

Ambient temperature and air pressure modulate hormones and behaviour in Greylag geese (*Anser anser*) and Northern bald ibis (*Geronticus eremita*)



Sebastian Dorn^{a,*}, Claudia A.F. Wascher^a, Erich Möstl^b, Kurt Kotrschal^a

^a Core facility Konrad Lorenz Forschungsstelle, University of Vienna, 4645 Grünau, Austria

^b Department of Biochemistry, University of Veterinary Medicine, Veterinärplatz 1, 1210 Vienna, Austria

ARTICLE INFO

Article history:

Received 14 December 2012

Received in revised form 30 July 2014

Accepted 7 August 2014

Available online 6 September 2014

Keywords:

Air pressure

Air temperature

Enzyme-immunoassay

Greylag goose

Hypothalamic-pituitary-adrenal axis

Northern bald ibis

ABSTRACT

Ambient temperature and air pressure are relevant stimuli that can elicit hormonal responses in alignment with adjusting individuals' physiology and behaviour. This study investigated possible changes in corticosterone (C) and testosterone (T) and contingencies with behaviour in response to ambient temperature and air pressure, and it evaluated the temporal response dynamics of these hormones in 12 individual Greylag geese (*Anser anser*) over 26 and 12 individual Northern bald ibis (*Geronticus eremita*) over 27 days, during late winter. Immunoreactive metabolites of C and T were analysed non-invasively from 626 fecal samples by means of group-specific antibodies and correlated to behaviour and weather factors. In both species, high C levels correlated with low temperatures 24 h before sampling, but low C levels correlated with high air pressure 6–12 h before sampling. In both species, C levels and behavioural activity were negatively correlated. In addition, temperature had a positive influence on T levels in both species 12–24 h before sampling. The fact that weather conditions influenced changes in levels of C, while social interactions did not, is indicative of a general mechanism of graduated physiological adjustment to environmental variations affecting metabolism, stress responses and behaviour.

© 2014 Elsevier B.V. All rights reserved.

1. Introduction

Individuals must be able to cope with the daily and annual variability of light regimes, temperature or air pressure (Jacobs, 1996). Some of the factors, such as season or light regime are predictable, individuals can adapt their circannual morphology, physiology or behaviour in anticipation of those changes. Other factors, however, such as temperature and air pressure, are less predictable from day to day (Wingfield and Kitaysky, 2002; Wingfield and Ramenofsky, 1999). In a previous study, Frigerio et al. (2004) showed a negative correlation in early winter between corticosterone (C) and low temperatures in male Greylag geese the night before and a positive correlation with low air pressure the previous afternoon. Generally these relationships could reflect the involvement of C in thermoregulation and of air pressure as a parameter used by the geese to predict the weather prior to reproduction and migration. Therefore, in this study we aim to evaluate whether and how air pressure and temperature relate to the fine-tuning of behaviour, C

and testosterone (T) metabolites as measured in the faeces of both sexes of semi-tame Greylag geese and Northern bald ibis. To estimate the reaction periods, we measured the impact of temperature and air pressure on C and T levels 6, 12 and 24 h prior to defecation. In addition, we examined possible influences of temperature, air pressure and C and T on behavioural parameters.

A primary mechanism, called allostasis, controlled by the hypothalamic–pituitary–adrenal axis and the production of catecholamines and glucocorticoids (McEwen and Seeman, 1998a), is used to cope with stress to respond to, and balance, unpredictable environmental variations (Wingfield and Ramenofsky, 1999; Elkins, 1988). Glucocorticoids may increase food intake, mobilize energy reserves by increased gluconeogenesis (Whirledge and Cidlowski, 2010), increase catabolism of fat and proteins (Wingfield and Ramenofsky, 1997) and may also affect the immune system in various ways (Greenberg and Wingfield, 1987; McEwen et al., 1997). In contrast, the production of T depends on light regime (Fail and Whitsett, 1988; Andersson et al., 1998; Frungieri et al., 2005), food availability, and social context (Wingfield et al., 1983; Wingfield et al., 1992).

Fluctuations of ambient temperature and air pressure act as external Zeitgebers (Elkins, 1988), which determine rhythms of

* Corresponding author. Tel.: +43 664 2226490; fax: +43 7616 85104.
E-mail address: dornseb@hotmail.com (S. Dorn).

physiology and behaviour (Nelson, 1995). In birds C is one central metabolic hormone, which is involved in maintaining body temperature at low ambient temperatures (Withers, 1992; Wingfield and Ramenofsky, 1999).

Therefore, during winter time birds can react with higher basal metabolic rates in combination with metabolic enzymes (Marsh, 1981; Lundgren and Kiessling, 1985; Lundgren and Kiessling, 1986; Lundgren, 1988; Pelters et al., 1999; Liknes and Swanson, 2011). In addition, C level changes can trigger spring migration (Von Holst, 1998; Elkins, 1965), reproduction and moult (Wingfield and Kenagy, 1991).

Inclement weather triggers the synthesis of C, which in turn, may inhibit T (in *Fringilla melodia*, Wingfield and Silverin, 1986; DeNardo and Sinervo, 1994b), affecting aggression (in *Melospiza melodia*; Wingfield and Silverin, 1986), male sexual behaviour and parental care (Deviche, 1983). The antagonistic interaction between C and T could be elicited by the blocking of the gonadotropin-releasing hormone (Dubey and Plant, 1985) and the luteinizing-hormone (Connolly and Callard, 1987; Etches et al., 1984) or by the binding of glucocorticoids to corticosteroid binding globulin (Deviche et al., 2001). In addition, a negative influence of the gonadotropin-inhibitory hormone on the luteinizing-hormone in combination with prolonged stress in male rats has been observed (Kirby et al., 2009).

In numerous birds, during late winter and spring time the highest amounts of T (Hannon and Wingfield, 1990; Garamszegi et al., 2005; Romero et al., 2006), of expression of androgen receptors (Leska et al., 2012), of C (Breuner and Orchinik, 2001; Deviche et al., 2001) and of corticosteroid binding globulins (Assenmacher et al., 1975; Silverin, 1986; Romero and Wingfield, 1998; Romero et al., 1998b) have been shown.

Greylag geese (*Anser anser*) adapt well to broad temperature variations and alternating weather conditions. They are facultative migrants depending on food availability (Lorenz, 1979; Rutschke, 1982; Bluhm, 1988). Generally, the annual life phases of different types of geese differ when responding to similar annual cycles of hormone T and C production, which implies that this response is ingrained (Dittami, 1981; Wingfield and Farner, 1980; Akesson and Raveling, 1981; Hirschenhauser et al., 1999b). In Greylag geese, T increases consistently from December to March to prepare courtship and mating (Hirschenhauser et al., 1999a,b). C begins to rise in February and remains elevated in March during courtship. During winter, geese show moderate levels of C and T (Hirschenhauser et al., 1999b). Blokpoel (1978) and Richardson (1978) showed a linkage between C levels and migration behaviour in snow geese (*Anser caerulescens*). This linkage, plus the findings that C levels are dependent on air pressure and temperature in male Greylag geese (Frigerio et al., 2004) during early winter, may hint at a generalized gradual reaction mechanism that adjusts physiology and behaviour patterns to environmental variations. Thus, for geese we expected that during late winter low temperature and higher air pressure would increase C in combination with decreased behavioural activity e.g., more standing and lying, less walking, feeding or preening.

In contrast, the other study species, Northern bald ibis (*Geronticus eremita*), is a member of the ibis family and hence, of tropical origin. Generally this would mean that the ibis' physiology is sensitive to cold temperatures. Similar to geese, ibis may adjust migration and reproductive behaviour in the spring and fall depending on ambient weather conditions and food availability (Del Hojo et al., 1992). In our study, focal birds faced winter, with cold environmental conditions, which should lead to physiological and behavioural reactions. As in other birds of tropical origin, T values are quite low in Northern bald ibis throughout the year, but the levels increase prior to mating (Sorato and Kotrschal, 2006; Heath et al., 2003; Garamszegi et al., 2005). C decreases

moderately from January to February, increasing again during mating time (Sorato and Kotrschal, 2006). No correlation between excreted C levels and previous night temperatures was found. A study of Fritz et al. (2006) showed that C levels in Northern bald ibis increase before migration, driving physiological adaptation in preparation for migration. This fact indicates that during winter-time the ibis' C and related activity levels fluctuate in response to ambient weather conditions. Thus, we expected that similar as in geese, decreased behavioural activity would accompany elevated C levels also in ibis. Since the ibis family is of tropical origin, we also expected a greater C response and more passive behaviour and possibly, a different timing of such a response, as compared to geese.

