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ORIGINAL PAPER

Habitat quality affects stress responses and survival in a bird wintering under extremely low ambient temperatures

Dina Cīrule[1] · Tatjana Krama[2,3] · Ronalds Krams[3] · Didzis Elferts[4,5] · Ants Kaasik[6] ·
Markus J. Rantala[7] · Pranas Mierauskas[8] · Severi Luoto[9] · Indrikis A. Krams[6,10]

Abstract Animals normally respond to stressful environmental stimuli by releasing glucocorticoid hormones. We investigated whether baseline corticosterone (CORT), handling-induced corticosterone concentration(s), and body condition indices of members of willow tit (*Poecile montanus*) groups differed while wintering in old growth forests and managed young forests in mild weather conditions and during cold spells. Willow tits spend the winter season in non-kin groups in which dominant individuals typically claim their priority to access resources, while subordinate individuals may experience greater levels of stress and higher mortality, especially during cold spells. We captured birds to measure baseline CORT and levels of handling-induced CORT secretion after 20 min of capture. Willow tits in the young forests had higher baseline CORT and a smaller increase in CORT in response to capture than individuals in the old forests. Baseline CORT was higher in females and juvenile birds compared to adult males, whereas handling-induced CORT secretion did not differ between birds of different ages. During cold spells, baseline CORT of willow tits increased and handling-induced CORT secretion decreased, especially in birds in young forests. Willow tits' survival was higher in the old forests, with dominant individuals surviving better than subordinates. Our results show that changes in CORT secretion reflect responses to habitat quality and climate harshness, indicating young managed coniferous forests as a suboptimal habitat for the willow tit.

Keywords Stress · Corticosterone · Habitat quality · Dominance hierarchy · Willow tits · Winter survival

Introduction

The decline of biological diversity as a consequence of habitat loss, deterioration, and fragmentation is a substantial concern in conservation biology (Hanski 1999; Fahrig 2003). Many species depend on particular features of their habitats that are necessary for reproduction and survival (Wiens 1989;

✉ Indrikis A. Krams
indrikis.krams@ut.ee

[1] Animal Health and Environment BIOR, Institute of Food Safety, Rīga, Latvia

[2] Department of Plant Protection, Institute of Agricultural and Environmental Sciences, Estonian University of Life Science, Tartu, Estonia

[3] Department of Biotechnology, Daugavpils University, Daugavpils, Latvia

[4] Department of Botany and Ecology, Faculty of Biology, University of Latvia, Rīga, Latvia

[5] Latvian State Forest Research Institute "Silava", Salaspils, Latvia

[6] Institute of Ecology and Earth Sciences, University of Tartu, Vanemuise 46, 51014 Tartu, Estonia

[7] Department of Biology, Turku Brain and Mind Centre, University of Turku, Turku, Finland

[8] Department of Environment Policy, Mykolas Romeris University, Vilnius, Lithuania

[9] English, Drama and Writing Studies, and School of Psychology, University of Auckland, Auckland 1010, New Zealand

[10] Department of Zoology and Animal Ecology, Faculty of Biology, University of Latvia, Rīga, Latvia

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Wingfield et al. 2015). High-quality habitats are regarded as areas with a high concentration of important resources and where individual fitness, survival, or other measures of performance are highest. Habitat destruction may create serious difficulties for organisms, potentially leading to local population extinction (Peres 2001; Fahrig 2003). Habitat destruction has recently been suggested to constitute a physiological stressor for animals (Homan et al. 2003; Romero 2004; Wikelski and Cooke 2006; Dantzer et al. 2014).

Free-living organisms face multiple stressors in their natural environments (Romero 2004; Romero et al. 2009) that can challenge homeostasis (Ots et al. 1998; Boonstra 2013). In vertebrates, the autonomic nervous system (Herman et al. 2016) and the hypothalamic–pituitary–adrenal (HPA) axis are among the principal mechanisms that evoke adaptive reactions when organisms face noxious environmental stimuli (Schulkin et al. 2005; Hõrak et al. 2006). Adaptive responses include alterations in life history strategy (Wingfield et al. 1998; Boonstra 2005) during which glucocorticoid hormones are secreted from the adrenal cortex (Sapolsky et al. 2000; Creel et al. 2013). If the stressor is brief and infrequent (Sapolsky et al. 2000; Uchoa et al. 2014; Ketterson et al. 2015), the adrenal gland increases glucocorticoid hormone production, and this boosts energy availability to respond properly to the presence of the stressor (Romero et al. 1997, 1998; Sapolsky et al. 2000; Landys et al. 2006; Ketterson et al. 2015). However, when there are insufficient reserves to satisfy the physiological cost of stress, resources must be shifted away from other biological functions such as reproduction, maintenance, growth, and immunity due to trade-offs between life history traits (Stearns 1992). Chronic stress and the accompanying sustained high concentration of circulating glucocorticoids may have significant effects on immunity and growth due to induction of severe protein loss in muscle and neural tissues, thus impairing health condition and reproductive function (Sapolsky and Pulsinelli 1985; McEwen 2000; Bergeon Burns et al. 2014).

