THIS IS A PREPRINT VERSION OF DOI: 10.1016/j.yhbeh.2021.104979

Factors modulating the behavioral and physiological stress responses: do they modify the relationship between flight initiation distance and corticosterone reactivity?

Zulima Tablado[1], Yves Bötsch[1], Veronika Bókony[2], Frédéric Angelier[3], Ádám Z. Lendvai[4], Susanne Jenni-Eiermann[1], and Lukas Jenni[1]

1 Swiss Ornithological Institute, CH-6204 Sempach, Switzerland.
2 Lendület Evolutionary Ecology Research Group, Plant Protection Institute, Centre for Agricultural Research, Eötvös Loránd Research Network, Herman Ottó u. 15, H-1022 Budapest, Hungary.
3 Centre d'Etudes Biologiques de Chizé, CNRS, 79360 Villiers en Bois, France.
4 Department of Evolutionary Zoology and Human Biology, University of Debrecen Egyetem tér 1, 4032 Debrecen, Hungary.

Corresponding author: Zulima Tablado (zutal@yahoo.es)

Authors' contributions: Z.T. participated in the study design, collected and analysed the data and wrote the manuscript. Y.B. helped with designing the study, collecting the data and worked on manuscript drafts. V.B., F.A. & A.Z.L. contributed to data collection and analyses and worked on manuscript drafts. S.J-E & L.J. helped with designing and coordinating the study, and worked on manuscript drafts.

Data availability: The datasets generated and analysed during the current study are available from the Swiss Ornithological Institute (https://zenodo.org/communities/vora?page=1&size=20).

Abstract

Understanding how vulnerable species are to new stressors, such as anthropogenic changes, is crucial for mitigating their potential negative consequences. Many studies have investigated species sensitivity to human disturbance by focusing on single behavioral or physiological parameters, such as flight initiation distance and glucocorticoid levels. However, little is known about the differential effect that modulating factors might have on behavioral versus physiological stress responses across species. This lack of knowledge make difficult to understand the relationship between both types of reactions, and thus to assess to what extent a behavioral reaction is representative of an internal physiological stress response or vice versa. We collected published data on bird flight initiation distances (FID) and corticosterone (CORT) responses, the two most frequently used indicators of stress reaction. We then investigated how spatio-temporal factors or species-specific characteristics relate to these behavioral and physiological stress responses, and potentially modify the relationship between them. Additionally, we evaluated the strength of the correlation between the two stress responses (behavioral and physiological). Our findings showed that FID and CORT responses were poorly correlated across species, and the lack of correlation was attributable to modulating factors (e.g. latitude and body mass) which influence behavior and physiology differently. These modulating factors, therefore, should be taken into consideration to better interpret FID and CORT responses in the context of species vulnerability to stress.

Keywords: adrenocortical response, baseline corticosterone, stress corticosterone, flight initiation distance, escape response, human disturbance, recreational activities, stress hormones.

Introduction

Wild animals are often exposed to threatening situations, such as encounters with predators or aggressive competitors, and have developed a series of mechanisms to cope with them (Wingfield, 2013). These mechanisms include immediate and short-term changes in both their physiology and behavior (Gormally and Romero, 2020). At the physiological level, changes entail increases in the secretion of stress-related neurotransmitters, catecholamines, and "stress" hormones (i.e. corticosteroids, through the hypothalamic–pituitary–adrenal (HPA) axis), as well as the activation of the immune system among others (Sapolsky et al., 2000; Tablado and Jenni, 2017). Behaviorally, responses to threats range from passive responses, such as hiding and freezing (Steen et al., 1988; Bracha, 2004), to active ones, like escaping or attacking (Lima, 1993; Bracha, 2004; Stankowich and Blumstein, 2005).

The combination of all these mechanisms is intended to improve individual survival by reallocating energetic resources towards essential processes, reducing the risk of being harmed, and preparing for potential injuries (Wingfield et al., 1998; Blumstein, 2010). However, the activation of all these defense mechanisms does not come without a cost. Anti-predatory reactions can lead, for example, to the temporary abandonment and exposure of offspring or eggs and to increased energy expenditure (Romero, 2004; Buckley, 2011). Moreover, if stress responses are activated too frequently they may result in chronic stress (i.e. disrupted HPA axis regulation and functioning), reduced individual fitness (i.e. reduced reproduction and/or survival), and even compromised population growth (Dickens and Romero, 2013; Tablado and Jenni, 2017).

Humans are often perceived as predators by wildlife (Frid and Dill, 2002), and therefore may trigger the same behavioral and physiological responses as other biotic stressors. That is why the increase in anthropogenic disturbance (e.g. outdoor sports and recreation, ecotourism, traffic or urbanization), which lead to frequent encounters between wildlife and humans, has created concern among researchers and conservationists about the consequences of these encounters for wild populations and species. In an attempt to better understand species vulnerability to human disturbance, some studies have compared stress responses across species by focusing on single parameters, either behavioral or physiological changes (see for example Blumstein et al., 2005; Lendvai et al., 2013). Escape responses (mostly flight initiation distance), especially in birds, have been particularly used as a “non-invasive” estimation of species sensitivity to human disturbance (Blumstein et al., 2005; Møller and Tryjanowski, 2014). However, it is still uncertain to which extent environmental and species-specific characteristic modulate behavior and physiology differently and thus, to which extent behavioral reactions are representative of physiological responses to stress and vice versa. Therefore, it is unclear if focusing on single parameters is enough if we aim at assessing variation in vulnerability to human disturbance across species.

The objective of this study was, therefore, to examine how various factors (including characteristics of the species and of the spatio-temporal context) modulate the behavioral and physiological stress responses across species, in order to understand whether they affect both types of responses in a similar way or not. By this, we explored the nature of the relationship between behavioral and physiological reactions across species. We focused on the well-studied taxon of birds and we chose the two most commonly measured short-term stress responses: flight initiation distance (FID) as the behavioral response and the increase of the most common glucocorticoid in birds, corticosterone (CORT), as the physiological response. Both these responses are well-conserved mechanisms across vertebrates, comparable among species, and have been extensively studied in the literature using standardized protocols (Sapolsky et al., 2000; Romero, 2002; Bracha, 2004; Stankowich and Blumstein, 2005; Tablado and Jenni, 2017).

We collected published data on FID and circulating corticosterone concentrations (baseline and stress-induced levels). Then, we analyzed the FID and CORT data to investigate the influence of modulating factors that have been previously suggested to affect the two measures (Stankowich and Blumstein, 2005; Hau et al., 2010; Tablado and Jenni, 2017). The factors investigated comprised both species-specific characteristics (e.g. body mass, longevity) and spatio-temporal variables (e.g. habitat type, life-history stage). For the subset of species for which we had data on both stress parameters, we additionally examined the strength of correlation between FID and CORT across species. We proposed two alternative hypotheses: (1) Modulating factors affect behavior and physiology in similar ways and lead to a positive correlation between CORT and FID, with a range going from sensitive species, showing both a stronger physiological response and a longer FID, to less sensitive species which have both a short FID and a weak CORT reactivity. (2) At least some of the modulating factors influence the behavioral and physiological response to a stressor differently, which causes a decoupling of the relationship between FID and CORT. This would highlight that these modulating factors are important to consider in order to better understand the differences in vulnerability to stress across species.

Materials and methods

Data collection

We did an exhaustive literature review and collected available information up to August 2014 on population-specific FID and CORT reactivity of bird species all over the world from scientific articles, books, dissertations, scientific reports, and unpublished data. This database was later updated with data from two published databases: HormoneBase (Vitousek et al., 2018) for CORT and the FID database of Livezey et al. (2016) (see Appendix A for the complete list of studies, world areas, and species). FID is defined and measured as the distance at which animals can be approached by humans before escaping either by flying, swimming or on foot, also called flushing distance, escape distance or approaching distance. The information collected on CORT reactivity consisted of circulating baseline and stress-induced levels of CORT following a standardized capture-restraint stress protocol (Wingfield et al., 1992). This protocol assumes to simulate a threatening situation and measures, first, baseline levels (i.e. mostly within 3 minutes after capture) and then examines changes in CORT levels in the blood as a response to capture, restraint and handling. The time intervals at which blood was sampled (*sampling time*) varied across studies, so we included this variable in further analyses. Only studies presenting CORT data for both sexes within a species, either separately or sex-combined values, were considered for further analyses. When male and female values were given separately, we averaged them for each species to reduce the extra variability resulting from the between-sex differences and, more importantly, to be consistent with FID data which were mostly presented for both sexes combined. We excluded data from populations which were explicitly mentioned to be in poor condition (e.g. data from polluted areas) or to which an experimental treatment had been applied.

When available from the same or related sources, we also recorded information on the degree of *urbanization* of the study area, *latitude*, *life-history stage*, and methodological details such as *FID-measurement technique*, bird *capture method*, *CORT-measurement assay*, and *laboratory* in which the measurements were done. *Urbanization* was categorized as either "urban", when the study sites were located within densely build-up areas as either mentioned in the source papers (i.e. urban and suburban areas) or identified on a map by the geographical coordinates, or "non-urban" when the source papers or coordinates indicated that the site was in a natural or rural area. *Life-history stage* was classified using six categories: "overwintering" (late autumn and winter), "early breeding" (including territory settlement, courtship and egg laying), "parental phase" (incubation and rearing offspring), "molt", "postbreeding" (mainly late summer and early autumn) and "migration". We added another category, "breeding", for cases when the exact breeding stage was not known or several breeding stages had been combined. *FID-measurement technique* was classified as either "standard direct measurement" if data were obtained using standard protocols consisting of measuring the distance at which a bird flushes when approached by human (see for example Blumstein et al., 2005) or "expert communication" (when the approaching distances were estimated by experts without standardized protocols; e.g. Ruddock and Whitfield, 2007). *Capture method* to measure blood CORT levels was categorized as "positive" (when birds were attracted to the traps with a positive stimulus, such as baiting), "negative" (when birds were caught directly by approaching them, for example in their burrows, or were attracted to mist nets using playbacks or decoys to simulate intrusion), "neutral" (when capture included passive mist netting or trapping) or "mixed" (when several methods were used, mainly mist netting plus bait trapping). *CORT-measurement assay* was categorized as either radioimmunoassay (RIA) or enzyme immunoassay (EIA).

