, and a significant relationship between dominance ranks and responses to acute stress, with an increasing response in more dominant animals.

Methods

Birds and observations

The experiments were carried out in December 2000 and January 2001 at the Centre d'Etudes Biologiques de Chizé (CEBC), in western France, using adult ducks descended from individuals caught in the wild. The birds were kept at the CEBC for at least 3 years before the start of the experiments and were therefore accustomed to their aviary environment. During the day, mallards were free to move in the field station's grasslands (approximately 1000 m²) with food and water ad libitum. Pintails were kept in separate 110 m² enclosures (50 m² grass, 60 m² concrete) equipped with a 10 m² pool. At night, the ducks were caged in two 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.

During the experiments, the birds were kept apart in two separate 10 × 10 m grass areas during the day and in 5 × 10 m concrete aviaries during the night, all equipped with a

10 m² pool. We used all the available pintails (6 adult males and 11 adult females). For the mallards, we selected individuals randomly from a larger flock (of 30 individuals, to obtain 8 males and 8 females). Food was provided ad libitum.

The birds were marked individually with plastic badges glued on their backs with non-toxic glue (3 × 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 December 18 to December 22 for mallards and from January 15 to January 19 for pintails. During each 45 min session, the group of birds was placed in a 2 × 4 m arena and videotaped using a digital video camera recorder (Sony, Digital handycam) positioned 2 m from the enclosure and 2 m from the ground 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 × 2 m) included a bowl of 400 g of wheat and a bowl with an area of 700 cm² of water. In the afternoon, a 1 m² pool of clear water replaced the bowl of water and two cameras covered the complete area of the enclosure. All interactions recorded on the videotapes, near food or elsewhere, were noted, including 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 to obtain a sufficient number of interactions during each observation session. This treatment caused no injuries or abnormal body mass variations during the experiment (mean = +0.18% ± 0.018 SD). All procedures used in this study adhered to ethical standards of animal use for scientific research. This programme was approved by the French Ministry for Environment and Sustainable Development and satisfied the requirements of the Animal Welfare Regulations from the Ministry of Research.

Blood sampling

Blood samples were first collected on the 14th and 15th of December 2000 for mallards and on the 11th and 12th January for pintails, 3 days before the behavioural observation sessions for each species. Birds were individually captured with a net, one after another. All birds were bled according to the following standardised technique (Wingfield, 1994): immediately after capture, an initial blood sample (600 µl) was collected from the brachial vein with a 1 ml heparinised syringe and a 25 gauge needle, and additional samples were taken 20 and 45 min later. To control for possible effect of handling time during initial bleeding on hormone levels, we measured, for each individual, the time elapsed between the onset of trapping and the end of initial blood sampling (mean = 99 s ± 46 SD, maximum: 261 s).

After each blood sample, birds were kept in an individual opaque cloth bag. Blood samples were put into ice and centrifuged as soon as possible; afterward, plasma (for corticosterone assay) was subsequently stored at –20°C. All birds were bled for the first time in the morning (9:30 to 10:30 a.m.) at the same time of the day to minimise the effect of diurnal fluctuations on plasma corticosterone levels (Breuner et al., 1999; Romero and Remage-Healey, 2000; Tarlow et al., 2003). Corticosterone levels (baseline, 20 and 45 min) were not correlated with time of day for any of the two species (Spearman, $P > 0.05$). This suggests that our protocol was effective in minimising this source of variation. One individual (a mallard) was difficult to bleed and could not be bled at 45 min, hence is not included in the sample.

Radio immunoassays

Corticosterone levels were determined at the CEBC following the procedure detailed in Lormée et al. (2003). Minimal detectable corticosterone levels were 0.4 ng mL⁻¹ (lowest measurement: 3.87 ng mL⁻¹). All samples were run in one assay; the coefficients of intra-assay variation, assessed using three reference plasmas, were 1.55% for mallards and 1.99% for pintails ($n = 5$ duplicates).