In addition, we expected higher levels of T in geese as compared to ibis, which, as other colonial species of tropical origin, should excrete lower T levels and similar amounts of T in males and females. This assumption bases on studies in American white ibis (*Eudocimus albus*, Heath et al., 2003) and other tropical species (Levin and Wingfield, 1992; Lormee et al., 2000), living in colonies. We did not expect a distinct antagonistic effect of increased C on T levels, because this has only been observed when inclement weather produces chronically high C for days (DeNardo and Licht, 1993; Deviche, 1983).

2. Materials and methods

2.1. Study animals

2.1.1. *Anser anser*

We focused on six male and six females in stable pair bonds with a wide range of ages (MW \pm SD: 6.08 \pm 4.06 year of age) which were part of a free-ranging, nonmigratory flock of Greylag geese, introduced into the Upper Austrian valley of the river Alm by Konrad Lorenz in 1973 (Lorenz, 1988). All study animals could be identified by specified colored rings on their legs. Geese are habituated to human presence and do not significantly change heart rate when familiar humans approach (Wascher et al., 2011). The flock is subject to natural selection (Hemetsberger, 2002) and is supplemented with food twice per day. From October to February, geese form a homogenous flock of around 160 individuals, consisting of families, couples and singletons. Geese are long-term monogamous and socially complex (Kotrschal et al., 2010; Lorenz, 1988; Rutschke, 1982). From December to March, geese were observed and their behaviours were recorded on a daily basis from 0730 to 0800 and 1500 to 1600 close to the Konrad Lorenz Research Station at the River Alm or in the Cumberland Game Park. At night the geese roost at a Lake (Almsee), 10 km to the south.

2.1.2. *Geronticus eremita*

A stable, nonmigratory and free-roaming population of this critically endangered species was re-established from zoo offspring at the Konrad Lorenz Forschungsstelle (KLF), starting in 1997. Within the colony, males are dominant over females and older birds rank higher than younger birds (Pegoraro, 1996; Del Hojo et al., 1992; Cramp, 1998; Sorato and Kotrschal, 2006). Focal birds (below) were part of a local colony of 30 individuals (Kotrschal, 2004) well habituated to the presence of humans. As in geese, ibis were identified by specified colored rings on their legs. During the daily observation period (from 0800 to 0900 and 1600 to 1700) the animals had access to an open aviary, which they use as a night roost but also during the day. Only during the winter months, ibis are fed in the aviary twice daily. In general their behaviour hardly differed from birds living in the wild, as judged by their independent reproduction and breeding (Tintner, 2000; Pegoraro, 1996).

In this study, 12 individuals (4 males, 8 females) were included, representing a range of age (MW \pm SD: 3.25 \pm 0.75 years of age) and dominance. As the colony consisted of young individuals (3 years old maximum), no paired individuals were available as focals.

2.2. Data collection

2.2.1. Behaviour

On days of fecal sampling each individual was observed twice per day for 3 min, one hour before feeding. Feeding times were dependent on daylight and presence of focus individuals on study site, resulting in a switch of around 1 h later during the 4 months examination period. In the case of paired geese, males and females were recorded at the same time. In geese, duration of behaviours were grouped in passive: standing, lying and head under wing and active: walking, swimming, flying, greeting, preening, nibbling, feeding, extreme head up, head up, head low and aggressive behaviours (Lorenz, 1988; Lambrecht, 1986). In Northern bald ibis we coded standing, ducking head and sunbathing as passive and walking, running, flying, picking, feeding, greeting, pecking, bathing, cleaning, threatening, and beating wings as active behaviours (Pegoraro, 1996).

2.2.2. Air pressure and temperature

The study area at the KLF is situated in an Alpine valley 550 m above sea level. Mean annual temperature is 7.3 °C, average rainfall is at 1550 mm, representing typical alpine pre-hibernal and hibernal weather conditions with quickly varying temperature and air pressure. Air pressure and temperature were continuously recorded by our local weather station. Over one minute intervals temperature and air pressure values were measured in degrees of Celsius (°C), respectively Pascal (Pa), by a solar-energy powered weather station (TMBogner & Lehner OEG), located close to the KLF, situated in a distance of up to 500 m to the areas where behaviour/faeces were sampled. Data were stored on an internal data logger. After being read out in weekly intervals 10 min means of temperature and air pressure were calculated. During observation period from 5th of December 2001 to 16th of March lowest temperature levels were measured between 2300 and 0900 and highest levels between 1300 and 1500. In the study of Frigerio et al. (2004; from 9th November to 14th December) lowest temperatures were measured between 2300 and 0100 and 1800 and 2000 and highest values from 0000 to 0300 and from 1100 to 1400. In contrast, in this study highest air pressures occurred from 2300 to 0200 and lowest from 1300 to 1600 and 2300 to 0100. In comparison to the study of Frigerio et al. (2004) minimum air pressure levels were found from 0000 to 0300 and 1200 to 1400 and maximum values between 2200 and 0100. Comparing the temperature values from this study with the study of Frigerio et al. (2004), the minimum temperature was -22.7 °C versus -16.7 °C, the maximum 20.9 °C versus 10.9 °C and the mean values were -6.5 °C versus -5.7 °C. Regarding the air pressure levels in this study the minimum value was 932 Pa, the maximum 974.3 Pa and the mean 955.4 Pa. During observation period the study of Frigerio et al. (2004), the minimum air pressure value was measured at 930.7 Pa, the maximum at 969.8 Pa and the mean at 952.8 Pa.

2.2.3. Fecal samples

Between 5th December 2001 and 16th March 2002 in geese on 26 and in ibis on 27 days fecal samples were collected for the analysis of immuno-reactive metabolites of corticosterone (C) and testosterone (T) by enzyme-immunoassay. In detail, one sample per individual and samples of individuals of one species were collected by day. Due to weather conditions or absence of individuals we did not manage to sample all individuals on all of these days (in geese, nine missing samples, in ibis one missing sample). Overall,

303 fecal samples were collected in geese and 323 in ibis. All samples were collected from 0730 to 1700 immediately after defecation and subsequently frozen at -20 °C within one hour of sampling as described by Hirschenhauser (1998). Non-invasive sampling was chosen, because animals do not need to be handled, which avoids stress; also, hormone values of fecal samples generally co-vary with systemic levels (Palme and Möstl, 1993; Hirschenhauser et al., 2000; Kotschal et al., 2000).

2.3. Assay of fecal steroids

Excreted metabolites were analyzed by enzyme immuno assay (EIA) by use of group-specific antibodies (Möstl et al., 1987). This method was validated for geese (Kotschal et al., 2000); generally, peaks of fecal metabolites appear in droppings with a time-lag of 2–4 h, (Möstl et al., 2005; Frigerio et al., 2004). Greylag geese have a short gut passage time of 2–3 h. The gut passage time of Northern bald ibis has not been evaluated until now, but in American white ibis, which is closely related to Northern bald ibis and has similar body size and food spectrum, gut passage time is 2–3 h (Adams et al., 2009) and hence, exactly in the range of geese.