Using sources such as bird handbooks and online databases (see Appendix B for full list of sources), we also obtained further information about species-specific variables: average *body mass*, main *diet* ("carnivore" (including insectivores), "omnivore" or "herbivore"), maximum *longevity* recorded in the wild, typical *habitat* type ("closed": forested areas; "open": mostly free of trees, such as grasslands or marshlands; "mixed": mixture of open and wooded areas or areas with medium-sized vegetation, such as shrubs), and *level of aggregation*. The latter was determined using descriptions of the usual group size for the given life-history stage in which the stress measures were taken and was classified as "solitary or pairs", "small group" (for flocks or colonies up to about 100 individuals) and "large group" (for aggregations larger than 100 individuals).

Additionally, we characterized the species' degree of cryptic coloration (from now on *degree of crypticity*) and probability of *disruptive coloration* (i.e. coloration that breaks up the body outline) to understand to which extent these aspects of coloration could act as camouflage and affect stress responses. These two variables were defined using a double-blinded system. First, an ornithologist unaware of the purpose of the study was asked to search online for three pictures per species and sex of birds in their typical breeding-season habitat. Then, three other ornithologists, also unaware of the purpose of the study, were asked to describe all these pictures (~ 2700) according to the following criteria. Firstly, the ornithologists were asked to estimate the percentage of matching of the bird's plumage with the background in terms of both color similarity and coloration patterns (distribution of color patches); the three estimates were averaged to quantify the *degree of crypticity*. Cases where there was large variability among the estimates of the three ornithologists were considered unreliable and omitted from further analyses. That is, we excluded species where the standard deviation of the three estimates was over twice the average standard deviation of all species. Secondly, the ornithologists were asked to classify bird coloration in the pictures as disruptive or non-disruptive; later, the probability that a species was defined as having a *disruptive coloration* by the observers was calculated as the number of times described as disruptive divided by the total number of evaluations for the given species.

Statistical analyses

First, in order to model the variation in FID and CORT data as a function of different modulating factors, we performed two phylogenetic linear mixed models, one with FID and the other with CORT concentrations as response variables. For each model we used all available data on either FID (332 species and 100 studies) or CORT (90 species and 99 studies), respectively. Both variables were log-transformed to better fit a normal distribution (log (FID+0.1) and log (CORT)), where log symbolizes the natural logarithm. For CORT, we were mostly interested in the association of modulating factors with CORT reactivity (i.e. on the increase in CORT as a response to a stressor), so we analyzed all CORT data together in the same model, including both baseline and stress-induced values measured at different times (times ranging from 1 to 60 minutes). To account for the variation in CORT values with time since capture we incorporated *sampling time* as explanatory variable in the CORT model both as linear and quadratic term, as well as the interactions of sampling time with all other explanatory variables to describe how the corticosterone reactivity curve is modulated by the different factors. Note that since we were interested in the increasing part of the CORT reactivity curve (i.e. CORT increase under stress), we included the interactions of *sampling time* only with its linear term, avoiding in this way unnecessary complexity and over-parameterization.

We then explored in both separate models the association of FID and CORT, respectively, with the spatial context (*urbanization*, *habitat* type, and *latitude* in absolute values, i.e. from 0-90º independent of the hemisphere), the temporal context (*life-history stage*), and the species-specific characteristics (*body mass*, *diet*, *level of aggregation*, *longevity*, *degree of crypticity,* and *disruptive coloration*). *Body mass* was incorporated as log-transformed in the models to account for the fact that the relationships with body mass may not be linear throughout the whole range but instead may reach an asymptote at larger body masses. FID has been shown to increase with body mass in previous studies (e.g. Blumstein 2006), but species with exceptionally large body masses may not flee earlier than medium-sized species. Similarly, CORT responses were also predicted to show an asymptotic relationship with body mass, although in this case, we expected CORT reactivity to decrease with body mass, due to a steady decrease in mass-specific metabolic rate with size (Gillooly et al., 2001; Hau et al., 2010; Jimeno et al., 2018). Potential non-linear effects of *longevity* and *disruptive coloration* were also examined by including their linear and quadratic terms.

We also included explanatory variables dealing with relevant aspects of the measurement methodology: *FID-measurement technique* in the FID model and *capture method* and *CORT-measurement* *assay* for the analyses of CORT values. Finally, in both models we accounted for within-species and within-study correlations by including *species* and *study* as random factors. In the CORT model we also included *laboratory* as random factor to control for inter-laboratory variation in corticosterone measurements (Fanson et al., 2017) and sample *ID* to account for the correlation of repeated measures (i.e. CORT levels at different sampling times) for each species within each study (see Table A.1 and A.2 for complete models). Phylogenetic linear mixed models were fitted with the R function and package MCMCglmm (Hadfield, 2010), using uninformative priors (V = 1, nu = 0.02), 200000 iterations, thinning every 100 iterations, and a burn-in period of 3000. The phylogeny to account for phylogenetic non-independence among species was obtained by calculating, through the R package phytools (Revell, 2012), the least-squares consensus tree out of 100 phylogeny subsets based on the Ericson backbone (Ericson et al., 2006) available from BirdTree.org (see Jetz et al., 2012 for more details).

To evaluate the effect of the modulating factors in the Bayesian framework we calculated, based on the posterior distribution of the model parameters, the posterior probability (PP) of the hypotheses that these variables had either a positive or a negative association with the response variable. The higher the probability (from 0.5 to 1), the greater the support for the effect of a given variable. For categorical variables (e.g. *habitat*), we additionally calculated for all pair-wise combinations of factor levels the posterior probability (PP) of the hypothesis that the mean values differed among categories. Again, the larger this probability (0.5 to 1), the stronger the support for the difference between categories. To make inferences about differences in corticosterone reactivity depending on the modulating variables (i.e. across predictor values or factor categories), we calculated the posterior probability that the fitted reactivity curves differed in three different aspects: 1) baseline levels (estimated as values at *sampling time* of 1 minute; PPb), 2) stress levels (i.e. values at *sampling time* of 30 minutes, as measured by most authors; PP30), and 3) the increment in corticosterone levels from 1 to 30 minutes (PPi). For the tables and figures, the posterior mean and 95% credible intervals (CrI) were also drawn from the posterior distribution of the model parameters.

Additionally, for subset of species (n = 48 species) for which we had data on both FID and CORT (even if mostly came from separate studies), we implemented a phylogenetic multivariate mixed model to compare the influence of modulating factors on both stress responses simultaneously. That is, FID and CORT reactivity were both included as response variables, permitting direct comparisons of the association of the explanatory variables with each of them. We used the same explanatory variables and random factors as in the two previous models; however, in this case we included only variables that are common to both dependent variables in order to be able to compare effect sizes on each response variable. Therefore, we did not include response-specific variables, such as *FID-measurement technique, capture method*, *CORT-measurement assay*, CORT *laboratory* or CORT *sampling time*. In this case, CORT reactivity was calculated as the slope of the increase from baseline CORT to CORT concentration at the time when stress-peak values were measured (range 20-30 min, mostly around 30 min after capture). Both variables were transformed to better fit a normal distribution (i.e. FID was log-transformed (log (FID+0.1)) and CORT slope was square-rooted to fulfil normality) (see Table A.6 for complete model). This phylogenetic multivariate mixed model was also performed using the R package *MCMCglmm* (Hadfield, 2010) with the same priors, iterations, thinning, burn-in the previous two models. Consensus trees (for this subset of species) were also obtained from BirdTree.org and used in the models to control for the effect of phylogeny.

Moreover, in order to assess the correlation between behavioral and physiological stress responses across species, we used the same subset of species for which we had data on both FID and CORT (n = 48 species) to calculate a Pearson correlation with phylogenetic data using the R package *phytools* (Revell, 2012). That is, we examined whether FID values were correlated with CORT reactivity (stress-induced increases in CORT) while controlling for shared ancestry. Both variables were transformed to fulfill normality similarly to phylogenetic multivariate mixed model (i.e. log (FID+0.1) and square root (CORT slope)). If several values were available per species for either FID or CORT slope, values were averaged to create species-specific averages, because very few studies (less than 1%) provided data on FID and CORT from the same individuals impeding direct correlations. We calculated repeatability of the traits using rptR package (Nakagawa and Schielzeth 2013) in R in this subset of the 48 species as above, and found that both FID and CORT slope were highly repeatable within species, which supports the use of species averages for the correlation analysis (R_{FID} =0.727 [95% confidence interval: 0.597, 0.806], n=261 FID data; $R_{CORTSLOPE}$ =

0.753 [0.623, 0.834], n=173 CORT slope records). For comparison's sake with the relationship at pre-stress corticosterone levels, we added a second phylogenetic correlation between FID and baseline CORT, both variables previously log-transformed.

Results

Our models showed that some modulating factors had similar relationships to both FID and CORT while other factors were associated to FID and CORT in different ways (Table 1). The results of phylogenetic multivariate mixed model, investigating the influence of modulators on both responses simultaneously, were unfortunately not conclusive enough. This is probably due to the limited sample size (only 48 species for which both FID and CORT reactivity was available). Despite the lack of robust results (Table A.6, Figure A.3), this multivariate model showed trends in agreement with the results observed in the separate phylogenetic linear mixed models (Figure 1 and 2). Therefore, given the lack of conclusive results from the multivariate model, we decided to focus on the qualitative comparison of the results from the two separate models, by comparing the direction (increasing or decreasing) and shape of the observed trends.