The fragmentation and deterioration of old growth forests by modern forestry have become serious threats to species diversity. In northern Europe, for example, the apparent population decline of some forest parid species resulted from the loss of high-quality wintering and breeding habitats (Virkkala and Liehu 1990; Niemi et al. 1998), where the old, natural forests had decreased in area and become fragmented (Järvinen 1982; Virkkala 1987; Veistola et al. 1997). Willow tits establish their territories in high-quality habitats, while they are absent in habitats of intermediate quality (Ekman 1998). Wintering willow tits have been observed to enter the sapling areas in their flock territories but only for short feeding bouts (Krams 1996). To survive the winter in the higher latitudes of northern Europe with severe continental climate, the physiological capacity of birds must be sufficient to withstand the lowest ambient temperature that may occur. Because of the

higher energy requirements or the inability to tolerate reduced body temperature (Reinertsen and Haftorn 1986), wintering individuals may experience greater levels of physiological stress and higher mortality, especially during sudden cold spells (Krams et al. 2010a, 2013). It has been shown that restricted food availability and accessibility (Rowher and Wingfield 1981; Wingfield et al. 1983; Wingfield 1985; Rogers 1987; Rogers et al. 1993; Smith et al. 1994; Raouf et al. 2006; Jenni-Eiermann et al. 2008), habitat harshness (Wingfield et al. 1995; Addis et al. 2011; Krause et al. 2015; Walker et al. 2015), or sudden snowstorms and temperature declines (de Bruijn and Romero 2011, 2013; Krause et al. 2016a, b) affect behavioral decisions (Glądalski et al. 2014; Senner et al. 2015; Briedis et al. 2017) and elicit secretion of plasma corticosterone (CORT), a main glucocorticoid of birds involved in regulation of the immune system, energy, and stress responses (Kitaysky et al. 2001). It has also been demonstrated that different bird species may differ considerably in their capacity to survive under low temperatures (Saarela et al. 1995). Importantly, in studies on dominance-structured groups of wintering birds, higher plasma CORT was found in subordinate group members (Silverin et al. 1984; Pravosudov et al. 2001; Holberton and Able 2002; Poisbleau et al. 2005; but see Pravosudov et al. 2003). It has been shown that subordinate individuals have restricted access to food sources, while the availability of food might be a crucial factor of survival in winter (Ekman and Askenmo 1984; Krams et al. 2010a). Arthropods dwelling in the tree canopy are among the most important food sources for the forest wintering passerines. These arthropods prefer branches with needles within canopies of coniferous trees (Gunnarsson 1990), while the canopies of mature coniferous trees contain more arthropods than canopies of younger trees (Krams 1998a; Krams et al. 2001). This makes old growth forests a better wintering habitat for willow tits than young managed forests (Krams et al. 2001).

Physiological stress caused by low ambient temperatures may interact with habitat quality to undermine the survival of birds wintering in forests affected by anthropogenic changes. For example, the American redstart (Setophaga ruticilla), a migratory songbird, had higher baseline CORT when wintering in low-quality habitats than when occupying high-quality habitats (Marra and Holberton 1998). Redstarts wintering in low-quality habitats exhibited a reduction in their ability to release CORT in response to capture stress (handling-induced CORT). This may suggest a reduction in the sensitivity of the HPA axis to environmental signals (Schwabl et al. 1991; Wingfield et al. 1992, 1994 a, b; Holberton et al. 1996; Silverin 1997), meaning that elevated baseline CORT levels minimized the redstarts' reactive homeostasis (Romero et al. 2009). While baseline CORT and handling-induced CORT secretion in American redstarts was not age-dependent, in many other forest-dwelling birds wintering in dominance-structured groups, the

subordinate individuals (often young birds) occupy habitats of lower quality which negatively affects their survival (Ekman and Askenmo 1984; Suhonen 1993; Krams 2001).

In this field study, we investigated whether three indices of condition (CORT concentration, muscle score, and body fat reserves) in members of willow tit (*Poecile montanus*) flocks differ across dominance hierarchies, weather conditions (ambient temperature), and between semi-natural old growth and young managed forests. The willow tit is a small hoarding sedentary resident passerine that is a widespread and common resident breeder throughout temperate and subarctic Europe and northern Asia (Snow and Perrins 1998). This species has undergone significant population declines during recent decades (Harrap and Quinn 1996). In northern Europe, willow tits prefer coniferous stands composed of pines and spruces. Willow tits form heterospecific flocks with non-kin conspecifics and other members of the Paridae guild during the non-reproductive season (Ekman 1998). These flocks remain stable in membership and space as members of flocks and jointly defend their territory from other flocks from mid-summer till the next breeding season in early spring. Several studies have shown that the flocks are dominance-structured, that male willow tits always dominate females and, within the sexes, adults dominate juveniles (e.g., Krams 1996, 1998b). In this study, natural temperature regimes ranged from mild to extremely low ambient temperature occurring during sudden cold spells.