EIA was employed for the quantitative analysis of C and T metabolites in faeces of geese and ibis (geese: Möstl et al., 1987; Kotschal et al., 1998; Hirschenhauser et al., 1999b; ibis: John Dittami, unpublished data). T metabolite levels were determined by an existing androgen assay mainly against 4-androsten-17 β -ol-3-one (potentially androstenedione and DHEA; Hirschenhauser et al., 1999b) and C concentrations by an assay against 11 β -hydroxyetiocholanolone (Frigerio et al., 2004). For cross-reactivity see references above. For T metabolites, the concentration limits for reliable measurements were between 0.05 ng/g and 99.23 ng/g in geese and between 0.73 ng/g and 174.31 ng/g in ibis. For C metabolites this range was between 1.1 ng/g and 288.7 ng/g in geese and 0.27 ng/g to 847.69 ng/g in ibis. The mean intra- and inter-assay coefficients of variation were calculated from 10 (from one plate), respectively 20 homogenized and pooled samples. In geese the intra-assay coefficient was 21.4% for T and 15.1% for C. In ibis it was 22.9% for T and 32.4% for C. In addition, the inter-assay coefficients were 36.8% and 19.7% for T and 24.3% and 21.3% for C in geese, respectively ibis. These values are relatively typical for this method (Kotschal et al., 2000; Sorato and Kotschal, 2006). For T the standard curves ranged from 0.33 to 80 pg/well and for C from 2.05 to 500 pg/well.

2.4. Statistics

We related behavioural parameters and hormone levels to the minimum and maximum temperatures and air pressures 6, 12 or 24 h before sampling, because both parameters may be used by individual geese and ibis to predict unfavourable weather conditions (Frigerio et al., 2004). In detail, we evaluated the minimum and maximum temperatures and air pressures within time frames of 6, 12 and 24 h before individual defecation times respectively sampling for correlation analysis. In geese and ibis, the mean sampling time points were nearly the same during observation time (in geese: MW = 1006 \pm 0205 SD; in ibis: MW = 1023 \pm 0139 SD), indicating a similar effect of weather on hormone levels. In this study we examined the influence of temperature and air pressure in a time period 24 h prior to sampling the droppings for hormone analysis on behaviour and on C and T levels. Via Generalized Linear Mixed Models (GLMMs), a multivariate regression analysis, we calculated random and fixed effects on non-normally distributed response variables. We calculated four GLMMs with Gamma error distribution and log link function. Response variables were ng/g C, ng/g T, duration of active and duration of passive behaviour. Date, sex, age, minimum temperature, minimum air pressure, each of

which a measure was taken 6 h, 12 h and 24 h prior to defecation and behaviour (active, passive) were used in the case of the C and T model. To account for repeated measures, individual and species were included as random factors. In order to select the best fitting model, we used a combination of stepwise model reduction and the second order Akaike's information criterion (AICc), starting with all main effects and stepwise reducing the least significant factor, which remained excluded from the model if dropping it reduced the AICc. When dropping non-significant factors did not improve the AICc, they were re-entered into the model. In order to exclude species differences in the effects of weather parameters on hormone excretion and behaviour, we included interactions between species (ibis, geese) and all fixed factors remaining in the final model, which were all non-significant, except for passive behaviour. For examining a possible relation between mean hourly temperature and mean hourly air pressure at days of behaviour and fecal sampling, a spearman's correlation for nonparametric data was done. All tests were performed in SPSS 19.0.

3. Results

Overall, hourly mean temperature was significantly and negatively correlated with mean hourly air pressure at the sampling days, (Spearman's correlation: $r_s = -0.6$; $n = 1272$, $P < 0.0001$).

3.1. Relationships of weather parameters and hormone excretion

In geese and ibis, males excreted more corticosterone (C) than females ($F = 5.439$, $df_1 = 1$, $df_2 = 613$, $P = 0.02$; Fig. 1). In males and females of geese and ibis high C excretion was significantly correlated with low minimum temperatures in the 24 h ($F = 23.243$, $df_1 = 1$, $df_2 = 613$, $P < 0.001$; Fig. 2A) before defecation. In addition, male and female geese and ibis excreted high C levels with high air pressure values (6 h: min: $F = 9.407$, $df_1 = 1$, $df_2 = 613$, $P = 0.02$; Fig. 2B; max: $F = 8.854$, $df_1 = 1$, $df_2 = 613$, $P = 0.003$; Fig. 2C; 12 h: $F = 9.108$, $df_1 = 1$, $df_2 = 613$, $P = 0.003$; Fig. 2D). In geese and

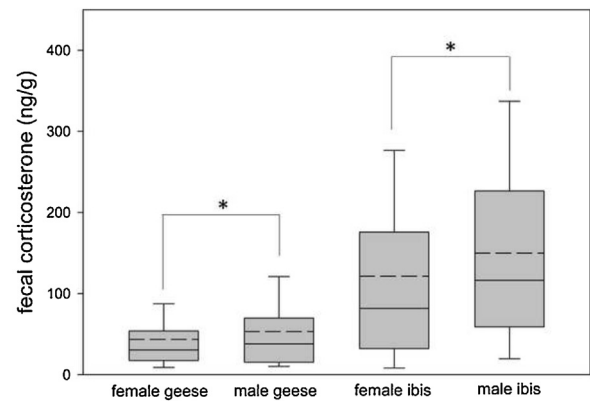


Fig. 1. Male geese and ibis excreted higher levels of C than female geese and ibis. The excreted levels of C of male and female geese and ibis are plotted as box plots with 25th–75th percentiles. The bars mark 90–10% intervals. The continuous midlines indicate the median and the dotted midlines the average. In both species the difference of C excretion between females and males was calculated by GLMM analysis (Section 2.4).

ibis, excreted high testosterone (T) levels significantly correlated with high minimum temperature ($F = 3.975$, $df_1 = 1$, $df_2 = 608$, $P = 0.047$; Fig. 3A) 12 h and maximum temperature ($F = 21.01$, $df_1 = 1$, $df_2 = 608$, $P < 0.001$; Fig. 3B) 24 h prior to excretion. Minimum temperature 24 h prior to excretion remained in the final model although it was not significant ($F = 3.547$, $df_1 = 1$, $df_2 = 608$, $P = 0.06$).

3.2. Weather, hormones and behaviour

In geese and ibis, males showed significantly less active behaviour than females ($F = 4.765$, $df_1 = 1$, $df_2 = 610$, $P = 0.029$; Fig. 4), in females and males less active behaviour significantly correlated with high C levels ($F = 4.106$, $df_1 = 1$, $df_2 = 610$,

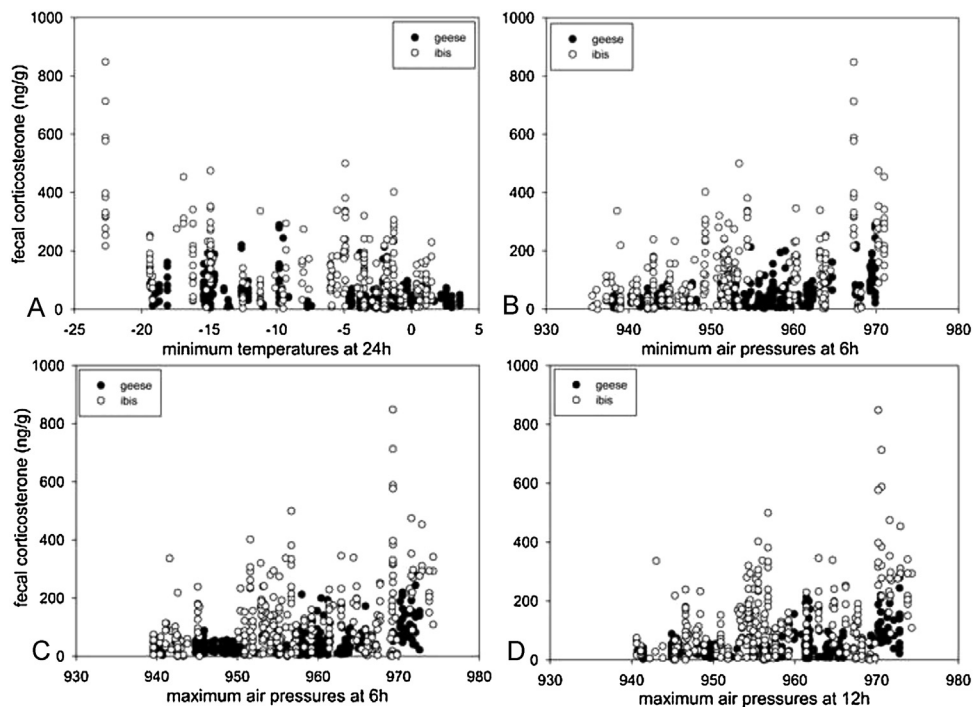


Fig. 2. Correlations of minimum temperature, minimum and maximum air pressures with excreted C levels 6–24 h before in geese and ibis. The individual C and the minimum temperature values with a time period of 24 h (A), the minimum air pressure values with a time period of 6 h (B) and the maximum air pressure values with time periods of 6 (C) and 12 h (D) before defecation are plotted.