There was no significant relationship between handling time and corticosterone levels measured during the initial bleeding (Mallards: $F_{[1,6]} = 1.798$, $P = 0.228$; Pintails: $F_{[1,4]} = 0.001$, $P = 0.977$). If the capture of a bird within the group caused some additional stress to the remaining individuals while they waited to be captured, we expected that the level of corticosterone would be positively correlated with the order of capture of the birds. In pintails, the capture order had no effect on the baseline concentrations of corticosterone in the plasma ($F_{[1,4]} = 0.312$, $P = 0.606$). In mallards, the order of capture and baseline corticosterone levels were negatively correlated ($F_{[1,6]} = 14.277$, $P = 0.009$; Spearman rank correlation, $r_s = -0.781$, $P < 0.05$). Thus, initial blood samples were considered to reflect baseline levels of corticosterone (Kitaysky et al., 1999b; Lormée et al., 2003; Wingfield et al., 1982).

Morphometric measurements and body condition

The ducks were weighed to the nearest gram after blood collection. Tarsus and culmen 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 to minimise observer biases.

Body mass to wing length, bill and tarsus ratios are commonly used to access body conditions in birds (Chastel et al., 1995). However, given the fact that captive ducks wear out their wings more rapidly than in natural conditions, 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., 1999b). Individuals that were heavy for their body size had high values and vice versa.

Statistical analysis

Interactions between birds were organised in sociometric matrices from which we calculated Kendall's coefficient of linearity K , Landau's linearity index h and the linearity index h' (De Vries, 1995), using MatMan 1.0 (Noldus Information Technology, 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 have not been observed to perform any agonistic interaction. Statistical significance of K is provided by a χ^2 test. For the h' index, a sampling process using 10,000 randomisations 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), first finding the rank order most consistent with a linear hierarchy by minimising the number of inconsistencies and then minimising the total strength of the inconsistencies (De Vries, 1998). The birds were ranked from 1 (most dominant) to 6 or 8 (most subordinate).

In the statistical analysis, initial data were tested for the assumptions of parametric statistical tests (Sokal and Rohlf, 1995). If the data violated assumptions, they were \log_{10} transformed and examined again. The difference in corticosterone levels between species was tested using a non-parametric Mann–Whitney U test. The relationships between continuous variables were tested by linear regression, while a Spearman rank correlation was used when testing for a relationship between continuous and discrete variables. Changes in corticosterone levels with time after capture were examined with a two-way repeated ANCOVA. Interspecific comparison of stress response to handling was performed with two-way repeated measures ANCOVA, where species was included as a factor and serial bleeds of the same bird during the stress protocol as repeated measures. Intraspecific comparisons of stress responses to handling were performed with two-way repeated measures ANCOVA, where the body condition index and rank were used as factors and serial bleeds of the same bird during the stress protocol as repeated measures. All statistical analyses were performed using SYSTAT 7.0 (release 9 for Windows; SPSS Inc., Chicago, USA, Wilkinson, 1997). Values are presented as means \pm standard error.

Results

Dominance relationships

In 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.

In 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.

Baseline corticosterone levels

Baseline corticosterone level was higher in pintail than in mallard plasma (Fig. 1; Mann–Whitney, $U = 6.000$, $P = 0.020$). In mallards, the baseline concentration was not significantly related to body condition (linear regression, $F_{[1,6]} = 3.523$, $P = 0.110$) or rank (Spearman rank correlation, $r_s = -0.405$, $P > 0.05$). Body condition and rank were not correlated (Spearman rank correlation, $r_s = 0.000$, $P > 0.05$). In pintails, baseline concentrations were not significantly related to body condition (linear regression, $F_{[1,4]} = 5.248$, $P = 0.084$) or rank (Spearman rank correlation, $r_s = 0.429$, $P > 0.05$). Body condition and rank order were not correlated (Spearman rank correlation, $r_s = 0.086$, $P > 0.05$).