These qualitative comparisons were supported by the high within-species repeatability observed (calculated using rptR package in R as above) in the two complete datasets of FID (n = 878 data, 262 species) and CORT levels (n = 574 data, 71 species) used in these two models. The repeatability without controlling for the modulating factors (except for *sampling time* in the CORT model) was $R_{FID} = 0.724$ [95% CI: 0.671, 0.769] and $R_{CORT} = 0.494$ [0.376, 0.588], while the values after accounting for the modulating factors were $R_{FID} = 0.751$ [0.706, 0.798] and $R_{CORT} = 0.418$ [0.307, 0.55] (see Taff et al., (2018) for reference on CORT repeatability). Moreover, potential bias caused by differences in the range of data available for each model (i.e. each subset of species) is not an issue in this study, since as shown in Supplementary Table A.5 the available variation in the explanatory variables does not differ substantially between the FID, the CORT, and the multivariate models.

With the two separate mixed models, with either FID or CORT as the dependent variable, we found that, after controlling for the methodological variables (See Supplementary information Figure A.1), modulating factors such as urbanization, life-history stage, disruptive coloration, and level of aggregation showed similar relationships with both FID and CORT (Table 1; Figure 1 and 2; Supplementary information Table A.1 and A.2). In contrast, other factors, like latitude, habitat type, or body mass, exhibited qualitatively different associations to FID and CORT (Table 1; Figure 1 and 2; Supplementary information Table A.1 and A.2). Note that the influence of modulators on the CORT reactivity curve can only be fully interpreted in the increasing part of the curve, which is the main focus of our study, because we included the interactions with *sampling time* only in its linear form in the CORT model (Figure 2a,b,e,f and Figure A.2).

Birds in urban environments had both shorter FID and lower CORT reactivity, although this trend was less strongly supported (i.e. had a smaller PP) for the physiological than for the behavioral response (Table 1; Figure 1a and 2a). Other spatial-context variables modulated FID and CORT levels differently. FID decreased with latitude while the CORT stress response increased towards the poles (Table 1; Figure 1b and 2b). Habitat type influenced FID, so that species in closed habitats allowed for a closer approach than species in mixed or open habitats, while no clear association was observed between habitat and CORT reactivity (Table 1; Figure 1c and 2c).

Regarding the temporal context, the behavioral and the physiological responses varied similarly across life-history stages. Birds had shorter FID and weaker CORT reactivity during the parental phases (i.e. incubation and chick rearing) and the molting period, while both FID and the CORT reactivity increased during migration, overwintering and the early breeding season (i.e. from territory settlement to egg-laying). Note that data for molting birds were only available for CORT (Figure 1d and 2d).

As for the species-specific characteristics, we found that the probability of disruptive coloration and the level of aggregation modulated both FID and CORT levels in similar ways (Table 1; Figure 1 and 2). Birds with more disruptive color patterns tended to have a shorter FID and lower CORT reactivity (Figure 1g and Figure 2g). Species in small groups showed a lower behavioral and physiological response to stress, whereas species that are more solitary or in large groups presented a higher reactivity (Table 1; Figure 1i and

2i). In contrast, FID and CORT showed different relationships with other species-specific variables, such as body mass, crypticity, diet, and longevity (Table 1; Figure 1 and 2). FID increased with increasing body mass while CORT reactivity showed an opposite relationship, with smaller species having a higher overall CORT reactivity (Table 1; Figure 1e and 2e). The degree of crypticity was negatively correlated with FID, while this trend was not so clearly supported in the case of CORT reactivity (Table 1; Figure 1f and 2f). Similarly, diet had a more marked association with FID than with CORT reactivity. Herbivorous species had the largest FID, but differences between diet categories were not observed regarding the CORT response (Table 1; Figure 1h and 2h). Longevity showed a quadratic relationship with FID (species with an intermediate longevity had the longest FID), while CORT reactivity showed only a weak tendency to be higher in species that live longer (Table 1; Figure 1j and 2j).

In species for which both FID and CORT were available, we found no strong correlation between these two responses to stress. While FID showed a strong positive relationship to baseline (i.e. pre-stress) levels of CORT (correlation coefficient = 0.6; p-value <0.0001; Figure 3a), stress-induced increases (i.e. slope) in CORT (CORT reactivity) did not show a clear association with FID (correlation coefficient = 0.1; p-value = 0.5; Figure 3b).

Discussion

This study showed that there is not a straightforward relationship between the two most commonly measured proxies for behavioral and physiological stress responses across avian species. The hormonal reactivity to stress (i.e. the increase of CORT levels in a standardized, threatening situation) showed no correlation with the behavioral response (i.e. escape distance from an approaching human), which demonstrates that FID is not necessarily representative of the intensity of a species' CORT reactivity to stress, and vice versa. However, we found a positive inter-specific correlation between FID and baseline CORT. This coincides with findings at the individual level in, for example, tree lizards and cottonmouth snakes (Thaker et al., 2009, Herr et al., 2017), showing that pre-stress circulating CORT levels enhance antipredator behavioral responses through the preparatory effects of corticosterone.

Our results from the models investigating the influence of multiple factors on both FID and CORT reactivity separately suggest that the lack of interspecific correlation between the physiological and behavioral stress responses could at least partially be due to the fact that some factors modulate behavioral and physiological responses differently. That is, whereas factors such as life-history stage had a similar relationship with both FID and CORT reactivity, other factors (e.g. latitude or body mass) seemed to modulate the two stress responses in different directions. Our findings are in line with the conceptual review of Killen et al. (2013), who suggest that environmental variables may alter general relationships between behavior and physiology.

In this way, spatial-context factors such as latitude seem to modulate the behavioral and physiological responses differently. We found that FID decreased with latitude whereas the CORT response showed the opposite trend, and therefore the two responses are likely shaped by different processes. For example, FID could be driven by the presence or absence of a coevolutionary history with predators/humans. Evolving in an environment with lower predation pressure, such as high latitudes, where the diversity and abundance of predators is lower (Schemske et al., 2009), could have resulted in bird species being more naïve towards humans (Diaz et al., 2013). This coincides with previous studies showing shorter FID on islands with low predation pressure than in areas with higher numbers of predators (Humphrey et al., 1987; Berger et al., 2007). On the other hand, we found that CORT response was larger at high latitudes than at lower latitudes, which agrees with previous studies that found higher CORT levels and reactivities at high latitudes and in extreme habitats (Dunlap and Wingfield, 1995; Bókony et al., 2009), although this reactivity is reduced during the breeding seasons (e.g. Silverin et al., 1997; O'Reilly and Wingfield, 2001). The positive correlation between latitude and CORT responses could be explained by the greater need for coping with extreme weather events at high latitudes and the association of cold environments with increased metabolic rates (Gillooly et al., 2001; Jimeno et al., 2017), which in turn is linked to CORT production (Jessop et al., 2013; Jimeno et al., 2018).

Habitat type also showed different associations with the behavioral versus the physiological response in our study. Species inhabiting habitats with closed, dense vegetation seemed to allow closer approach than species in more open habitats; however, corticosterone reactivity did not differ across habitats. This divergence of patterns could be explained by vegetation density acting as a shield that both reduces predator/human detection by birds and also provides birds with a sense of shelter, thus delaying active behavioral reactions (Stankowich and Blumstein, 2005; Thiel et al., 2007; Tablado and Jenni, 2017). In contrast, stress-induced corticosterone levels represent the physiological response to an actual predation threat (Sapolsky et al., 2000; Tablado and Jenni, 2017), in this case the capture, restraint and handling protocol, and may be therefore independent of previous variation in probability of predator detection.

On the other hand, we found a tendency towards both lower FID and CORT levels in urban study sites. This could be explained by urbanization creating environments where frequent human disturbance selects for bolder personalities within and/or among species, therefore, resulting in urban populations reacting less to humans (Atwell et al., 2012; Rebolo-Ifran et al., 2014; Sprau and Dingemanse, 2017). To a certain extent, habituation could also play a role, in that urban birds get used to human presence and do not perceive their approach as a threat, shaping their behavioral responses towards shorter FIDs (Vincze et al., 2016; Cavalli et al., 2018). Similar mechanisms might have also led to reduced CORT reactivity in some urban-dwelling birds, although within-species studies so far have produced mixed results (Bonier, 2012; Sepp et al., 2018; Iglesias-Carrasco et al., 2020).

Regarding the temporal context, behavior and physiology in our study seemed to respond similarly to changes in life-history stage. Birds showed shorter FID and smaller CORT responses during the parental phases of reproduction (i.e. incubation and chick rearing) or molting periods than during other periods of the annual cycle. This pattern agrees with previous studies, which partially investigated this question within single-species systems or across specific life-history stages (Romero et al., 1998; Romero, 2002; Tablado and Jenni, 2017). Both behavioral and physiological stress responses promote self-maintenance (Wingfield and Sapolsky, 2003; Cornelius et al., 2011), therefore both responses are suppressed to a certain extent during parental stages of the life cycle in order to allow for successful reproduction (Romero, 2002; Wingfield and Sapolsky, 2003; Angelier and Wingfield, 2013). Molting birds are also limited in their capacity to behaviorally or physiologically respond to stressors (Romero, 2002; Tablado and Jenni, 2017; Jenni and Winkler, 2020).

As for the species-specific characteristics, the level of aggregation showed a similar relationship to both behavioral and physiological responses, with species living in small groups having lower CORT response and shorter FID than species living either in larger groups or solitarily. Forming groups has the advantage of decreasing the probability of being predated through risk dilution and reducing the per-individual amount of vigilance time, as well as increasing the likelihood of finding food (Elgar, 1989; Roberts, 1996; Stankowich and Blumstein, 2005). All this would result in lower levels of overall stress and therefore to lower reactions to disturbance; however, when groups are too large, increases in stressful social interactions (such as increased intragroup competition) and in likelihood of arousal lead to higher probabilities of triggering antipredator behavioral and/or physiological responses (Pride, 2005; Tablado and Jenni, 2017).