Based on the willow tit groups' social structure, habitat structure, and possible substantial changes in weather conditions, we had four predictions related to CORT levels and body condition of individual willow tits of different age, sex, and social rank. To test our predictions, each bird was captured twice: we took the first sample under mild conditions and the second one under low ambient temperatures. On each occasion, we took two CORT samples: the first within 2 min of capture to obtain baseline CORT and the second after 20 min of capture to obtain levels of handling-induced CORT secretion of individual birds (Marra and Holberton 1998). We hypothesized (i) lower levels of willow tit baseline CORT, higher handling-induced CORT secretion, and a better condition of the pectoral muscle in the birds captured in old forests than in the young forests under conditions of low ambient temperatures where chronic physiological stress can lead to suppressed stress responsiveness. Since rank-related access to resources often results in better winter survival among dominants (Ekman and Askenmo 1984; Koivula et al. 1995; Krams et al. 2001, 2010a), we expected (ii) higher mortality in subordinate willow tits. We also predicted (iii) a positive correlation between dominance rank and the condition of the pectoral muscle, while higher baseline CORT and lower levels of handling-induced CORT secretion were expected in subordinate individuals in the young managed forests under conditions of extremely low ambient temperatures. Finally, we tested whether (iv) willow tits wintering in high-quality territories have higher baseline CORT, lower pectoral muscle scores, and body fat scores because of higher energetic demands required to defend their territories more actively than birds wintering in low-quality territories (Mazerolle and Hobson 2002).

Materials and methods

Study site and birds

The study was conducted near the town of Krāslava in southeastern Latvia (55° 87′ N, 27° 23′ E) in December 2009 and January 2012. The study area covers approximately 12 km^2 of mainly coniferous forests of different ages, from open clearcut areas and bogs to closed forests, dominated by Scots pine (*Pinus sylvestris*) and Norwegian spruce (*Picea abies*) (Rytkönen and Krams 2003). The data were obtained from willow tits of 12 mixed-species flocks (6 flocks in 2009 consisting of 6 adult males, 6 adult females, 6 juvenile males, and 6 juvenile females; 6 flocks in 2012 consisting of 6 adult males, 6 adult females, 6 juvenile males, and 6 juvenile females) in young 35–55-year-old managed pine plantations with a sparse understory. We also obtained the data from willow tits of 11 mixed-species flocks (6 flocks in 2009 containing 6 adult males, 6 adult females, 9 juvenile males, and 7 juvenile females; 5 flocks in 2012 containing 5 adult males, 5 adult females, 7 juvenile males, and 5 juvenile females) in unmanaged 105–155-year-old mixed forests dominated by Norwegian spruce. The mixed-species flocks contained 4–5 willow tits (mean number of individuals 4.26 ± 0.45, mean ± SD; 98 individuals in total; all flocks consisted of one adult male, one adult female, one to two juvenile males, and one juvenile female). The flocks also consisted of other species such as crested tits (*Lophophanes cristatus*), coal tits (*Periparus ater*), great tits (*Parus major*), marsh tits (*Poecile palustris*), blue tits (*Cyanistes caeruleus*), treecreepers (*Certhia familiaris*), and nuthatches (*Sitta europaea*). Aggressive behavior of more dominant crested tits, nuthatches, and great tits may make flocking less attractive to subordinate willow tits, and they often forage as members of smaller conspecific sub-flocks around midday under mild weather conditions (Hogstad 1988a, 1988b).

Each flock of willow tits inhabits a territory of about 9 ha (Krams 1996). To detect boundaries of territories of the flocks, we used a Magellan GPS receiver (MiTAC Digital Corporation, Santa Clara, CA, USA). An observer recorded the flock's coordinates every 5 min while following adult willow tits (Krama et al. 2015). This was done to ensure that willow tits inhabit only one type of forest.

The birds were trapped by mist nets (Ecotone, Sopot, Poland) at temporary feeders baited with sunflower seeds. Each bird was banded with metal and a unique combination of colored plastic rings in September. Willow tits were sexed

and aged (as adult or juvenile). The shape of the rectrices of willow tits was used to determine age (Laaksonen and Lehikoinen 1976), while sexual dimorphism in wing and tarsus length was used to sex individuals (Koivula and Orell 1988). We also used a method developed by Vinogradova et al. 1976: willow tits with wings shorter than 61 mm were identified as females, and those with wings longer than 67 mm were considered males. In addition, the sex of adult willow tits was known from previous breeding seasons. Finally, we continued observations of individual willow tits also outside the wintering season. Observed fights and territorial behavior, singing behavior and parental roles during the breeding season were used to determine the sex of those individuals with overlapping biometrical parameters. In this study, only flocks with all individuals properly sexed were included into analyses.