Adrenocortical response to acute stress

Both species responded to acute stress by a rapid and significant response of the adrenocortical system to the stress of being captured and held (repeated measures GLM between metric 0, 20 and 45 min, $F_{[2,24]} = 13.234$, $P <$

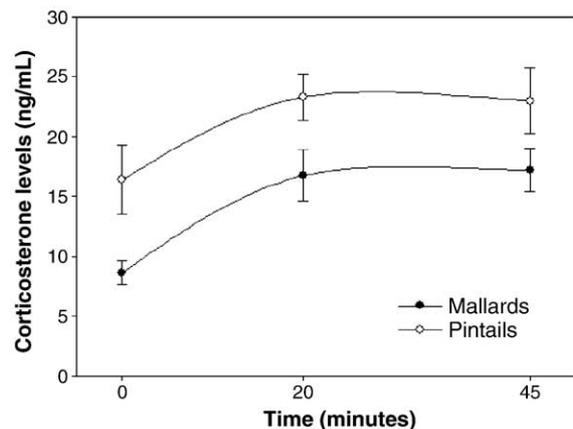


Fig. 1. Corticosterone concentration over 45 min of capture and handling for mallards (●) and pintails (○). Time 0 corresponds to the baseline corticosterone values, i.e. from the blood samples taken immediately after capture.

0.001). Maximum corticosterone levels were reached after 20 min of handling and restraint (repeated measures GLM between metric 20 and 45 min, $F_{[1,12]} = 0.345$, $P = 0.568$, Fig. 1). Although the responses were qualitatively similar, “species” had a significant effect in the repeated measures ANOVA ($F_{[1,11]} = 10.092$, $P = 0.009$), which reflected a difference in corticosterone concentration in the plasma between pintail and mallard at each time step. The mallard baseline level was half that of pintails. The stress response is moderate for both species, only twice the baseline for mallards and 1.5 times the baseline for pintails.

In mallards, the magnitude of the stress response was unaffected by body condition (repeated measures GLM between metric 0, 20 and 45 min, $F_{[1,4]} = 1.350$, $P = 0.310$). Stress responses were significantly correlated with rank in male mallards (repeated measures GLM between metric 0, 20 and 45 min, $F_{[1,4]} = 10.501$, $P = 0.032$) with dominant male mallards showing stronger corticosterone response to stress than subordinates (Fig. 2a). In pintails, the adrenocortical response was significantly and negatively correlated with body condition (repeated measures GLM between metric 0, 20 and 45 min, $F_{[1,3]} = 51.002$, $P = 0.006$). Stress responses were also significantly correlated with rank order in male pintails (repeated measures GLM between metric 0, 20 and 45 min, $F_{[1,3]} = 10.180$, $P = 0.050$) with dominant male pintails showing a stronger corticosterone response to stress than subordinates (Fig. 2b). There was no significant interaction between body condition and dominance on the stress response in pintails ($F_{[1,2]} = 2.903$, $P = 0.231$), hence their effects were additive: dominant individuals always had a greater stress response than subordinates for a given body condition (Fig. 3).

Discussion

Dominance and baseline levels of corticosterone

Our results were in accordance with the only other study on dominance and corticosterone in wintering birds (Pravosudov et al., 2003), and contrary to the usual

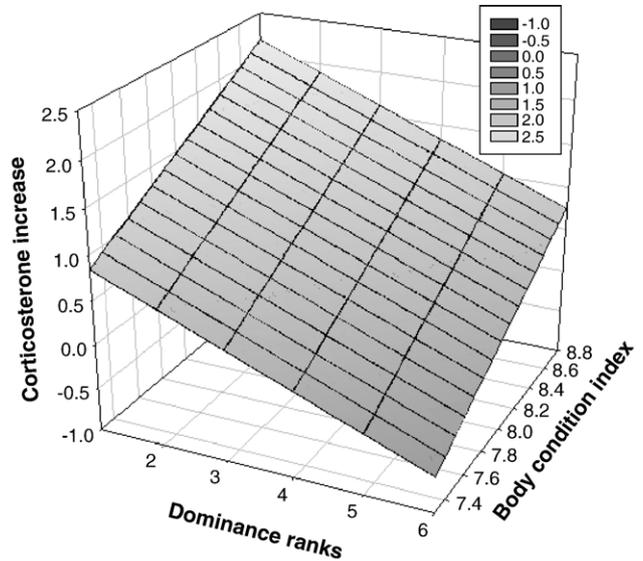


Fig. 3. Relationships between the body condition index, dominance rank and increases in corticosterone levels for pintails. Corticosterone increase = 0.901. Body condition index -0.288 . Dominance rank -5.451 .