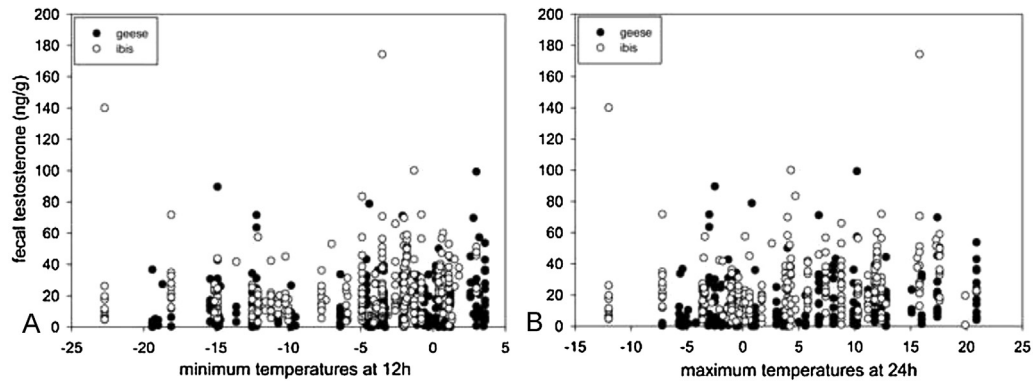


Fig. 3. Minimum temperatures 12 and maximum temperatures 24 h correlated with the excretion of T metabolites in geese and ibis. The minimum temperature values 12 (A) and the maximum temperature values 24 h (B) prior to defecation and the individual excreted T levels are shown.

$P=0.043$; Fig. 5A) and with maximum air pressure ($F=14.153$, $df_1=1$, $df_2=610$, $P<0.0001$; Fig. 5B) 6 h prior to defecation; more active behaviour correlated with minimum air pressure ($F=10.771$, $df_1=1$, $df_2=610$, $P<0.001$; Fig. 5C) and maximum temperature ($F=28.845$, $df_1=1$, $df_2=610$, $P<0.0001$; Fig. 5D) 24 h prior to defecation.

Time spent with more passive behaviour in ibis and geese significantly correlated with maximum air pressure 12 h ($F=6.361$, $df_1=1$, $df_2=620$, $P=0.012$; Fig. 6A) and minimum air pressure 24 h ($F=6.208$, $df_1=1$, $df_2=620$, $P=0.013$; Fig. 6B) prior to defecation. Furthermore, less passive behaviour correlated with minimum temperature ($F=69.250$, $df_1=1$, $df_2=620$, $P<0.0001$; Fig. 6C) 24 h prior to defecation.

3.3. Hormone relations

We found a significant interaction between T and species onto excreted C ($F=5.686$, $df_1=2$, $df_2=613$, $P=0.004$; Fig. 7). As expected, excreted T significantly decreased with increasing C metabolites in geese whereas in ibis we found no such effect.

4. Discussion

In this study, we examined the influence of the environmental factors temperature and air pressure in late winter on behaviour and on corticosterone (C) and testosterone (T) levels in the 24 h period prior to being excreted in Greylag geese and Northern bald

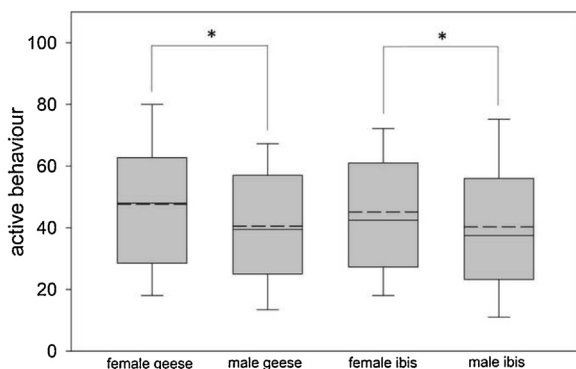


Fig. 4. Female geese and ibis showed more active behaviour patterns than male geese and ibis. The graph shows comparisons of overall active behaviour of female and male geese and ibis during observation period plotted as box plots with 25th to 75th percentiles. The bars mark 90 to 10% intervals. The continuous midlines represent the median and the dotted midlines the average. For the analysis of difference of active behaviour between females and males in both species GLMM analysis was used (Section 2.4).

ibis. When temperatures were low 24 h before sampling, geese and ibis excreted high C levels. In contrast, in both species, low C levels correlated with high air pressure 6–12 h before sampling. In geese and ibis, behavioural activity was negatively correlated with C levels and temperature 24 h prior to excretion and positively correlated with air pressure 6–24 h prior to excretion. In both species, T levels correlated in a positive way with temperature values 12–24 h before sampling.

We found low active behaviour to be correlated with high levels of C, which may support the maintenance of homeostasis (Wingfield and Ramenofsky, 2011). Especially during wintertime, when extreme environmental conditions increase the energetic demands of thermoregulation higher levels of C can be produced, which can lead as a consequence to lower activity to ensure survival. Although no higher levels of feeding were observed, a reduction of active behaviour can be associated with gain of mass in preparation of migration (Gwinner, 1990; Klaassen and Biebach, 1994) or to outlast extreme weather conditions (Wingfield and Ramenofsky, 1999). Behavioural activity was positively associated with maximum temperature of a time period of 24 h prior to defecation. However, we found a negative correlation of behavioural activity with minimum temperature 24 h before. These findings support the assumption that enhanced C levels were connected to low rates of active behaviour in the context of maintaining physiological balance. Geese and ibis are migratory birds and temperature essentially influences migration preparation and is involved in timing of the departure of migration. In addition, food availability is also an important factor for triggering migration. Our study individuals are part of free-ranging, nonmigratory flocks, which show behavioural patterns of restlessness during fall and early spring before courtship (geese: Lorenz, 1979; Rutschke, 1982; ibis: Fritz et al., 2006). The birds are able to stay during winter because they are food-supplemented. Therefore, during wintertime they are exposed to cold temperatures and are expected to react physiologically to these conditions for survival and migration preparation.

Similarly, high testosterone (T) levels can contribute to a higher degree of fat deposition (Wingfield et al., 1990), and a stronger muscle anabolism (Tonra et al., 2011; Ramenofsky and Wingfield, 2006) may be related to enhanced locomotory activity (Wada, 1986; Ketterson and Nolan, 1992; Wikelski et al., 1999). In the present study, we did not observe a co-variation of T levels with active or passive behaviour.