Regarding camouflage, we observed that both behavioral and physiological responses decreased with the probability of disruptive coloration of the species. The species more likely to be described as "disruptively colored" escaped later and showed lower CORT responses. Similarly, we found that stress responses decreased with the degree of crypticity, especially in the case of FID, which coincides with results of previous studies in birds and other taxa (Heatwole, 1968; Møller et al., 2019). This could be explained by evolutionary processes favoring crypticity and disruptive coloration as adaptations to reduce predation, through decreasing the probability of predators detecting prey or discerning their vital parts, respectively (Schaefer and Stobbe, 2006; Stevens and Merilaita, 2009), thus, alleviating the evolutionary pressure towards the development of strong behavioral or physiological anti-predator responses.

Body mass showed contrasting associations with FID versus CORT reactivity. While escape distances increased with body mass, especially in the lower part of the body mass range, CORT response decreased, with larger species showing a weaker CORT reactivity under stress. These results agree with previous research investigating FID and CORT separately. On the one hand, larger species might be able to perceive predators from longer distances given their bigger eyes and body size (Kiltie, 2000). Moreover, their larger size might limit fast flushing responses, forcing them to react in advance (Blumstein et al., 2005; Tablado and Jenni, 2017). On the other hand, CORT production is closely linked to mass-specific metabolic rate, which tends to increase with decreasing body size, therefore allowing for a stronger relative CORT response in smaller species (Jessop et al., 2013; Tablado and Jenni, 2017).

Diet type also modulated behavioral and hormonal stress responses differently. The largest flight initiation distances were observed in herbivore species. This is consistent with the predation risk hypothesis, since predation risk is likely to be higher for herbivores than for non-herbivore species, and furthermore, the cost of moving to alternative breeding sites when disturbed might also be lower for herbivorous species (Gill et al., 2001; Capellini et al., 2008; but see Blumstein, 2006). However, when looking at the CORT response, we found no clear differences among the three types of species.

Finally, although we did not observe a strong relationship between longevity and CORT responses, there seems to be a quadratic association between longevity and FID, with stronger escape responses occurring at intermediate longevities. This is consistent with previous research suggesting that “slow” species, with long lives and smaller yearly reproductive output, invest more in self-maintenance and less in reproduction when facing challenges (Breuner, 2010; Hau et al., 2010; Møller and Garamzegi, 2012). However, beyond a certain longevity threshold, birds might face less threats and predator pressures in general, and thus, they may not perceive human approaches as such a strong risk as species with intermediate life spans. A link between naivety to predation and low behavioral reactions has been shown e.g. on islands (Berger et al., 2007). Moreover, extremely long-lived species may also accumulate more experience about predators and have more opportunities to learn that humans are not dangerous, and this may result in reduced stress responses (Lendvai et al., 2013; Sol et al., 2016).

In conclusion, even though flight initiation distance and corticosterone reactivity are both mechanisms used by animals for self-protection under threatening situations, the two responses are not entirely correlated across avian species, especially outside the breeding season. Both physiology and behavior are modulated differently by intrinsic and extrinsic factors. We acknowledge that our results are based on qualitative comparisons and that future studies should focus on measuring both physiological and behavioral stress responses under the same circumstances in the same individuals to allow for more quantitative comparisons. However, this limitation does not invalidate the general patterns found here. We suggest that flight initiation distance patterns are mainly driven by evolution under different predation pressures, including variations in the amount and diversity of predators, probabilities of detection or of being detected and attacked, and thus threat perception in general. In contrast, CORT reactivity patterns seem to be influenced by more complex evolutionary pressures, since CORT levels respond not only to predation threats, but are also associated with metabolic changes that help the organism to cope with multiple stressors including starvation, disease and extreme weather. Furthermore, measures of flight initiation distance are not only affected by the animals' perception of risk but also by the probability of detecting the predator/human in the first place, while the standard measurement of CORT response involves the actual capturing and handling of the individuals, filtering out the effect of probability of detection. Therefore, the usually measured behavioral and physiological stress responses are not always representative of each other. This means that, when the two kinds of responses are studied separately, the results should be interpreted carefully. For example, a species that flees from longer distances is not necessarily more sensitive physiologically to various stressors; similarly, a species producing high CORT responses to the capture-restraint protocol is not necessarily the one most impacted behaviorally by human disturbance. Thus, for protecting wildlife in a world increasingly affected by urbanization and other forms of anthropogenic environmental change, we suggest that assessments of conservation status take into consideration modulating factors in order to better interpret single stress responses, and, if possible, take into account multiple (both behavioral and physiological) measures of stress responses simultaneously.

Acknowledgements

We thank Trond Amundsen, Torkild Tveera, Megan Price, Ron Summers, Mariette Wheeler, Patrick-Jean Guay, Paolo Galeotti, and András Kosztolányi, for providing data otherwise inaccessible to us, and institutions such as the Document Delivery Service, University of Tasmania Library for sending us copies of work not available online for us. We are grateful to Fränzi Korner-Nievergelt for her statistical advice. Special thanks go to Doris Thalmann, Tobias Lötscher, Johann von Hirschheydt, Bruno Meyer and Flurin Leugger for their help with the tedious work of searching for pictures of the study species and assess them to create the camouflage variables. We thank the members of the lab at the Swiss Ornithological Institute for their input at previous stages of the study. VB was supported by the János Bolyai Research Scholarship of the Hungarian Academy of Sciences and the ÚNKP-20-5 New National Excellence Program ("Bolyai+ Scholarship") of the Ministry for Innovation and Technology from the source of the National Research, Development and Innovation Fund of Hungary (NKFIH K-135016).

References

Angelier, F., Wingfield, J.C., 2013. Importance of the glucocorticoid stress response in a changing world: theory, hypotheses and perspectives. Gen. Comp. Endocrinol. 190, 118–128.

Atwell, J.W., Cardoso, G.C., Whittaker, D.J., Campbell-Nelson, S., Robertson, K.W., Ketterson, E.D., 2012. Boldness behavior and stress physiology in a novel urban environment suggest rapid correlated evolutionary adaptation. Behav. Ecol. 23, 960–969.

Berger, S., Wikelski, M., Romero, L.M., Kalko, E.K.V., Rödl, T., 2007. Behavioral and physiological adjustments to new predators in an endemic island species, the Galapagos marine iguana. Horm. Behav. 52, 653–663.

Blumstein, D.T., 2006. Developing an evolutionary ecology of fear: how life history and natural history traits affect disturbance tolerance in birds. Anim. Behav. 71, 389–399.

Blumstein, D.T., 2010. Flush early and avoid the rush: a general rule of antipredator behavior? Behav. Ecol. 21, 440–442.

Blumstein, D.T., Fernandez-Juricic, E., Zollner, P., Garity, S., 2005. Inter-specific variation in avian responses to human disturbance. J. Appl. Ecol. 42, 943–953.

Bókony, V., Lendvai, A.Z., Liker, A., Angelier, F., Wingfield, J.C., Chastel, O., 2009. Stress response and the value of reproduction: are birds prudent parents? Am. Nat. 173, 589–598.

Bonier, F., 2012. Hormones in the city: Endocrine ecology of urban birds. Horm. Behav. 61, 763–772.

Bracha, D., 2004. Freeze, Flight, Fight, Fright, Faint: Adaptationist Perspectives on the Acute Stress Response Spectrum. CNS Spectr. 679–685.

Breuner, C.W., 2010. Stress and reproduction in birds. In: Hormones and Reproduction of Vertebrates. (eds. Norris, D.O., Lopez, K.H.. London: Academic Press., pp. 129–151.

Buckley, R., 2011. Tourism and Environment. Annu. Rev. Environ. Resour. 36, 397–416.

Capellini, I., Barton, R.A., McNamara, P., Preston, B.T., Nunn, C.L., 2008. Phylogenetic analysis of the ecology and evolution of mammalian sleep. Evol. Int. J. Org. Evol. 62, 1764–1776.

Cavalli, M., Baladrón, A.V., Isacch, J.P., Biondi, L.M., Bó, M.S., 2018. The role of habituation in the adjustment to urban life: An experimental approach with burrowing owls. Behav. Processes 157, 250–255.
Cornelius, J.M., Perfito, N., Zann, R., Breuner, C.W., Hahn, T.P., 2011. Physiological trade-offs in self-maintenance: plumage molt and stress physiology in birds. J. Exp. Biol. 214, 2768–2777.
Cyr, N.E., Romero, L.M., 2009. Identifying hormonal habituation in field studies of stress. Gen. Comp. Endocrinol. 161, 295–303.
Diaz, M., Møller, A.P., Flensted-Jensen, E., Grim, T., Ibañez-Alamo, J.D., Jokimäki, J., et al., (2013. The Geography of Fear: A Latitudinal Gradient in Anti-Predator Escape Distances of Birds across Europe. PLoS ONE, 8, e64634.
Dickens, M.J., Romero, L.M., 2013. A consensus endocrine profile for chronically stressed wild animals does not exist. General and Comparative Endocrinology 191, 177–189.
Dunlap, K.D., Wingfield, J., 1995. External and internal influences on indices of physiological stress. I. Seasonal and population variation in adrenocortical secretion of free-living lizards, *Sceloporus occidentalis*. J. Exp. Zool. 271, 36–46.
Elgar, M.A., 1989. Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. Biol. Rev. 64, 13–33.
Ericson, P.G., Anderson, C.L., Britton, T., Elzanowski, A., Johansson, U.S., Källersjö, M., et al., (2006. Diversification of Neoaves: integration of molecular sequence data and fossils. Biol. Lett. 2, 543–547.
Fanson, K.V., Németh, Z., Ramenofsky, M., Wingfield, J.C., Buchanan, K.L.; (2017. Inter-laboratory variation in corticosterone measurement: Implications for comparative ecological and evolutionary studies. Methods Ecol. Evol. 1–10.
Frid, A., Dill, L.M., 2002. Human-Caused Disturbance Stimuli as a Form of Predation Risk, 6(1): 11.
Gill, J.A., Norris, K., Sutherland, W.J., 2001. Why behavioural responses may not reflect the population consequences of human disturbance. Biol. Conserv. 97, 265–268.
Gillooly, J.F., Brown, J.H., West, G.B., Savage, V.M., Charnov, E.L., 2001. Effects of Size and Temperature on Metabolic Rate. Science 293, 2248–2251.
Gormally, B.M., Romero, L.M., 2020. What are you actually measuring? A review of techniques that integrate the stress response on distinct time-scales. Functional Ecology 34, 2030–2044.
Hadfield, J.D., 2010. MCMC methods for multiresponse generalized linear mixed models: the MCMCglmm R package. J. Stat. Softw. 33, 1–22.
Hau, M., Ricklefs, R.E., Wikelski, M., Lee, K.A., Brawn, J.D., 2010. Corticosterone, testosterone and life-history strategies of birds. Proc. R. Soc. B Biol. Sci. 277, 3203–3212.
Heatwole, H., 1968. Relationship of Escape Behavior and Camouflage in Anoline Lizards. Copeia 1968, 109–113.
Herr, M.W., Graham, S.P., Langkilde, T., 2017. Stressed snakes strike first: Hormone levels and defensive behavior in free ranging cottonmouths (*Agkistrodon piscivorus*). Gen. Comp. Endocrinol. 243, 89–95.
Iglesias-Carrasco, M., Aich, U., Jennions, M.D., Head, M.L., 2020. Stress in the city: meta-analysis indicates no overall evidence for stress in urban vertebrates. Proceedings of the Royal Society B 287, 20201754.
Jenni, L., Winkler, R., 2020. The Biology of Moult in Birds. Bloomsbury Publishing.
Jessop, T.S., Woodford, R., Symonds, M.R.E., 2013. Macrostress: do large-scale ecological patterns exist in the glucocorticoid stress response of vertebrates? Funct. Ecol. 27, 120–130.
Jetz, W., Thomas, G., Joy, J., Hartmann, K., Mooers, A., 2012. The global diversity of birds in space and time. Nature 491, 444–448.
Jimeno, B., Hau, M., Verhulst, S., 2017. Strong association between corticosterone levels and temperature-dependent metabolic rate in individual zebra finches. J. Exp. Biol. 220, 4426–4431.
Jimeno, B., Hau, M., Verhulst, S., 2018. Corticosterone levels reflect variation in metabolic rate, independent of 'stress.' Sci. Rep. 8, 13020.