predictions, this study demonstrated that baseline corticosterone was not correlated to dominance rank for mallards and pintails. Our results suggest no evidence for either subordination stress (Abbott et al., 2003; Nuñez-De La Mora et al., 1996) or dominance cost (Carlson et al., 2004; Muller and Wrangham, 2004; Sands and Creel, 2004) in our groups. Subordinates were not continuously more stressed by aggressive interactions or submissive behaviours from dominant birds as shown for chicks of the blue-footed boobies *Sula nebouxii* (Nuñez-De La Mora et al., 1996). Although subordinates were involved in and lost more aggressive interactions than intermediate rank individuals, this was not visible in their baseline corticosterone levels but would have probably appeared if blood samples had been taken during or immediately after the behavioural experiments. Similarly, dominants not only won more but also initiated more interactions, presumably to maintain their social rank, but also this did not show in their baseline levels. Contrary to many studies, we found that baseline corticosterone was independent of frequency and social

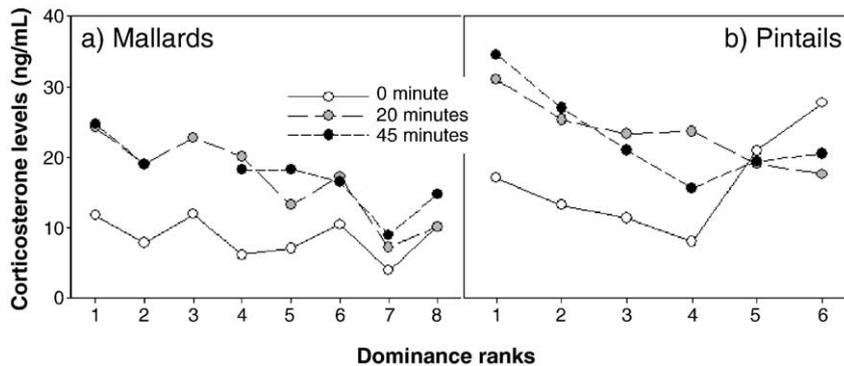


Fig. 2. Relationships between dominance rank, baseline corticosterone level (0 min) and corticosterone levels at 20 and 45 min after handling. (a) Mallards; (b) pintails.

orientation of aggressive behaviours (see review in De Vries et al., 2003) and also independent of social status (see review in Creel, 2001). It is also possible that our sample sizes were too small to detect weak relationships, a permanent constraint in analysing the results of our experiments.

The fact that baseline levels of corticosterone were not correlated to social status may be because our groups were formed long before our behavioural observations. This would have favoured the establishment of fairly stable dominance relationships, maintained by individual recognition and social inertia (Archwaranon et al., 1991; Sorenson et al., 1997), hence minimising violent fights and therefore, corticosterone secretion.

The only previous study in Anatidae concerning social stress and corticosterone levels showed that social stress in greylag geese ganders *Anser anser* was caused mainly by competition between males and by limited access to females during the mating season, and by parental commitment during the rest of year (Kotschal et al., 1998). Our study took place just before the mating season when courtship behaviours and pair formation had not begun or were very infrequent. Thus, it was a period with little competition for access to mates and with no parental stress. This could also explain the absence of correlation between rank and baseline corticosterone level in our dabbling ducks.