Previously, Frigerio et al. (2004) showed C to correlate negatively with minimum temperature during the night before in male Greylag geese during early winter. Here, we found this effect with a time delay of 24 h, showing that animals reacted gradually over a time period of 24 h. This timing of birds' C synthesis as response to minimum temperature may enable them the adjustment of their

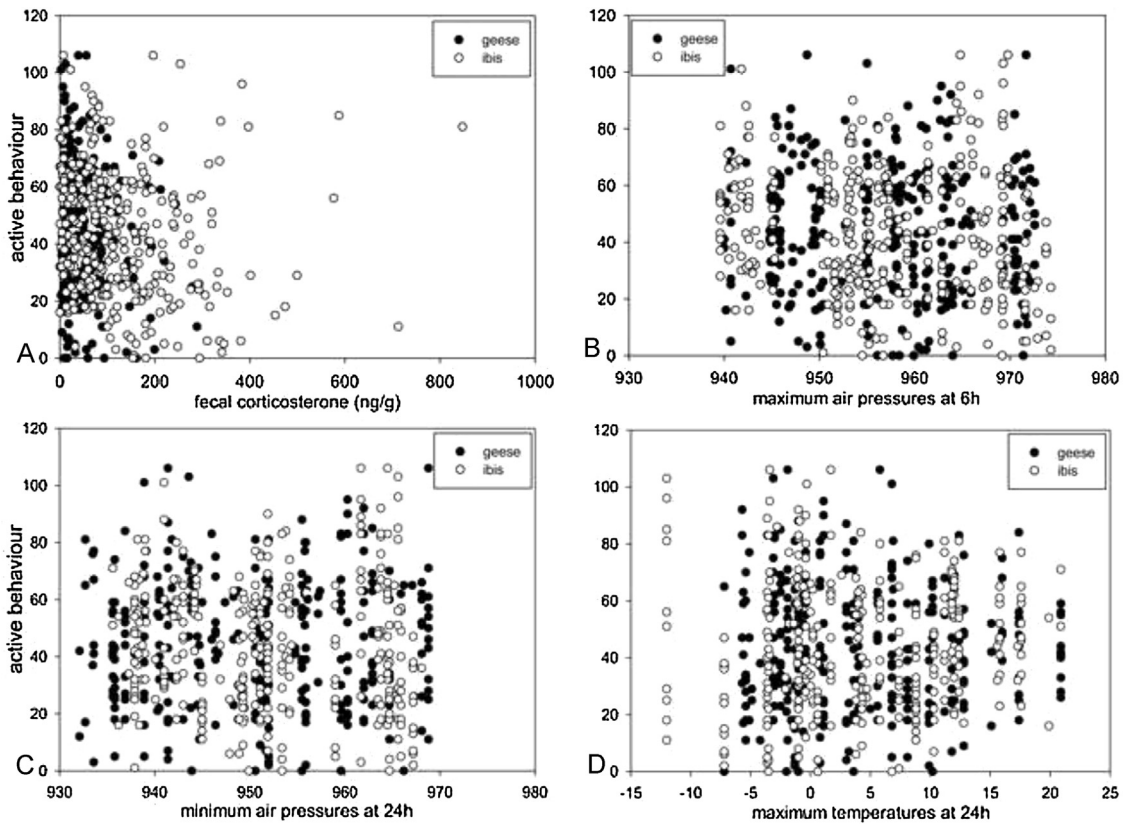


Fig. 5. C levels and minimum air pressure 24 h, maximum air pressure 6 h and maximum temperature before 24 h influenced the frequency of active behaviour patterns of geese and ibis. The graph shows the individual excreted C levels (A), the maximum air pressure values with a time period of 6 h (B), the minimum air pressure values with a time period of 24 h (C), the maximum temperature values with a time period of 24 h (D) before defecation and the active behaviour of geese and ibis.

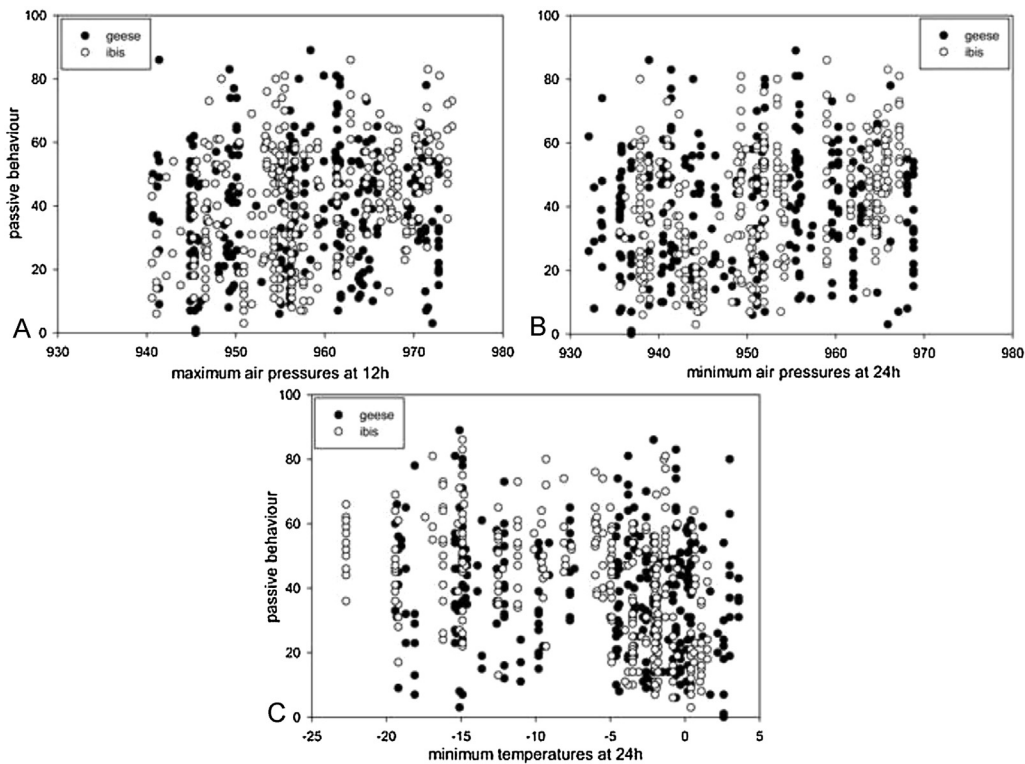


Fig. 6. Correlations of maximum air pressure 12 h, minimum air pressure 24 h and minimum temperature 24 h before defecation with produced C levels in Greylag geese and Northern bald ibis. The individual C levels are shown in combination with the maximum levels of air pressure 12 h, the minimum levels of air pressure 24 h and the minimum temperature levels of 24 h prior to excretion.

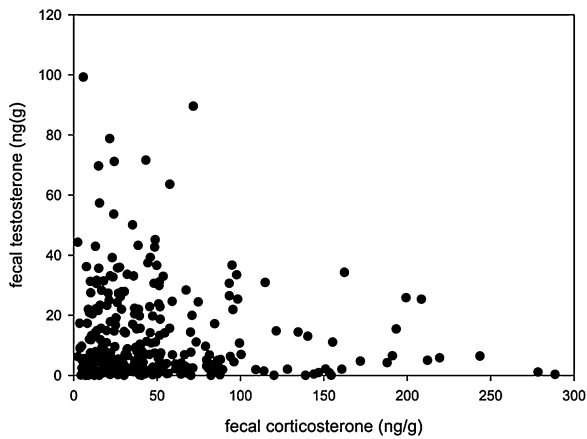


Fig. 7. Excreted T levels are negatively correlated with C levels in Greylag geese. The individual T and C levels are shown over the entire examination period.

physiology in case of cold weather (Hofer and East, 1998; Wingfield et al., 1983; Wingfield et al., 1997b) to ensure allostasis (McEwen, 1998b) and the preparations of migration or reproduction.

Further, we found a negative relationship between C and T in geese, but not in ibis. An inhibiting effect of C on T is well described (Viau, 2002; Lynn et al., 2010). Why we found this effect in geese but not in ibis remains unclear. Either geese were better able to prepare for their socio-sexual phase or migration, both of which occurs earlier in the year than in ibis (Hirschenhauser et al., 1999b), or geese, due to the Northern family origin, were simply better regulators than the ibis, which come from a family of subtropical origin. In addition, we suggest that low T could be a hint that geese responded to exposed stressful and unfavourable weather situations with higher energy mobilization than did the ibis.

We found positive correlations of high temperature with excreted T with a time delay of 12 and 24 h, possibly because high C levels constrained T production in response to adverse conditions (Silverin, 1986; DeNardo and Sinervo, 1994b; Viau, 2002; Lynn et al., 2010). In this context, high C levels support survival and migration preparation, also by temporary down-regulating of non-essential behavioural and metabolic activities, including T.