Killen, S.S., Marras, S., Metcalfe, N.B., McKenzie, D.J., Domenici, P., 2013. Environmental stressors alter relationships between physiology and behaviour. Trends Ecol. Evol. 28, 651–658.

Kiltie, R.A., 2000. Scaling of visual acuity with body size in mammals and birds. Funct. Ecol. 14, 226–234.

Lendvai, A.Z., Bókony, V., Angelier, F., Chastel, O., Sol, D., 2013. Do smart birds stress less? An interspecific relationship between brain size and corticosterone levels. Proc. R. Soc. B Biol. Sci. 280(1770), 20131734.

Lima, S.L., 1993. Ecological and Evolutionary Perspectives on Escape from Predatory Attack: A Survey of North American Birds. Wilson Bull. 105, 1–47.

Livezey, K.B., Fernández-Juricic, E., Blumstein, D.T., 2016. Database of Bird Flight Initiation Distances to Assist in Estimating Effects from Human Disturbance and Delineating Buffer Areas. Journal of Fish and Wildlife Management.

Møller, A.P., Garamzegi, L.Z., 2012. Between individual variation in risk-taking behavior and its life history consequences. Behav. Ecol. 23, 843–853.

Møller, A.P., Liang, W., Samia, D.S.M., 2019. Flight initiation distance, color and camouflage. Curr. Zool. 65(5), 535-540.

Møller, A.P., Tryjanowski, P., 2014. Direction of approach by predators and flight initiation distance of urban and rural populations of birds. Behav. Ecol. aru073.

Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods Ecol. Evol. 4, 133–142.

O'Reilly, K.M., Wingfield, J.C., 2001. Ecological Factors Underlying the Adrenocortical Response to Capture Stress in Arctic-Breeding Shorebirds. Gen. Comp. Endocrinol. 124, 1–11.

Pride, R.E., 2005. Optimal group size and seasonal stress in ring-tailed lemurs (*Lemur catta*). Behav. Ecol. 16, 550–560.

Rebolo-Ifran, N., Carrete, M., Sanz-Aguilar, A., Rodriguez-Martinez, S., Cabezas, S., Marchant, T.A., et al., 2014. Links between fear of humans, stress and survival support a non-random distribution of birds among urban and rural habitats. Sci. Rep. 5, 13723–13723.

Revell, L.J., 2012. phytools: an R package for phylogenetic comparative biology (and other things). Methods Ecol. Evol. 3, 217–223.

Roberts, G., 1996. Why individual vigilance declines as group size increases. Anim. Behav. 51, 1077–1086.

Romero, L.M., 2002. Seasonal changes in plasma glucocorticoid concentrations in free-living vertebrates. Gen. Comp. Endocrinol. 128, 1–24.

Romero, L.M., 2004. Physiological stress in ecology: lessons from biomedical research. Trends Ecol. Evol. 19, 249–255.

Romero, L.M., Soma, K.K., Wingfield, J.C., 1998. Hypothalamic-pituitary-adrenal axis changes allow seasonal modulation of corticosterone in a bird. Am. J. Physiol. - Regul. Integr. Comp. Physiol. 274, R1338–R1344.

Ruddock, M., Whitfield, D.P., 2007. A Review of Disturbance Distances in Selected Bird Species. Report from Natural Research (Projects) Ltd. to Scottish Natural Heritage. Natural Research, Banchory, UK.

Sapolsky, R.M., Romero, L.M., Munck, A.U., 2000. How Do Glucocorticoids Influence Stress Responses? Integrating Permissive, Suppressive, Stimulatory, and Preparative Actions. Endocr. Rev. 21, 55–89.

Schaefer, H.M., Stobbe, N., 2006. Disruptive coloration provides camouflage independent of background matching. Proc. R. Soc. B Biol. Sci. 273, 2427–2432.

Schemske, D.W., Mittelbach, G.G., Cornell, H.V., Sobel, J.M., Roy, K., 2009. Is there a latitudinal gradient in the importance of biotic interactions? Annu Rev Ecol Evol Syst. 40, 245–269.

Sepp, T., McGraw, K.J., Kaasik, A., Giraudeau, M., 2018. A review of urban impacts on avian life-history evolution: Does city living lead to slower pace of life? Glob. Change Biol. 24, 1452–1469.

Silverin, B., Arvidsson, B., Wingfield, J., 1997. The adrenocortical responses to stress in breeding willow warblers *Phylloscopus trochilus* in Sweden: effects of latitude and gender. Funct. Ecol. 11, 376–384.

Sol, D., Sayol, F., Ducatez, S., Lefebvre, L., 2016. The life-history basis of behavioural innovations. Philos. Trans. R. Soc. B Biol. Sci. 371, http://dx.doi.org/10.1098/rstb.2015.0187.

Sprau, P., Dingemanse, N.J., 2017. An Approach to Distinguish between Plasticity and Non-random Distributions of Behavioral Types Along Urban Gradients in a Wild Passerine Bird. Front. Ecol. Evol. 5, 92.
Stankowich, T., Blumstein, D.T., 2005. Fear in animals: a meta-analysis and review of risk assessment. Proc. R. Soc. B Biol. Sci. 272, 2627–2634.
Steen, J.B., Gabrielsen, G.W., Kanwisher, J.W., 1988. Physiological aspects of freezing behaviour in willow ptarmigan hens. Acta Physiol. Scand. 134, 299–304.
Stevens, M., Merilaita, S., 2009. Defining disruptive coloration and distinguishing its functions. Philos. Trans. R. Soc. B Biol. Sci. 364, 481–488.
Tablado, Z., Jenni, L., 2017. Determinants of uncertainty in wildlife responses to human disturbance. Biol. Rev. 92(1), 216–233.
Taff, C.C., Schoenle, L.A., Vitousek, M.N. (2018). The repeatability of glucocorticoids: a review and meta-analysis. Gen. Comp. Endocrinol. 260, 136–145.
Thaker, M., Lima, S.L., Hews, D.K., 2009. Acute corticosterone elevation enhances antipredator behaviors in male tree lizard morphs. Horm. Behav. 56, 51–57.
Thiel, D., Menoni, E., Brenot, J., Jenni, L., 2007. Effects of recreation and hunting on flushing distance of capercaillie. J. Wildl. Manag. 71, 1784–1792.
Vincze, E., Papp, S., Preiszner, B., Seress, G., Bókony, V., Liker, A., 2016. Habituation to human disturbance is faster in urban than rural house sparrows. Behav. Ecol. 27, 1304–1313.
Wingfield, J.C., Maney, D.L., Breuner, C.W., Jacobs, J.D., Lynn, S., Ramenofsky, M., et al., (1998. Ecological bases of hormone-behavior interactions: the “emergency life history stage.” Am. Zool. 38(1), 191–206.
Vitousek, M.N., Johnson, M.A., Donald, J.W., Francis, C.D., Fuxjager, M.J., Goymann, W., Hau, M., Husak, J.F., Kircher, B.K., Knapp, R., 2018. HormoneBase, a population-level database of steroid hormone levels across vertebrates. Scientific data 5, 180097.
Wingfield, J.C., 2013. The comparative biology of environmental stress: behavioural endocrinology and variation in ability to cope with novel, changing environments. Animal Behaviour 85, 1127–1133.
Wingfield, J.C., Sapolsky, R.M., 2003. Reproduction and Resistance to Stress: When and How. J. Neuroendocrinol. 15, 711–724.
Wingfield, J.C., Vleck, C.M., Moore, M.C., 1992. Seasonal changes of the adrenocortical response to stress in birds of the Sonoran Desert. J. Exp. Zool. 264, 419–428.

Table 1. Summary of the qualitative results from the separate models with either FID or CORT as the dependent variable and all modulating factors as independent variables, after controlling for the methodological variables (see Appendix Table A.1 and A.2 for the full model output).