Dominance ranks

Dominance order was measured within each flock using pairwise interactions between birds at the temporary feeders in the beginning of November. An individual was dominant over another if it chased the other away from the food, caused the withdrawal of the other by approaching, or forced the other to wait by occupying the feeder (Koivula and Orell 1988; Krams et al. 2010a). The dominant won more interactions than the subordinate within each dyad (two-tailed sign test, $P < 0.001$). Adult males had the highest rank, and males were dominant over females in both age groups. We assigned rank 1 to the highest-ranking individual (adult male), while juvenile females were assigned rank 4 or 5 dependent on whether the flock consisted of four or five willow tits. The dominance hierarchy was linear in the flocks.

Weather conditions

The first sampling of birds was done before a cold spell arrived. The second set of samples was obtained from the same willow tits during a cold spell when the ambient temperature decreased to −35 °C within some days, and remained extremely cold for at least 2 weeks. Two to four days before the weather forecast predicted the onset of a cold spell in mid-December 2009 and mid-January 2012, we captured willow tits from six mixed-species flocks in mid-December 2009 and six flocks in mid-January 2012 in the young managed forests, and from six flocks in mid-December 2009 and five flocks in mid-January 2012 in the old forests. Before the cold spell arrived, the weather was mild with the average temperature in the night within the range of 5 to −3 °C while the mean daytime temperatures varied from 8 to 0 °C. The average night-time temperature during the cold spell was within the range of −28 to −32 °C, with mean daytime temperatures from −18 to −24 °C. January 2012 was colder than December 2009.

Measurements and samples

We captured the birds using mist nets located at permanent feeders provided with ad libitum sunflower seeds between 10:00 and 13:30 h. Within 1–2 min of capture, ca. 100 μl of whole blood was collected from the tarsal vein into heparinized microcapillary tubes (Saerstedt AG & Co, Nümbrecht, Germany). This sample provided the baseline level of plasma CORT. We identified each bird and took basic morphological measurements of wing and tarsus length, muscle score, and body mass. The birds were weighed to the nearest 0.5 g using a 30-g Pesola spring balance. Muscle score was assessed by visually inspecting the pectoral muscle around the keel bone on a 0–3 scale according to Bairlein (1995). Fat score was obtained when checking the amount of fat in the furcular hollow on a 0–4 scale (Krams 2002; Krams et al. 2010a, 2013).

The birds were kept in bird holding bags (Ecotone, Gdynia, Poland) individually. We took a second blood sample 20 min after capture to provide the profile of handling-induced CORT secretion, and then released the bird. It has previously been shown that CORT of wintering willow tits peaks within ca. 20 min of capture-related stress (Silverin et al. 1989). Plasma was separated from blood cells by 10-min centrifugation at 10,000 rpm and stored at −35 °C until analyzed. Correlate EIA kit (Cat No. 900-097; Assay Designs Inc., Ann Arbor, MI) was used for measurements of plasma CORT levels. Plasma samples were diluted 1:3 with assay buffer in the kit, and standard protocol was followed (see online manual: http://www.assaydesigns.com/objects/catalog//product/extras/900-097.pdf). Samples were randomly assigned to microplate wells along with blanks and five standards (32–200,000 pg ml^{-1} CORT). Plates were read on a Multiscan FC microplate reader (ThermoFisher Scientific, Waltham, MA, USA) at 405 nm. The samples, standards, and controls were assayed in duplicate. The average recovery of the assay was uniformly high (mean ± SD = 86 ± 2.4%; $n = 10$) and we did not correct for it. The sensitivity for CORT detection was 27 pg/ml, according to the manufacturer's protocol. The repeatability of CORT measurements was high ($r = 0.88$, $n = 25$ pairs of repeated samples), calculated as intraclass correlation coefficients from one-way ANOVA according to Lessells and Boag (1987). The intra- and interassay variations were 8.24 and 10.41%, respectively, which is typical in this kind of study (Tilgar et al. 2009). We obtained CORT measurements from 23 adult males, 23 adult females, 29 juvenile males, and 23 juvenile females.

Survival

We estimated the survival of the willow tits at the end of February 2010 and 2012. We checked for the presence/absence of flock members for 4–5 days by observing color-banded individuals with binoculars (using 10× magnification) at bird feeders baited with sunflower seeds (Krams et al. 2001;

Krama et al. 2015). The birds that disappeared in the course of winter but were found again outside the study area in spring were included in the analysis as survivors.