In this study, we found air pressures 6–24 h prior to defecation to be negatively correlated with excretion of C metabolites and positively correlated with behavioural activity. High levels of C in combination with less active behaviour could be based on the repeated weather conditions of high air pressure with deep temperatures during observation period (compare significant negative correlation between mean temperature and air pressure) to save energy and survival (Wingfield and Ramenofsky, 1999). In addition, air pressure can work as Zeitgeber for migration preparation and migration, as it varies very quickly within few hours (Blokpoel, 1978; Richardson, 1978, reviewed by Alerstam, 1993). High pressure systems can trigger movements of birds during spring (reviewed by Alerstam, 1993; Zalakevicius, 1994; Dokter et al., 2013). Hence, the results of this study could indicate that the study birds are able to adjust their physiology by changing C levels and behaviour to preceding fluctuations of temperature in combination with changes of air pressure for migration preparation.

Males reacted to low temperature and high air pressure 6–24 h before with significantly higher levels of C and a greater decrease in active behaviour than females. In geese, this could be explained by the fact that males excrete significant more T than females during wintertime (Hirschenhauser et al., 1999a), requiring a higher production of C to counteract serve environmental conditions. In

ibis, males and females excreted similar amounts of T, but different amounts of C. This is in alignment with previous findings of behavioural and hormonal similarity between sexes in this species (Sorato and Kotschal, 2006) and in white ibis (Heath et al., 2003). The similar T productions of females and males could be explained by a hypothesis of Wingfield and Farner (1993), stating small difference of T levels between sexes, due to minimal sexual dimorphism and similar sex specific behaviours. The higher C production of males during examination period could reflect a higher sensitivity to unfavourable weather, which could be associated with their general higher status in colony hierarchy.

In summary, the results of our study are parallel to Frigerio et al. (2004). However, there were differences regarding the reaction times of geese in the former study and geese and ibis in this study. In Frigerio et al. (2004) C levels of male geese co-varied with minimum temperatures in early morning and minimum air pressure levels in the previous afternoon. In addition, no correlations were observed between T levels and temperature or air pressure values, nor between temperature and air pressure values. In contrast we found that minimum temperatures 12 h prior to defecation and maximum temperature levels 24 h prior to defecation correlated positively with T levels; minimum temperature 24 h prior to defecation correlated negatively with C levels and minimum air pressure values 6 and 12 h prior to defecation correlated positively with C levels. These differences could be explained by different weather conditions in the two study periods. In the former study, observations were conducted November to mid of December, in contrast to December to March in our study, which was characterized by lower minimum temperature and mean temperature values during the observation time and lower values of minimum and maximum temperatures in the overlapping period between both studies. And finally, during late winter the animals' energy management probably differs from early winter. This is supported by the observed negative influence of C on T in this study in geese, which may be indicative of a higher demand of energy in late winter than during early winter. Another difference between the two studies became evident in the timing of animals' physiological reaction to minimum temperature and air pressure. The percentage of minimum temperature 6 h prior to defecation shifted from 56.5% of the former study to 47.2% of this study in comparison to 12 h and 24 h prior to defecation, respectively, could support a minor importance of minimum temperature of early morning on same day in comparison to minimum temperature of morning on the day before. Regarding the percentage of minimum air pressure in a time frame of 24 h prior to defecation, 65.2% of the former study was decreased to 57.4% of this study, indicating a higher relevance of minimum air pressure 6–12 h before on C production. Sorato and Kotschal (2006) found no correlations between excreted C levels and previous night temperatures in Northern bald ibis. This examination period contained the months January to April (only 4 weeks are overlapping) and thus a big part of the mating time. Therefore, the birds responded more with stronger C levels on social interactions than on extreme weather conditions to satisfy their higher energy demands.

In conclusion, our results show contingencies between weather conditions, hormones and behaviour in two bird species, illustrating fine-tuned physiological and behavioural adjustments to environmental variations. We conclude that these contingencies may be interpreted as allostatic responses to environmental stress (e.g. reduction of reproduction and growth; Wingfield et al., 1997a), but not to social conflicts. Hence, C levels are not only associated with social context, but may be primarily impacted by abiotic factors during periods of high environmental variability, but also depending on seasonal necessities, such as the timing of migration or reproduction status.

Acknowledgements

Funding was provided by the FWF project P15766. In addition, this study was supported by the “Verein der Förderer der Konrad Lorenz Forschungsstelle”. We would like to thank two anonymous reviewers for helpful comments.