	Stress Response	
Modulating Factor	**FID**	**CORT reactivity**
Urbanization	Non-Urban > Urban	Non-Urban > Urban
Absolute latitude	Low > High	High > Low
Type of habitat	Mixed, Open > Closed	Closed ~ Mixed ~ Open
Life-history stage	Migration, Overwintering and Early breeding > Parental phase	Migration, Overwintering and Early breeding > Parental phase and Molt
Bodymass	High > Low	Low > High
Degree of crypticity	Low > High	Low ~ High
Disruptive coloration	Low > High	Low > High
Type of diet	Herbivorous > Omnivorous and Carnivorous	Herbivorous ~ Omnivorous ~ Carnivorous
Level of aggregation	Large and Solitary > Small	Large and Solitary > Small
Longevity	Intermediate > Low and High	Low ~ Intermediate ~ High

Figure 1. Graphical presentation of effect sizes for factors influencing flight initiation distance (estimated means ± 95% credible intervals) derived from the model presented in Appendix Table A.1. Posterior probabilities (PP ranging from 0.5 to 1) represent the strength of the support for a given effect. For factors with more than two categories, we used different letters to represent categories diverging with a PP > 0.9, as a reference of the magnitude of the probability with which the categories differ (complete pairwise PPs are shown in Table A.3). Note that we had no available data on FID of molting birds, thus, this category was not included in panel d.

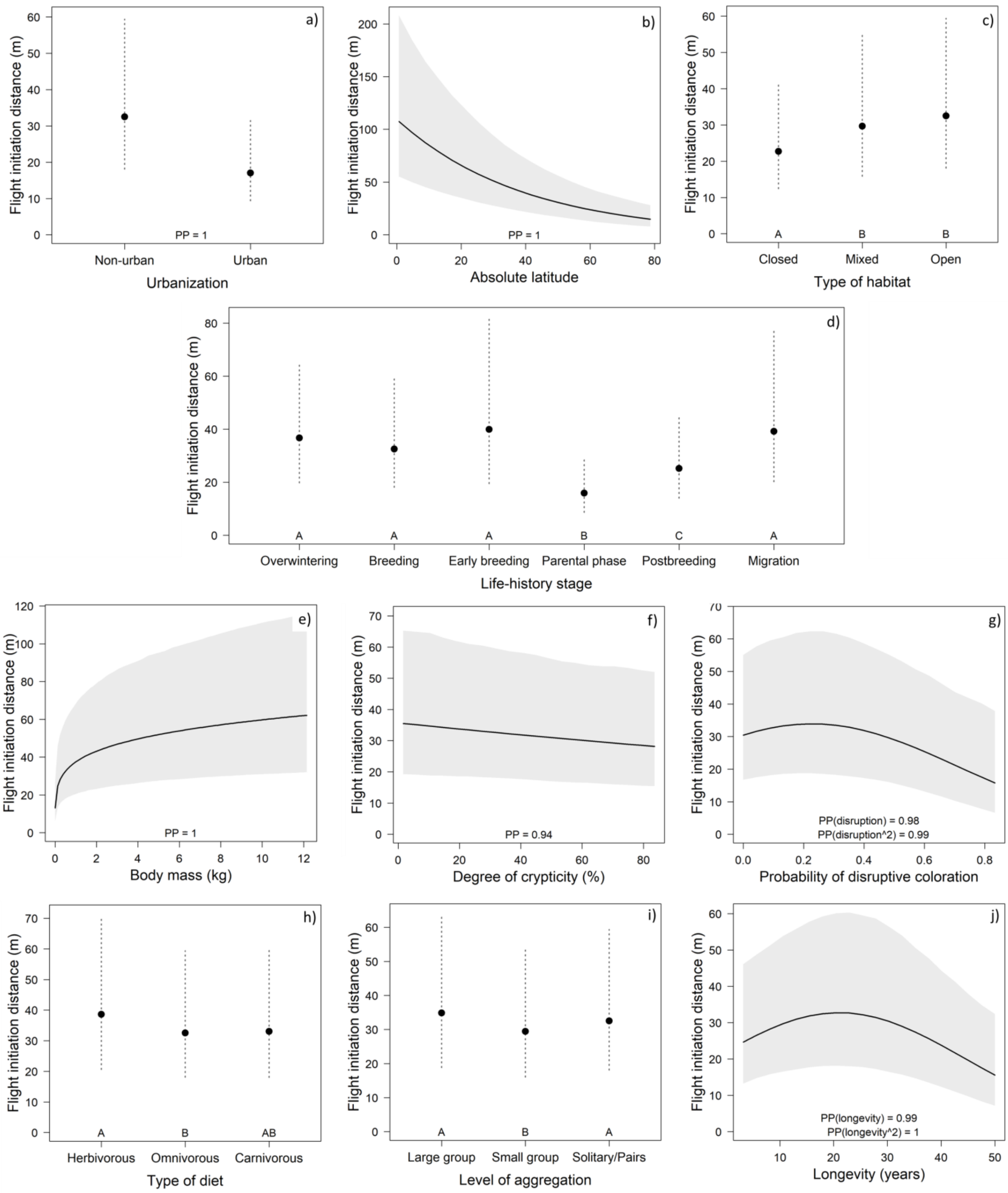


Figure 2. Graphical presentation of effect sizes for factors related to CORT levels, derived from the model presented in Appendix Table A.2. For factors with only two categories, estimated CORT levels (± 95% credible intervals) are plotted across the whole sampling-time range (a), whereas for factors with more than two categories, for simplicity, we only show levels at baseline (1 min; black squares) and at 30 min after capture (black triangles), with their credible intervals (dashed lines). The increase in CORT from 1 to 30 min is indicated with the solid grey line (c, d, h and i; see complete plots in Figure A.2). Similarly, for continuous variables with a linear or logarithmic effect we plotted CORT levels across the whole sampling-time range by selecting the highest and lowest values of the dataset (b, e, f), whereas in the continuous variables with quadratic effect we selected three values (lowest, highest, and intermediate, i.e. middle point of the range) and represented them in the same way as factors with several categories (g, j). Posterior probabilities (PP; ranging from 0.5 to 1) represent the likelihood of a given difference. That is, PPb, PP30 and PPi denote the probability of having differences between two categories or levels in baseline CORT, in stress-induced CORT at 30 min, or in the increment from baseline to stress-induced CORT, respectively. Letters indicate whether categories (or levels of continuous variables) differ from each other with a PPb (lower), PP30 (higher), or PPi (middle position; grey) higher than 0.9. We used this cut-off value as a reference for representation, but complete PPs for the pairwise comparisons are shown in Table A.4. Note the differences in the y-axes.

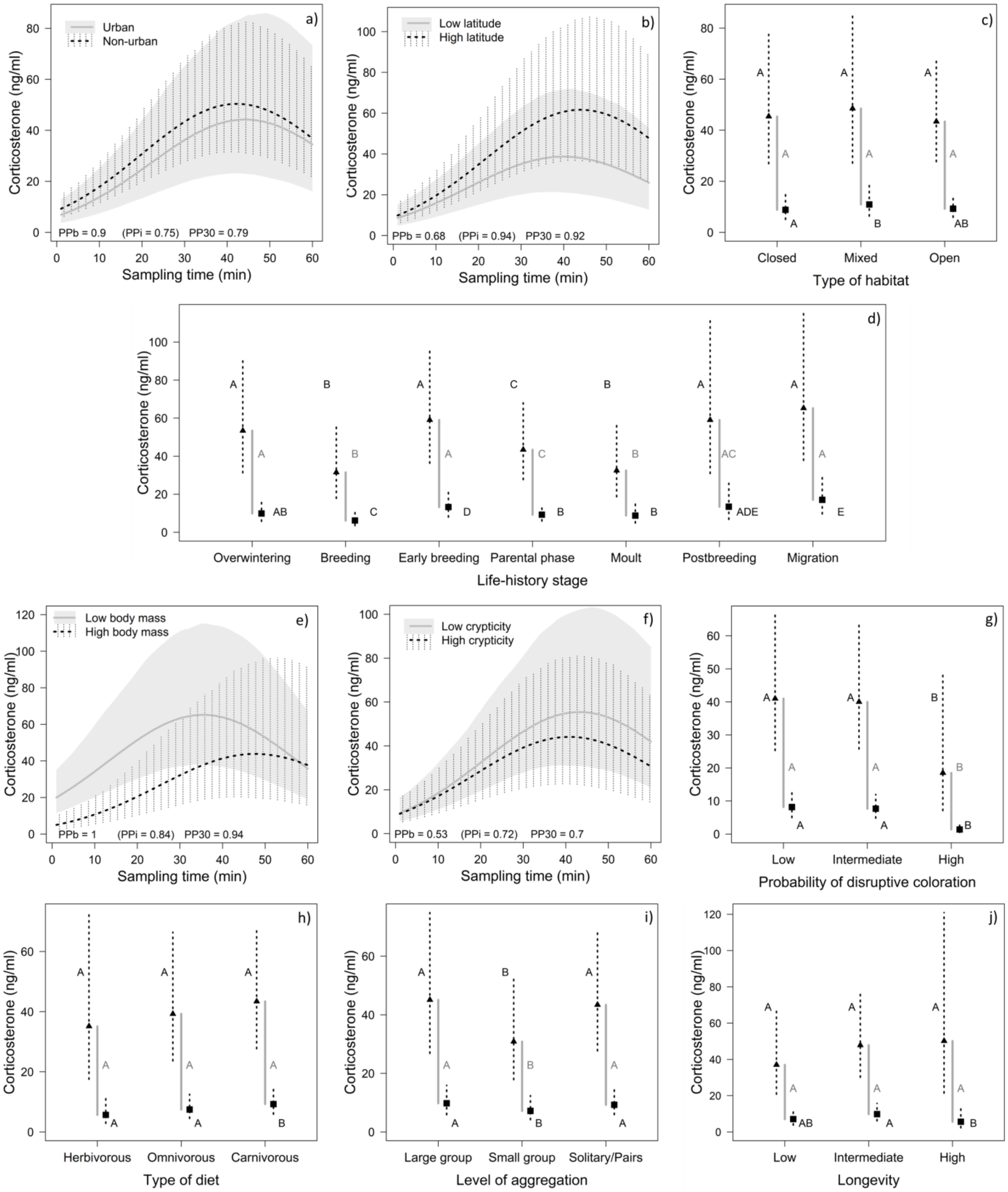
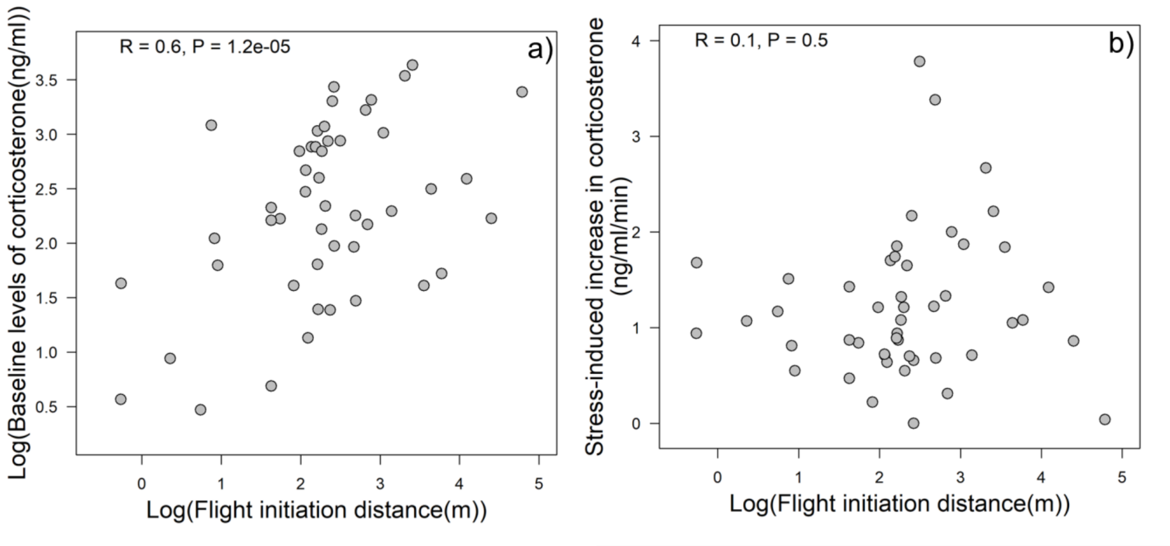