Statistics

We used linear mixed effects models to account for possible correlations between the data points that either come from the same individual or from different individuals from the same flock. Individual IDs nested under flock number were used as random effects. For testing the significance of model parameters corresponding to fixed effects, Satterthwaite correction was used to estimate the degrees of freedom for the F-distribution corresponding to the null hypothesis. Interactions up to the third order were included in the models. If third-order interactions were not significant, models were refit without them. For all models, model residuals were screened to detect possible departures from the model assumptions (normally distributed residuals with constant variance) and no violations were detected. In the case of CORT concentrations (dependent variable), separate models were made for baseline and for handling-induced CORT concentrations. Habitat, age, year, sex, weather conditions, fat score, and muscle score were included as fixed effects. For models where fat scores and muscle scores were analyzed as dependent variables, habitat, age, year, sex, and weather conditions were used as fixed factors. We used R 3.4.0. software. Models were fitted using the lme4 package and P values were calculated by lmerTest package. Post hoc tests for significant interactions were performed with lsmeans packages (Bates et al. 2015; Kuznetsova et al. 2016; Lenth 2016; R Core Team 2017).

Generalized linear mixed effects model with binomial error structure was used to test survival probability of willow tits. Baseline CORT concentration, year, sex, habitat, fat score, and dominance rank were used as fixed factors. The flock number was used as a random effect. Calculations of a possible relationship between survival and social dominance were based on the following categories assigned to each member of the flock: the number 1 was assigned to the highest-ranking individual and the numbers 4 or 5, based on variation in flock size, were assigned to the most subordinate willow tits. Only young birds ($n = 52$) were included in this analysis because there was no mortality observed among adult individuals.

Results

CORT values

The overall model for the handling-induced CORT concentration showed significant interaction only between habitat and weather (Table 1). In contrast, there were five significant second- and third-order interactions for the baseline CORT

Table 1 Linear mixed effects model main effects of habitat, age, sex, weather conditions, fat score, muscle score, and their interactions on concentration of plasma baseline CORT of willow tits (numDF for all factors and interactions is 1)

	Sum Sq	denDF	F value	P value
Habitat	157.76	20.651	172.13	< 0.0001
Age	1950.51	169.672	2128.16	< 0.0001
Year	0.00	19.914	0.00	0.9745
Sex	25.25	170.984	27.55	< 0.0001
Weather	945.07	165.918	1031.14	< 0.0001
Muscle score	0.39	180.829	0.43	0.5147
Fat score	0.08	175.781	0.08	0.7734
Habitat × age	20.31	162.107	22.16	< 0.0001
Habitat × sex	1.65	161.973	1.80	0.1814
Habitat × weather	203.53	161.380	222.07	< 0.0001
Age × sex	0.04	162.788	0.04	0.8445
Age × weather	16.08	162.575	17.55	< 0.0001
Sex × weather	9.39	162.242	10.25	0.0016
Age × sex × weather	4.48	162.008	4.89	0.0285

concentration (Table 2). The concentrations of baseline CORT of adult willow tits ($t_{169.6} = -46.1$, $P < 0.001$, Fig. 1) and males ($t_{170.9} = 5.2$, $P < 0.001$, Fig. 1) were lower than baseline CORT of juveniles and females, respectively. However, handling-induced CORT concentrations did not significantly differ between sexes or age groups (all Ps > 0.05, Table 2). The birds had lower baseline and handling-induced CORT under mild ambient temperatures (16.22 ± 5.03 and 29.54 ± 2.06 ng/ml, respectively; mean ± SD) than in the cold weather (21.38 ± 4.94 and 32.25 ± 1.99 ng/ml). The willow tits' baseline and handling-induced CORT levels under mild

Table 2 Linear mixed effects model main effects of habitat, age, sex, weather conditions, fat score, muscle score, and their interactions on concentration of plasma handling-induced CORT of willow tits (numDF for all factors and interactions is 1)

	Sum Sq	denDF	F value	P value
Habitat	171.845	21.897	79.972	< 0.0001
Age	6.158	175.247	2.866	0.0922
Year	39.862	20.778	18.551	0.0003
Sex	7.636	176.958	3.553	0.0611
Weather	289.034	170.114	134.508	< 0.0001
Muscle score	0.081	178.342	0.038	0.8464
Fat score	3.593	181.329	1.672	0.1976
Habitat × age	5.260	164.569	2.448	0.1196
Habitat × sex	1.739	164.557	0.809	0.3696
Habitat × weather	8.466	163.450	3.940	0.0488
Age × sex	0.176	165.698	0.082	0.7749
Age × weather	0.977	165.232	0.455	0.5011
Sex × weather	0.164	164.738	0.076	0.7826