References

- Adams, E.M., Frederick, P.C., Larkin, I.L., Guillette Jr., L.J., 2009. Sublethal effects of methylmercury on fecal metabolites of Testosterone, estradiol, and corticosterone in captive juvenile White ibises (*Eudocimus albus*). *Environ. Toxicol. Chem. Vol. 28* (5), 982–989.
- Akesson, T.R., Raveling, D.G., 1981. Endocrine and body weight changes of nesting and nonnesting Canada Geese. *Biol. Reprod.* 25, 792–804.
- Alerstam, T., 1993. *Bird Migration*. Cambridge University Press, Cambridge, UK.
- Andersson, H., Rydhmer, L., Lundström, K., Wallgren, M., Andersson, K., Forsberg, M., 1998. Influence of artificial light regimens on sexual maturation and boar taint in entire male pigs. *Anim. Reprod. Sci.* 51 (1), 31–43.
- Assenmacher, I., Astier, H., Daniel, J.Y., Jallageas, M., 1975. Experimental studies on the annual cycles of thyroid and adrenocortical functions in relation to the reproductive cycle of drakes. *J. Physiol. (Paris)* 70, 507–520.
- Blokpoel, H., 1978. Weather and spring migration of snow geese across southern Manitoba. *Oikos* 30, 350–363.
- Bloom, C.K., 1988. Temporal patterns of pair formation and reproduction in annual cycles and associated endocrinology in waterfowl. In: Johnston, R.F. (Ed.), *Current Ornithology*, 5, pp. 123–185.
- Breuner, C.W., Orchinik, M., 2001. Seasonal Regulation of Membrane and Intracellular corticosteroid receptors in the house sparrow brain. *J. Neuroendocrinol.* 13, 412–420.
- Connolly, P.B., Callard, I.P., 1987. Luteinizing hormone secretion from the quail pituitary in vitro. *Biol. Reprod.* 36, 1238–1246.
- Cramp, S., 1998. *The Complete Birds of the Western Palearctic*. University Press, Oxford, OptiMedia, Cd-ROM.
- Del Hojo, J., Elliott, A., Sargatel, J., 1992. *Handbook of the Birds of the World, 1. Ostrich to Ducks*. Lynx Edicions, Barcelona.
- DeNardo, D.F., Licht, P., 1993. Effects of corticosterone on social behavior of male lizards. *Horm. Behav.* 27, 184–199.
- DeNardo, D.F., Sinervo, B., 1994b. Effects of steroid hormone interaction on activity and home range size of free-living male lizards. *Horm. Behav.* 28, 53–62.
- Deviche, P., 1983. Interactions between adrenal function and reproduction in male birds. In: Mikami, S., Ishii, S., Wada, M. (Eds.), *Avian Endocrinology: Environmental and Ecological Perspectives*. Japan Science Society Press and Springer, Verlag, pp. 243–245.
- Deviche, P., Breuner, C., Orchinik, M., 2001. Testosterone, corticosterone, and photoperiod interact to regulate plasma levels of binding globulin and free steroid hormone in Dark-eyed Juncos, *Junco hyemalis*. *Gen. Comp. Endocrinol.* 122, 67–77.
- Dittami, J.P., 1981. Seasonal changes in the behavior and plasma titers of various hormones in barheaded geese. *Anser indicus*. *Zeitschrift für Tierpsychologie* 55, 289–324.
- Dokter, A.M., Shamoun-Baranes, J., Kemp, M.U., Tijm, S., Holleman, I., Saino, N., 2013. High altitude bird migration at temperate latitudes: a synoptic perspective on wind assistance. *PLoS ONE* 8 (1), e52300.
- Dubey, A.K., Plant, T.M., 1985. A suppression of gonadotropin secretion by cortisol in castrated male rhesus monkeys (*Macaca mulatta*) mediated by the interruption of hypothalamic gonadotropin-releasing hormone release. *Biol. Reprod.* 33, 423–431.
- Elkins, N., 1965. The effect of weather on the long-tailed Duck in Lewis. *Bird Study* 12, 132–134.
- Elkins, N., 1988. *Weather and Bird Behavior*. T & AD POYSER, 111–127.
- Etches, R.J., Williams, J.B., Rzasza, J., 1984. Effects of corticosterone and dietary changes in the hen on ovarian function, plasma LH and steroids and the response to exogenous LH-RH. *J. Reprod. Fertil.* 70, 121–130.
- Fail, P.A., Whitsett, J.M., 1988. Influence of photoperiod, ambient temperature and melatonin on testosterone synthesis and release during reproductive maturation in male deer mice. *J. Androl.* 9 (1), 21–30.
- Frigerio, D., Dittami, J., Mostl, 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.
- Fritz, J., Feurle, A., Kotrschal, K., 2006. Corticosterone pattern in Northern Bald Ibises during a human-led migration. *Abstr. J. Ornithol.* 147/5, 168.
- Frungerio, M.B., Mayerhofer, A., Zitta, K., Pignataro, O.P., Calandra, R.S., Gonzalez-Calvar, S.I., 2005. Direct effect of melatonin on Syrian hamster testes: melatonin subtype 1a receptors, inhibition of androgen production, and interaction with the local corticotropin-releasing hormone system. *Endocrinology* 146 (3), 1541–1552.
- Garamszegi, L.Z., Eens, M., Hurtrez-Bousses, S., Moller, A.P., 2005. Testosterone, testes size, and mating success in birds: a comparative study. *Horm. Behav.* 47, 389–409.
- Gwinner, E., 1990. Circannual rhythms in bird migration: Control of temporal patterns and interactions with photoperiod. In: Gwinner, E. (Ed.), *Bird Migration: Physiology and Ecophysiology*. Springer-Verlag, Berlin, pp. 257–268.
- Greenberg, N., Wingfield, J.C., 1987. Stress and reproduction: reciprocal relationships. In: Norris, D.O., Jones, R.E. (Eds.), *Reproductive Endocrinology of Fishes, Amphibians and Reptiles*. Wiley, New York, pp. 389–426.
- Hannon, S.J., Wingfield, J.C., 1990. Endocrine correlates to territoriality, breeding stage and body molt in free-living willow ptarmigan of both sexes. *Can. J. Zool.* 68, 2130–2134.
- Heath, J.A., Frederick, P.C., Edwards, T.M., Guillette, L.J., 2003. Reproductive physiology of free-living White Ibises (*Eudocimus albus*) in the Florida Everglades. *Gen. Comp. Endocrinol.* 133, 118–131.
- Hemetsberger, J., 2002. *Die Entwicklung der Grünauer Graugansschar (Anser anser) seit 1973*. Institute of Zoology, University of Vienna, Austria, Ph.D. thesis.
- Hirschenhauser, K., 1998. Steroidhormone aus Kot und Sozialverhalten bei Graugänsen (*Anser anser*). Institute of Zoology, University of Vienna, Austria, Ph.D. thesis.
- Hirschenhauser, K., Möstl, E., Kotrschal, K., 1999a. Within testosterone covariation and reproductive output in Greylag Geese *Anser anser*. *British Ornithologists' Union, Ibis* 141, 577–586.
- Hirschenhauser, K., Möstl, E., Kotrschal, K., 1999b. Seasonal patterns of sex steroids determined from feces in different social categories of greylag geese (*Anser anser*). *Gen. Comp. Endocrinol.* 114, 67–79.
- Hirschenhauser, K., Möstl, E., Peczeley, P., Wallner, B., Dittami, J., Kotrschal, K., 2000. Seasonal relationships between plasma and fecal testosterone in response to GnRH in domestic ganders. *Gen. Comp. Endocrinol.* 118, 262–272.
- Hofer, H., East, M.L., 1998. *Biological Conservation and Stress*. Academic Press 1998. *Adv. Study Behav.* 27, 405–497.
- Jacobs, L.F., 1996. The economy of winter: phenotypic plasticity in behavior and brain structure. *Biol. Bull.* 191, 92–100.
- Ketterson, E.D., Nolan Jr., V., 1992. Hormones and life histories: an integrative approach. *Am. Nat.* 140 (suppl), 33–62.
- Kirby, E.D., Geraghty, A.C., Ubuka, T., Bentley, G.E., Kaufer, D., 2009. Stress increases putative gonadotropin inhibitory hormone and decreases luteinizing hormone in male rats. *Proc. Natl. Acad. Sci. USA* 106, 11324–11329.
- Klaassen, M., Biebach, H., 1994. Energetics of fattening and starvation in the long-distance migratory garden warbler, *Sylvia borin*, during the migration phase. *J. Comp. Physiol. B* 164, 362–371.
- Kotrschal, K., Hirschenhauser, K., Möstl, E., 1998. The relationship between social stress and dominance is seasonal in greylag geese. *Anim. Behav.* 55, 171–176.
- Kotrschal, K., Dittami, J., Hirschenhauser, K., Möstl, E., Peczeley, P., 2000. Effects of physiological and social challenges in different season on fecal testosterone and corticosterone in male domestic geese. *Acta Ethol.* 2 (2), 115–122.
- Kotrschal, K., 2004. News from the Grunau semi-wild colony of Waldrapp ibis. *IAGNBI News* n., 1.
- Kotrschal, K., Scheiber, I.B.R., Hirschenhauser, K., 2010. Individual performance in complex social systems. In: Kappeler, P. (Ed.), *Animal Behaviour: Evolution & Mechanism*. Springer Verlag, Heidelberg, pp. 121–148.
- Lambrecht, J., 1986. Structure and causation of the dominance hierarchy in a flock of bar-headed geese (*Anser indicus*). *Behavior* 96, 28–46.
- Leska, A., Kiezun, J., Kaminska, B., Dusza, L., 2012. Seasonal changes in the expression of the androgen receptor in the testes of the domestic goose (*Anser anser f. domestica*). *Gen. Comp. Endocrinol.* 179, 63–70.
- Levin, R., Wingfield, J.C., 1992. Control of territorial aggression in tropical birds. *Ornis Scandinavica* 23, 284–291.
- Liknes, E.T., Swanson, D.L., 2011. Phenotypic flexibility in passerine birds: seasonal variation of aerobic enzyme activities in skeletal muscle. *J. Therm. Biol.* 36, 430–436.
- Lormee, 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.
- Lorenz, K., 1979. *The Year of the Greylag Goose*. Eyre Methuen, London.
- Lorenz, K., 1988. *Hier bin ich—wo bist du? Ethologie der Graugans*. Piper Verlag, Munich, Germany.
- Lundgren, B.O., Kiessling, K.H., 1985. Seasonal variation in catabolic enzyme activities in breast muscle of some migratory birds. *Oecologia* 66, 468–471.
- Lundgren, B.O., Kiessling, K.H., 1986. Catabolic enzyme activities in the pectoralis muscle of premigratory and migratory juvenile reed warblers *Acrocephalus scirpaceus* (Herm.). *Oecologia* 68, 529–532.
- Lundgren, B.O., 1988. Catabolic enzyme activities in the pectoralis muscle of migratory and non-migratory goldcrests, great tits and yellowhammers. *Ornis Scandinavica* 19, 190–194.
- Lynn, S.E., Stamplis, T.B., Barrington, W.T., Weida, N., Hudak, C.A., 2010. Food, stress, and reproduction: short-term fasting alters endocrine physiology and reproductive behavior in the zebra finch. *Horm. Behav.* 58, 214–222.
- Marsh, R.L., 1981. Catabolic enzyme activities in relation to premigratory fattening and muscle hypertrophy in the gray catbird (*Dumetella carolinensis*). *J. Comp. Physiol. B* 141, 417–423.
- McEwen, B.S., Biron, C.A., Brunson, K.W., Bulloch, K., Chambers, W.H., Dhabhar, F.S., Goldfarb, R.H., Kitson, R.P., Miller, A.H., Spencer, R.L., Weiss, M., 1997. Neural–endocrine–immune interactions: the role of adrenocorticoids as modulators of immune function in health and disease. *Brain Res. Rev.* 23, 79–133.
- McEwen, B.S., Seeman, T., 1998a. Protective and damaging effects of mediators of stress. *Ann. NY Acad. Sci.* 896, 30–47.
- McEwen, B.S., 1998b. Stress, Adaptation, and Disease: Allostasis and Allostatic Load. *Ann. NY Acad. Sci.* 840, 33–44.