To our knowledge, our study is the first which provides baseline corticosterone levels in adult dabbling ducks; nonetheless, they were comparable with levels found in duckling mallards, 8 ng mL⁻¹ (Harvey et al., 1980) and in early breeding harlequin ducks, 10 ng mL⁻¹ (Perfito et al., 2002). In our study, male pintails showed higher levels of baseline corticosterone than male mallards. This difference may be due to the mass difference with heavier duck species having less corticosterone, perhaps because large body size allows more fat storage and hence more hormone dilution in the blood. Along similar lines, various monospecific studies showed that corticosterone levels were often negatively correlated with the body condition of individuals (e.g. Kitaysky et al., 2001a,b; Perfito et al., 2002; Schoech et al., 1997). However, we found no significant correlation between body condition or mass and baseline corticosterone in either species, although there was such a trend in our pintails. This does not imply the absence of any relationship, but may be that the range of parameter values within each species was too small to show any difference. However, this shows that the pattern found in our results was not primarily due to body condition.

Corticosterone response to stress and linear social dominance

Mallards like pintails showed a rapid response to handling stress. After 20 min, corticosterone levels did not vary and these were their maximum levels of corticosterone. However, the intensity of this response was moderate

compared to other studies. For example, the corticosterone levels of captive starlings *Sturnus vulgaris* increased over four times the baseline in the same handling time (Romero and Ramage-Healey, 2000) as in artic-breeding shorebirds (O'Reilly and Wingfield, 2001). Harvey et al. (1980) also showed a major increase in mallards *A. platyrhynchos*: more than five times the initial level. In mallards and pintails, stress responses were similar in shape but the increase was greater in mallards. The difference in sex-ratio between mallard and pintail in our experiment could have played a role, but we would have expected the mallard to be more stressed as there were more males hence more interactions, even outside the mating season. It is possible that pintails were more stressed by captive conditions, which would explain their higher baseline corticosterone levels and could not increase their corticosterone levels more.

Our results are in accordance with those of Pravosudov et al. (2003), as dominant ducks both in mallards and pintails groups showed a stronger response to stress than subordinates. A possible alternative, but not exclusive, hypothesis could be a physiological one. Each stress response has a cost and this cost may be more or less acceptable according to the physiological status of the bird. If a short-term increase in corticosterone may not be very costly for the organism, the cost of reacting to a stressor can be high, in energy (e.g. flying) or in time (e.g. loss of feeding time). A bird can have an important response to stress if it has many body reserves and/or good access to food but a bird without reserves must limit its energetic expenditures. Hence, dominants, with easier access to food, may allow themselves to react strongly to stress. Dominants can be considered as living in a more predictable environment through their better access to resources than subordinates even if they do not always exhibit a better body condition. On the contrary, subordinates live in a more aggressive and less predictable environment and consequently response to stress may be more costly. When facing a threat or a brutal environmental change, the dominant's response may thus be quicker and of greater magnitude than those of subordinates that cannot afford the same magnitude of response.

In winter, minimising the costs of competition and maintaining acquisition of sufficient energetic reserves is often a paramount problem for each individual (Pravosudov and Lucas, 2000), especially in gregarious species. Individuals must make a trade-off between short and long-term survival and this trade-off is dependant on numerous parameters like physiological status and the predictability of access to resources, which can be mediated by social status. Our results showed no evidence for the existence of stress subordination or stress dominance during the winter period in these gregarious species, but dominants seem to be able to have greater response to chronic stress. This may suggest that dominant ducks can cope better with the costs of gregariousness in wintering quarters, such as increased predator attraction (Fritz et al., 2000) or resource depletion (Guillemain and Fritz, 2002). To our knowledge, this is the

first study comparing stress response and dominance status in wintering ducks, and these calls for the investigation of the role of social hierarchies in the wintering strategies of these migratory bird species. Recently, it was demonstrated that active stress-induced free corticosteroid levels differ between individuals because of differences in corticosteroid-binding globulin levels (Breuner et al., 2003). It would be interesting to test if these results are more or less pronounced when we assay only the active plasmatic corticosterone. It would also be very informative to replicate these experiments in other seasons to understand the relationship between dominance and corticosterone secretion at different stage of the life cycle of these migratory birds.

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