Fig. 1 Concentration of plasma CORT (mean and SD) at the time of capture (0) (baseline CORT) and 20 min after capture (20) (handling-induced CORT) in willow tits in **a** old/young forests and **b** in willow tit juveniles/adults under conditions of mild weather and during a cold spell. Numbers below error-bars indicate the sample size of each group. There was a significant difference between conditions ($P < 0.05$) in each combination of duration and sex, age, or habitat type

and cold weather were significantly lower in the old forest (17.58 ± 5.27 and 29.72 ± 1.77 ng/ml) than in the young forest condition (20.07 ± 5.68 and 32.13 ± 2.42 ng/ml). In 2009, handling-induced CORT concentrations were higher than in 2012 but there were no significant difference for the baseline CORT across the years (Tables 1 and 2). Fat score and muscle score were not associated with baseline and handling-induced CORT concentrations ($P > 0.05$).

Body condition: fat reserves and muscle score

Three second-order interactions and one third-order interaction were significant for the fat reserves model. Under mild weather, males were leaner than females but the difference was smaller than during cold weather ($F_{1,93.0} = 13.4$, $P < 0.001$, Fig. 2). Overall, adults had lower body fat reserves than juvenile birds, but the difference was smaller in mild compared to cold temperatures ($F_{1,93.0} = 14.8$, $P < 0.001$; Table 3). Furthermore, a significant interaction between sex and age showed that for adult birds the difference between sexes was greater than for juvenile birds ($F_{1,70.0} = 8.6$, $P = 0.005$; Table 3). No other significant interactions were revealed.

Muscle scores were higher under mild compared to cold weather ($F_{1,94.3} = 18.5$, $P < 0.001$, Fig. 3). Males had higher scores than females ($F_{1,71.9} = 10.6$, $P = 0.002$), older birds had higher scores than juvenile birds ($F_{1,71.6} = 32.6$, $P < 0.001$), and birds in the old forests had higher scores than in the young forests ($F_{1,20.2} = 4.7$, $P = 0.043$). The only significant interaction was between age, sex, and weather conditions ($F_{1,94.3} = 5.9$, $P = 0.017$; Table 4). Older females had higher scores than young females under both weather conditions, but males showed difference only under the cold weather.

Survival

The survival of willow tits in the old forests (91.50%) was significantly higher than in the young forests (72.92%) (Chisq = 7.3334, $df = 1$, $P = 0.0068$, Table 5) between the beginning of November and the end of February. Birds with higher dominance rank had significantly higher survival probability (Chisq = 4.3236, $df = 1$, $P = 0.0376$) (86.4% for dominance rank 2 and only 40% for dominance rank 4). There was no relationship between fat score (Chisq = 1.2252, $df = 1$, $P = 0.2683$) or baseline CORT concentration (Chisq = 0.0135, $df = 1$, $P = 0.9074$) and survival rate.

Discussion

The main finding of this study was that willow tits wintering as members of dominance-structured flocks differed in levels

Fig. 2 Fat scores (mean and SD) of willow tits in **a** old/young forests and **b** willow tit juveniles/adults under conditions of mild weather and during a cold spell. Numbers below error-bars indicate the sample size of each group

of baseline CORT and capture handling-induced CORT across habitats, weather, sex, and age. Prior studies on forest passerines show that individuals living in old forests are often in a better physiological condition than those inhabiting heavily managed forests, suggesting a link between habitat and the level of physiological stress in birds (Krams et al. 2010b; Saari et al. 1994; Suorsa et al. 2003, 2004; Grava et al. 2013). Greater stress levels and lower survival in birds inhabiting young, highly managed and fragmented forests

may be due to a lower availability of food resources and a higher risk of predation. Frequent changes of habitats may also increase predation risk especially around habitat edges, where birds have to change their anti-predator strategies, which are different in young and old forests (Krams 1996). Food abundance is crucial for the survival of parids wintering in forests (Jansson et al. 1981; Krams et al. 2001). The preference for mature habitats is due to a higher availability of arthropods to foliage-gleaning passerines in older and larger trees (Krams et al. 2001). The number of some parids has recently decreased manifoldly (Virkkala 1988; Virkkala 1990; Virkkala and Liehu 1990; Fuller et al. 2005; Hewson et al. 2007; Eaton et al. 2009), probably because of a year-round food shortage in managed, highly deteriorated and often young forests (Virkkala 1987; Krams et al. 2010b).