a)
Urban
Non-urban
Corticosterone (ng/ml)
Sampling time (min)
PPb = 0.9 (PPi = 0.75) PP30 = 0.79
b)
Low latitude
High latitude
Corticosterone (ng/ml)
Sampling time (min)
PPb = 0.68 (PPi = 0.94) PP30 = 0.92
c)
Corticosterone (ng/ml)
Closed
Mixed
Open
Type of habitat
d)
Corticosterone (ng/ml)
Overwintering
Breeding
Early breeding
Parental phase
Moult
Postbreeding
Migration
Life-history stage
e)
Low body mass
High body mass
Corticosterone (ng/ml)
Sampling time (min)
PPb = 1 (PPi = 0.84) PP30 = 0.94
f)
Low crypticity
High crypticity
Corticosterone (ng/ml)
Sampling time (min)
PPb = 0.53 (PPi = 0.72) PP30 = 0.7
g)
Corticosterone (ng/ml)
Low
Intermediate
High
Probability of disruptive coloration
h)
Corticosterone (ng/ml)
Herbivorous
Omnivorous
Carnivorous
Type of diet
i)
Corticosterone (ng/ml)
Large group
Small group
Solitary/Pairs
Level of aggregation
j)
Corticosterone (ng/ml)
Low
Intermediate
High
Longevity

Figure 3. Phylogenetic correlations between FID and baseline corticosterone level (a) or corticosterone reactivity (b) across species. The stress-induced increase in corticosterone corresponds to the slope of the increase from baseline CORT levels to peak stress-induced CORT levels.



Appendix A: List of sources for the FID and CORT data used in the analyses. Indicated are the species for which data were available, the type of data (Flight initiation distance; FID corticosterone reactivity; CORT), and the study area.

REFERENCE	SPECIES	DATA TYPE	STUDY AREA
(Ackerman *et al.* 2004)	*Anser albifrons*	FID	California, USA
(Adams *et al.* 2005)	*Pterodroma macroptera*	CORT	New Zealand
(Addison *et al.* 2008)	*Cerorhinca monocerata*	CORT	British Columbia, Canada
(Albrecht & Klvana 2004)	*Anas platyrhynchos*	FID	Trebon Biosphere Reservoir, Czech Republic
(Alvarez *et al.* 1984)	*Alectoris rufa, Ardea cinerea, Bubulcus ibis, Calidris alba, Caprimulgus ruficollis, Egretta garzetta, Himantopus himantopus, Larus argentatus, Pica pica, Upupa epops, Vanellus vanellus*	FID	Donana Biological Park, Spain
Amundsen, T. personal communication	*Pagodroma nivea*	FID	Dronning Maud Land, Antarctica
(Angelier *et al.* 2007)	*Rissa tridactyla*	CORT	Kongsfjorden, Svalbard
(Angelier *et al.* 2007)	*Pagodroma nivea*	CORT	Pointe Géologie archipelago, Antarctica
(Angelier *et al.* 2009)	*Pagodroma nivea*	CORT	Pointe Géologie archipelago, Antarctica
(Angelier *et al.* 2013)	*Daption capense*	CORT	Pointe Géologie archipelago, Antarctica
Angelier, F. personal communication	*Aptenodytes patagonicu, Thalassarche melanophrys*	FID	Kerguelen Islands
Angelier, F. personal communication	*Daption capense, Pagodroma nivea, Pygoscelis adeliae*	FID	Pointe Géologie archipelago, Antarctica
Angelier, F. personal communication	*Diomedea exulans*	FID	Possession Island
Angelier, F. personal communication	*Rissa tridactyla*	FID	Svalbard
(Astheimer *et al.* 1994)	*Zonotrichia leucophrys*	CORT	Toolik Lake Arctic Research Station, Alaska; Yakima County, Washington, USA
(Astheimer *et al.* 1995)	*Calcarius lapponicus*	CORT	Toolik Lake Arctic Research Station, Alaska
(Astheimer *et al.* 2000)	*Spizella arborea*	CORT	Toolik Lake Arctic Research Station, Alaska
(Atwell *et al.* 2012)	*Junco hyemalis*	FID	California, USA
(Baines & Richardson 2007)	*Tetrao tetrix*	FID	North Pennines, UK
(Barron *et al.* 2012)	*Cardinalis cardinalis*	FID	Fort Hood, Texas, USA
(Baudains & Lloyd 2007)	*Charadrius marginatus*	FID	South Africa
(Baugh *et al.* 2013)	*Parus major*	CORT	Arnhem, The Netherlands
(Beale & Monaghan 2004)	*Arenaria interpres*	FID	East Lothian coast of Scotland
(Bears *et al.* 2003)	*Junco hyemalis*	CORT	Jasper national park, Alberta, Canada
(Bety & Gauthier 2001)	*Chen caerulescens*	FID	Bylot Island, Canada
(Blakney 2004)	*Thinornis rubricollis*	FID	Australia
(Blumstein *et al.* 2003)	*Haematopus longirostris, Larus novaehollandiae, Limosa lapponica, Pelecanus conspicillatus, Threskiornis molucca, Vanellus miles*	FID	New South Wales, Australia

(de Boer & Longamane 1996)	*Calidris ferruginea, Numenius phaeopus, Numenius phaeopus, Pluvialis squatarola, Tringa nebularia*	FID	Mozambique
(Bötsch *et al.* 2018)	*Aegithalos caudatus, Certhia brachydactyla, Coccothraustes coccothraustes, Cyanistes caeruleus, Dendrocopos major, Erithacus rubecula, Fringilla coelebs, Parus major, Parus palustris, Phylloscopus collybita, Sitta europaea, Troglodytes troglodytes, Turdus merula, Turdus philomelos*	FID	Foret de Chaux, France
Bötsch, Y. unpublished data	*Cyanistes caeruleus, Parus major*	CORT	Foret de Chaux, France
(Boughton *et al.* 2006)	*Aphelocoma coerulescens*	CORT	Archbold Biological Station, Florida, USA
(Bregnballe *et al.* 2009)	*Anas crecca, Anas penelope, Anas platyrhynchos, Anser anser, Ardea cinerea, Fulica atra, Phalacrocorax carbo, Tringa nebularia, Vanellus vanellus*	FID	Denmark
(Breuner *et al.* 2006)	*Sterna hirundo*	CORT	Bird Island, Massachusetts, USA
(Breuner & Orchinik 2001)	*Passer domesticus*	CORT	Arizona, USA
(Brooks 1960)	*Agelaius phoeniceus, Carduelis tristis, Dendroica petechia, Empidonax traillii, Geothlypis trichas, Melospiza georgiana, Melospiza melodia*	FID	Wisconsin, USA
(Burger & Gochfeld 1991)	*Anthornis melanura, Carduelis flammea, Emberiza citrinella, Fringilla coelebs, Petroica australis, Prunella modularis, Rhipidura fuliginosa, Turdus merula, Turdus philomelos, Zosterops lateralis*	FID	Kaikoura, New Zealand
(Burger & Gochfeld 1983)	*Larus argentatus, Larus marinus*	FID	New Hampshire, USA
(Burger & Gochfeld 1991)	*Acridotheres tristis, Corvus corone, Corvus splendens, Passer domesticus, Streptopelia decaocto*	FID	Northern India
(Burhans & Thompson 2001)	*Cardinalis cardinalis, Icteria virens, Passerina cyanea, Spizella pusilla*	FID	Missouri, USA
(Cárdenas *et al.* 2005)	*Cacatua roseicapilla*	FID	Jervis Bay, Australia
(Chastel *et al.* 2005)	*Rissa tridactyla*	CORT	Kongsfjorden, Svalbard
(Clucas & Marzluff 2012)	*Corvus brachyrhynchos, Corvus cornix, Passer domesticus, Sturnus vulgaris, Turdus migratorius*	FID	Seattle, USA; Berlin, Germany
(Cockrem *et al.* 2006)	*Pygoscelis adeliae*	CORT	Ross Island, Antarctica
(Cockrem *et al.* 2008)	*Pygoscelis adeliae*	CORT	Ross Island, Antarctica
(Cockrem *et al.* 2009)	*Pygoscelis adeliae*	CORT	Ross Island, Antarctica
(Cooke 1980)	*Alauda arvensis, Carduelis carduelis, Carduelis chloris, Corvus frugilegus, Corvus monedula, Cyanistes caeruleus, Emberiza citrinella, Erithacus rubecula, Fringilla coelebs, Fringilla coelebs, Motacilla alba, Parus major, Passer domesticus, Prunella modularis, Sturnus vulgaris, Sylvia communis, Turdus merula, Turdus philomelos*	FID	UK
(Cornelius *et al.* 2012)	*Loxia curvirostra*	CORT	Coastal Washington; Grand Teton National Park, Wyoming
(Diaz *et al.* 2013)	*Acrocephalus palustris, Acrocephalus schoenobaenus, Acrocephalus scirpaceus, Aegithalos caudatus, Alauda arvensis, Alectoris rufa, Anas crecca, Anas platyrhynchos, Anser anser, Anthus*	FID	Brønderslev, Denmark; Budapest, Hungary; Granada, Spain; Olomouc, Czech Republic; Oslo, Norway; Paris, France; Poznan, Poland;