- Möstl, E., Meyer, H.H., Bamberg, E., Hegel, von, G., 1987. Oestrogen determination in faeces of mares by enzyme immunoassay on microtitre plates. Proc. of the Symp. Anal. Steroids, Sopron, Hungary, 219–224.
- Möstl, E., Rettenbacher, S., Palme, R., 2005. Measurement of corticosterone metabolites in bird's droppings: an analytical approach. Ann. NY Acad. Sci. 1046, 17–34.
- Nelson, R.J., 1995. An Introduction to Behavioral Endocrinology. Sinauer Associates, Sunderland, MA, USA.
- Palme, R., Möstl, E., 1993. Biotin-Streptavidin enzyme immunoassay for the determination of oestrogens and androgens in boar faeces. In: Proc. of the 5th Symp. on the Analysis of Steroids. (ed. S.GÖRÖG) Szombathely, Hungary.
- Pegoraro, K., 1996. Der Waldrapp. Aula Verlag.
- Pelsters, M.M., Lutgerink, J.T., Nieuwenhoven, F.A., Tandon, N.N., van der Vusse, G.J., Arends, J.W., Hoogenboom, H.R., Glatz, J.F., 1999. A sensitive immunoassay for rat fatty acid translocase (CD36) using phage antibodies selected on cell transfectants: abundant presence of fatty acid translocase/CD36 in cardiac and red skeletal muscle and up-regulation in diabetes. Biochem. J. 337, 407–414.
- Richardson, W.J., 1978. Timing and amount of bird migration in relation to weather: a review. Oikos 30, 224–272.
- Ramenofsky, M., Wingfield, J.C., 2006. Behavioral and physiological conflicts in migrants: the transition between migration and breeding. J. Ornithol. 147, 135–145.
- Romero, L.M., Wingfield, J.C., 1998. Seasonal changes in adrenal sensitivity alter corticosterone levels in Gambel's white-crowned sparrows (*Zonotrichia leucophrys gambelii*). Comp. Biochem. Physiol. 119 (C), 31–36.
- Romero, L.M., Soma, K.K., Wingfield, J.C., 1998b. Hypothalamic–pituitary–adrenal axis changes allow seasonal modulation of corticosterone in a bird. Am. J. Physiol. 274, 1338–1344.
- Romero, L.M., Cyr, N.E., Romero, R.C., 2006. Corticosterone responses change seasonally in free-living house sparrows (*Passer domesticus*). Gen. Comp. Endocrinol. 149, 58–65.
- Rutschke, E., 1982. Stability and dynamics in the social structure of the Greylag goose (*Anser anser*). Aquila 89, 39–55.
- Silverin, B., 1986. Corticosterone-binding proteins and behavioral effects of high plasma levels of corticosterone during the breeding period in the pied flycatcher. Gen. Comp. Endocrinol. 64, 67–74.
- Sorato, E., Kotrschal, K., 2006. Hormonal and behavioral symmetries between the sexes in the Northern bald ibis. Gen. Comp. Endocrinol. 146, 265–274.
- Tintner, A., 2000. Sozialer Einfluss auf Wachstum und Verhaltensentwicklung bei Waldrapp-Nestlingen. Diplomarbeit Uni Wien.
- Tonra, C.M., Marra, P.P., Holberton, R.L., 2011. Early elevation of testosterone advances migratory preparation in a songbird. J. Exp. Biol. 214, 2761–2767.
- Viau, V., 2002. Functional cross-talk between the hypothalamic–pituitary–gonadal and –adrenal axes. J. Neuroendocrinol. 14, 506–513.
- Von Holst, D., 1998. The Concept of Stress and Its Relevance for Animal Behavior. Academic Press 1998. Adv. Study Behav. 27, 2–109.
- Wada, M., 1986. Circadian rhythms of testosterone-dependent behaviors, crowing and locomotor activity, in male Japanese quail. J. Comp. Physiol. 158, 17–25.
- Wascher, C., a, F., Scheiber, I.B.R., Braun, A., Kotrschal, K., 2011. Heart rate responses to induced challenge situations in greylag geese (*Anser anser*). J. Comp. Psychol. (Washington, D.C.: 1983) 125, 116–119.
- Whirledge, S., Cidlowski, J.A., 2010. Glucocorticoids, stress, and fertility. Minerva Endocrinol. 35 (2), 109–125.
- Wikelski, M., Lynn, S., Breuner, C., Wingfield, J.C., Kenagy, G.J., 1999. Energy metabolism, testosterone and corticosterone in white-crowned sparrows. J. Comp. Physiol. A 185, 463–470.
- Wingfield, J.C., Farner, D.S., 1980. Control of seasonal reproduction in temperate-zone birds. Prog. Reprod. Biol. 5, 66–101.
- Wingfield, J.C., Moore, M.C., Farner, D.S., 1983. Endocrine responses to inclement weather in naturally breeding populations of white-crowned sparrows (*Zonotrichia leucophrys pugetensis*). Auk 100, 56–62.
- Wingfield, J.C., Silverin, B., 1986. Effects of Corticosterone on territorial behavior of free-living song sparrows *Melospiza melodia*. Horm. Behav. 20, 405–417.
- Wingfield, J.C., Schwabl, H., Mattocks, P.W.J., 1990. Endocrine mechanisms of migration. In: Gwinner, E. (Ed.), Bird migration. Springer, Berlin, pp. 232–256.
- Wingfield, J.C., Kenagy, G.J., 1991. Natural regulation of reproductive cycles. In: Schreibman, M., Jones, R.E. (Eds.), Vertebrate Endocrinology: Fundamentals and Biomedical Implications. Academic Press, New York, USA, pp. 181–241.
- Wingfield, J.C., Hahn, T.P., Levin, R., Honey, P., 1992. Environmental predictability and control of gonadal cycles in birds. J. Exp. Zool. 261, 214–231.
- Wingfield, J.C., Farner, D.S., 1993. Endocrinology of reproduction in wild species. In: Farner, D.S., King, J.R., Parkes, K.C. (Eds.), Avian biology. Academic Press, San Diego, California, pp. 163–327.
- Wingfield, J.C., Ramenofsky, M., 1997. Corticosterone and facultative dispersal in response to unpredictable events. Ardea 85, 155–166.
- Wingfield, J.C., Hunt, K., Breuner, C., Dunlap, K., Fowler, G.S., Freed, L., Lepson, J., 1997a. Environmental stress, field endocrinology and conservation biology. In: Clemmons, R., Buchholz, R., 564 (Eds.), Behavioural Approaches to Conservation in the Wild. Cambridge University Press, Cambridge, UK, pp. 95–131.
- Wingfield, J.C., Breuner, C., Jacobs, J., 1997b. Corticosterone and behavioural response to unpredictable events. In: Harvey, S., Etches, R.J. (Eds.), Perspectives in Avian Endocrinology, Journal of Endocrinology Ltd. Bristol, UK, pp. 267–278.
- Wingfield, J.C., Ramenofsky, M., 1999. Hormones and the behavioral ecology of stress. Sheffield Academic Press, pp. 1–44.
- Wingfield, J.C., Kitaysky, A., 2002. Endocrine responses to unpredictable environmental events: Stress or anti-stress hormones? Integr. Comp. Biol., 42600–42609.
- Wingfield, J.C., Ramenofsky, M., 2011. Hormone-behavior interrelationships of birds in response to weather. Adv. Study Behav. 43, 93–188.
- Withers, P.C., 1992. Comparative Animal Physiology. Saunders HBJ, pp. 81–121.
- Zalakevicius, M., 1994. Species specificity of bird migration control. Acta Ornithologica Lithuanica 9, 3–11.