It has previously been shown that a long-term lack of food may cause chronic physiological stress (Romero and Wikelski 2001), often resulting in a suppressed immune system and decreased disease resistance (Suorsa et al. 2003), all of which are detrimental to survival (Wasser et al. 1997; Romero and Wikelski 2001; Griesser et al. 2007). We found higher baseline CORT levels in willow tits inhabiting young forests under extremely low temperatures, while the increase in CORT in response to handling-induced stress was significantly lower in the birds in young forests compared to the birds in old forests under mild and cold weather. Young forests might therefore represent the worst habitat for willow tits, especially under extremely low ambient temperatures. The finding that willow

Table 3 Linear mixed effects model main effects of habitat, age, sex, weather conditions, and their interactions on fat scores of willow tits (numDF for all factors and interactions is 1)

	Sum Sq	denDF	F value	P value
Habitat	0.032	19.244	0.195	0.6641
Age	18.866	69.640	113.431	< 0.0001
Year	0.229	18.882	1.394	0.2524
Sex	35.323	70.156	214.649	< 0.0001
Weather	10.464	92.993	63.590	< 0.0001
Habitat × age	0.001	69.640	0.003	0.9558
Habitat × sex	0.011	70.156	0.069	0.7936
Habitat × weather	0.470	92.993	2.854	0.0945
Age × sex	1.409	70.064	8.560	0.0046
Age × weather	2.429	92.993	14.761	0.0002
Sex × weather	2.202	92.993	13.381	0.0004
Habitat × age × weather	0.828	92.993	5.029	0.0273

Fig. 3 Muscle scores (mean and SD) of willow tits in **a** old/young forests and **b** willow tit juveniles/adults under conditions of mild weather and during a cold spell. Numbers below error-bars indicate the sample size of each group

tit handling-induced CORT secretion increased less in 2012 (a more severe winter) than in 2009 also highlights the role of habitat quality in facilitating survival during cold weather. The higher baseline CORT in the young forests during cold weather may indicate a physiological response to meet higher energy requirements to compensate for decreased food availability, while the reduced handling-induced CORT secretion may be a response to avoid the deleterious effects that high CORT concentrations have on the physiological condition of individuals (Kitaysky et al. 2003; Blas et al. 2007; Spencer and

Verhulst 2007, 2008; Müller et al. 2009), as suggested by the lower body mass of birds in the young forest.

We suggest that levels of handling-induced CORT concentrations revealed in this study and by Silverin et al. (1989) reflect the maximum secretion capability in willow tits. This is supported by the significant differences in handling-induced CORT found in willow tits between habitats and weather conditions. Thus, the most likely explanation for our results is a reduction in the responsiveness of the HPA axis. This can occur through inhibiting the hypothalamic-releasing hormone, suppressing adrenocorticotropin, or diminishing levels of both hormones, which can be followed by a decline in the capacity of the adrenocortical tissue to react to those hormones (Sapolsky et al. 2000; Romero 2004; Charmandari et al. 2005; Smith and Vale 2006). These responses allow an organism to avoid the impairment that high concentrations of CORT

Table 4 Linear mixed effects model main effects of habitat, age, sex, weather conditions, and their interactions on muscle scores of willow tits (numDF for all factors and interactions is 1)

	Sum Sq	denDF	F value	P value
Habitat	0.2750	20.165	4.651	0.0433
Age	1.9259	71.619	32.564	< 0.0001
Year	0.0123	20.022	0.208	0.6530
Sex	0.6258	71.880	10.581	0.0017
Weather	1.0930	94.308	18.480	< 0.0001
Habitat × age	0.1604	71.619	2.713	0.1039
Habitat × sex	0.0005	71.880	0.009	0.9245
Habitat × weather	0.0008	94.308	0.013	0.9084
Age × sex	0.0001	71.830	0.002	0.9632
Age × weather	0.1026	94.308	1.734	0.1911
Sex × weather	0.0187	94.308	0.316	0.5751
Age × sex × weather	0.3499	94.308	5.917	0.0169

Table 5 Generalized linear mixed effects model main effects of habitat, dominance rank, baseline CORT level, fat score, sex, and year on the survival probability of young willow tits

	Chisq	df	P value
Habitat	7.3334	1	0.0068
Dominance rank	4.3236	1	0.0376
Baseline CORT	0.0135	1	0.9074
Fat score	1.2252	1	0.2683
Sex	0.2120	1	0.6452
Year	0.3318	1	0.5646

can have on the immune system, nerve cell function, and muscle catabolism (e.g., Sapolsky 1993; Belden et al. 2005). Such modulation of the CORT stress response has been observed during activities characterized by extremely high levels of CORT secretion, which require considerable energy investment (Wingfield et al. 1983; Wingfield and Silverin 1986; Holberton et al. 1996; Marra and Holberton 1998; Fokidis et al. 2011, 2012; Angelier and Wingfield 2013) and may be associated with protein sparing (Cherel et al. 1988a; Cherel et al. 1988b). In addition, high concentrations of CORT often cause immune suppression which may decrease the memory of the adaptive immune system (Uchoa et al. 2014) and affect skin inflammatory responses and immune cell influx to wounds (Dhabhar and McEwen 1999; Dhabhar 2002). This is especially relevant to wintering birds, because the skin acts as a barrier against the influences of the biotic and abiotic environments such as invading pathogens and subzero temperatures (Dhabhar and McEwen 1999).

Thus, the quality of a winter habitat is crucial: better habitats might lessen interference competition for food resources and provide cover against attacking predators (Ekman 1998). These effects are relevant to parids, because skin wounds may be a common consequence of failed predation attempts and territorial conflicts, which are common stressors experienced by prey living in groups (Dhondt 2011). Future research should test whether the decline in handling-induced CORT secretion in willow tits wintering in suboptimal habitats (i.e., young forests and cold conditions) is an adaptation to avoid using skeletal muscle protein to cover metabolic requirements or to facilitate skin inflammatory responses and immune cell influx to wounds.

In the present study, we found that subcutaneous fat reserves increased in subordinate birds and remained the same in alpha males under cold weather conditions, while muscle scores decreased for all willow tits. The decrease in the muscle score and the increase in handling-induced CORT suggest a response to stressors which promotes gluconeogenesis, resulting in a source of glucose substrates from non-carbohydrate sources such as skeletal muscle during considerable transitions in weather conditions (Cherel et al. 1988a; Cherel et al. 1988b). In high latitudes, thermoregulatory adjustments of birds should be sufficient to ensure survival under extreme ambient temperatures, which cause great levels of stress and higher mortality under conditions of unexpected cold spells. This is especially true in the case of dominance-structured groups where the competitive superiority of dominant individuals may add uncertainty to feeding opportunities and survival prospects of subordinate flock members. However, in non-hoarding great tits, dominants usually respond to low temperatures by increasing their subcutaneous fat reserves, whereas subdominant birds tend to decrease the amount of their underskin fat (Krams et al. 2010a, 2013). The substantial differences in fattening strategies of food hoarding

willow tit and great tit, a non-hoarding species, may indicate the influence of caching behavior and hoarded food reserves on survival strategies and stress responses. All these possibilities need to be addressed in future research.

Overall, our study provides evidence for the role that sociality and dominance hierarchies within the groups have on winter energetics and survival of subordinate individuals. However, we did not find any significant interaction between age and sex in willow tit CORT secretion. This was what we expected, since juvenile males usually dominate adult females in parids, with the effects of age and sex consequently canceling each other out (Saitou 1979; Gosler 1996; Krams 1998b). The lack of interaction between age and sex in CORT secretion may be further explained by mate protection in parids (Hogstad 1995; Krams et al. 2006). Because alpha pairs of willow tits (consisting of adults in this study) stay within their territory year-round and remain mated across years (Hogstad 2015), these individuals have close relationships, with males protecting their mates and females receiving less aggression from other flock members (Hogstad 1992). The alpha females also have a higher foraging rate when accompanied by their mate (Hogstad 2015).

Elevated levels of baseline CORT of subordinate willow tits may have adverse effects on their immune system, metabolic mechanisms, and behavior, especially in suboptimal habitats in years with cold winters (Saino et al. 2003; Spencer and Verhulst 2007, 2008; Müller et al. 2009). However, higher baseline CORT levels may allow subordinate birds to modify their behavioral and physiological reactions to cope with unexpected environmental changes (Angelier and Wingfield 2013). For example, elevated baseline CORT levels may enhance foraging activity of subordinate individuals under low temperatures while it might be less important for dominant individuals in the flock because they always have an optimal access to food resources. Such glucocorticoid stress responses may be partly heritable and their mechanism is likely selected to optimize survival and fitness of individual birds (Breuner et al. 2008; Angelier et al. 2011; Krause et al. 2016b; Lattin et al. 2016). To distinguish between positive and negative effects of high baseline CORT levels, it would be important to find out (among other things) if there is a link between environmentally increased secretion of baseline CORT and shortening of telomeres via oxidative damage, which has already been observed in domestic (Haussmann et al. 2012; Tissier et al. 2014) and wild birds (Quirici et al. 2016).

Taken together, the observed changes in survival and CORT secretion in wintering willow tits reflect responses to habitat quality and suggest young managed coniferous forests to be a suboptimal habitat for this species. If habitat degradation acts as a stressor and leads to negative long-term consequences for individual birds, it may also affect bird populations. Across the distribution range of willow tits, previously continuous

forests have been turned into managed forests, where small forested patches are usually separated by clear-cuts and young successional forests (Gustafson and Parker 1992). These changes may result in food shortage for forest dwellers (Zanette et al. 2000; Krams et al. 2001), explaining the dramatic decline of willow tit populations (Lewis et al. 2007).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethics statement All animal manipulations were carried out in accordance with the legal and ethical standards of the Republic of Latvia. The project had the permission of the Nature Conservation Agency of the Republic of Latvia (No. 16/2012).

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