	pratensis, Anthus spinoletta, Anthus trivialis, Ardea cinerea, Athene noctua, Aythya fuligula, Branta leucopsis, Bucephala clangula, Buteo buteo, Carduelis cannabina, Carduelis carduelis, Carduelis chloris, Carduelis spinus, Certhia brachydactyla, Certhia familiaris, Charadrius hiaticula, Coccothraustes coccothraustes, Columba livia, Columba oenas, Columba palumbus, Corvus corax, Corvus cornix, Corvus frugilegus, Corvus monedula, Cuculus canorus, Cyanistes caeruleus, Cyanopica cyana, Delichon urbica, Dendrocopos major, Emberiza calandra, Emberiza citrinella, Emberiza schoeniclus, Erithacus rubecula, Falco tinnunculus, Ficedula hypoleuca, Fringilla coelebs, Fulica atra, Galerida cristata, Gallinago gallinago, Garrulus glandarius, Haematopus ostralegus, Hippolais icterina, Hippolais polyglotta, Hirundo rustica, Lagopus mutus, Lanius collurio, Lanius senator, Larus argentatus, Larus canus, Larus fuscus, Larus marinus, Larus ridibundus, Lullula arborea, Luscinia luscinia, Luscinia megarhynchos, Luscinia svecica, Merops apiaster, Motacilla alba, Motacilla cinerea, Motacilla flava, Muscicapa striata, Nucifraga caryocatactes, Numenius arquata, Oenanthe oenanthe, Oriolus oriolus, Parus cristatus, Parus major, Parus montanus, Parus palustris, Passer domesticus, Passer montanus, Perdix perdix, Periparus ater, Phalacrocorax carbo, Phasianus colchicus, Phoenicurus ochruros, Phoenicurus phoenicurus, Phylloscopus collybita, Phylloscopus trochilus, Pica pica, Picoides syriacus, Prunella modularis, Pyrrhula pyrrhula, Regulus ignicapillus, Regulus regulus, Riparia riparia, Saxicola rubetra, Saxicola torquata, Serinus serinus, Sitta europaea, Streptopelia decaocto, Streptopelia turtur, Sturnus unicolor, Sturnus vulgaris, Sylvia atricapilla, Sylvia borin, Sylvia communis, Sylvia curruca, Sylvia melanocephala, Tadorna tadorna, Tringa nebularia, Tringa totanus, Troglodytes troglodytes, Turdus iliacus, Turdus merula, Turdus philomelos, Turdus pilaris, Turdus viscivorus, Upupa epops, Vanellus vanellus		Rovaniemi, Finland; Toledo, Spain
(Douglas *et al*. 2009)	*Aethia cristatella*	CORT	Big Koniuji Island, Alaska
(Dwyer 2010)	*Anas penelope, Anas platyrhynchos, Haematopus ostralegus, Numenius arquata, Tadorna tadorna, Tringa totanus*	FID	Forth estuary, Scotland
(Eason *et al*. 2006)	*Turdus migratorius*	FID	Kentucky, USA
(Ellenberg *et al*. 2007)	*Megadyptes antipodes*	FID, CORT	Otago, South Island, New Zealand
(Erwin 1989)	*Rynchops niger, Sterna hirundo, Sterna maxima*	FID	Virginia and North Carolina, USA
(Falsone *et al*. 2009)	*Anthus trivialis, Cyanistes caeruleus, Erithacus rubecula, Ficedula hypoleuca,*	CORT	Col de bretolet, between Switzerland and France

	Fringilla coelebs, Motacilla flava, Parus major, Periparus ater, Turdus philomelos		
(Fernandez-Juricic *et al.* 2001)	*Columba palumbus, Passer domesticus, Pica pica, Turdus merula*	FID	Madrid, Spain
(Fernandez-Juricic *et al.* 2004)	*Molothrus badius*	FID	La Quebrada Reserve; Argentina
(Fernandez-Juricic *et al.* 2009)	*Passerculus sandwichensis*	FID	California, USA
(Ferrari *et al.* 2012)	*Calidris fuscicollis, Limosa haemastica, Numenius phaeopus*	FID	Santa Cruz, Argentina
(Forbes *et al.* 1994)	*Anas americana, Anas clypeata, Anas discors, Anas platyrhynchos, Anas strepera, Aythya affinis*	FID	Saskatchewan, Canada
(Fowler 1999)	*Spheniscus magellanicus*	FID	Chubut, Argentina
(Fraser *et al.* 1985)	*Haliaeetus leucocephalus*	FID	Minnesota, USA
(Galeotti *et al.* 2000)	*Asio otus*	FID	Northern Italy
(Geist *et al.* 2005)	*Platycercus elegans, Strepera graculina*	FID	Booderee National Park, Australia
(Glover *et al.* 2011)	*Vanellus miles*	FID	South-eastern Australia
(Goutte *et al.* 2010)	*Pagodroma nivea*	CORT	Pointe Géologie archipelago, Antarctica
(Guay *et al.* 2013)	*Cygnus atratus*	FID	Melbourne, Australia
(Gulbransen *et al.* 2006)	*Chenonetta jubata, Cracticus tibicen*	FID	New South Wales, Australia
(Gutzwiller & Marcum 1997)	*Cardinalis cardinalis, Dendroica coronata, Melanerpes carolinus, Mimus polyglottos, Parus carolinensis, Regulus calendula, Turdus migratorius*	FID	Texas, USA
(Gutzwiller *et al.* 1998)	*Dendroica coronata, Parus gambeli, Perisoreus canadensis, Turdus migratorius*	FID	Wyoming, USA
(Heidinger *et al.* 2010)	*Sterna hirundo*	CORT	Bird Island, Massachusetts, USA
(Holberton & Able 2000)	*Junco hyemalis*	CORT	Yalobusha County, Mississippi and Albany County, New York, USA
(Holberton & Wingfield 2003)	*Passerculus sandwichensis, Spizella arborea, Zonotrichia leucophrys*	CORT	Toolik Lake Arctic Research Station, Alaska
(Holberton *et al.* 1996a)	*Aptenodytes patagonicus, Pygoscelis papua*	CORT	South Georgia Islands
(Holberton *et al.* 1996b)	*Dendroica coronata, Dumetella carolinensis*	CORT	Block Island, Rhode Island, USA
(Holmes 2007)	*Aptenodytes patagonicus, Pygoscelis papua*	FID	Macquarie Island, Australia
(Holmes *et al.* 1993)	*Aquila chrysaetos, Buteo lagopus, Buteo regalis, Falco columbarius, Falco mexicanus, Falco sparverius*	FID	Colorado, USA
(Hood *et al.* 1998)	*Spheniscus magellanicus*	CORT	Chubut, Argentina
(Hope *et al.* 2014)	*Calidris mauri*	FID	British Columbia, Canada
(Horton & Holberton 2010)	*Zonotrichia albicollis*	CORT	Penobscot Experimental Forest, Maine
(Humphrey *et al.* 1987)	*Cathartes aura, Gallinago gallinago, Haematopus ostralegus, Larus dominicanus, Larus dominicanus, Nycticorax nycticorax, Stercorarius antarcticus, Troglodytes aedon*	FID	Falkland Islands; Chubut, Argentina
(Ikuta & Blumstein 2003)	*Ardea alba, Ardea herodias, Calidris mauri, Calidris minutilla, Egretta thula, Larus delawarensis, Pluvialis squatarola, Tringa semipalmata*	FID	California, USA
(Jungius & Hirsch 1979)	*Phoebastria irrorata*	FID	Galapagos Islands

(Kight & Swaddle 2007)	*Sialia sialis*	FID	Virginia, USA
(Kitaysky *et al.* 1999)	*Rissa tridactyla*	CORT	Cook Inlet, Alaska
(Kitchen *et al.* 2011)	*Grallina cyanoleuca*	FID	Melbourne, Australia
(Koch & Paton 2014)	*Arenaria interpres, Calidris alba, Calidris alpina, Calidris canutus, Calidris minutilla, Calidris pusilla, Charadrius semipalmatus, Haematopus palliatus, Limnodromus griseus, Pluvialis squatarola, Tringa semipalmata*	FID	Massachusetts, USA
(Kosztolanyi *et al.* 2012)	*Charadrius alexandrinus*	CORT	Lake Tuzla, Turkey
(Landys-Ciannelli *et al.* 2002)	*Limosa lapponica*	CORT	Wadden Sea, Netherlands
(Lattin *et al.* 2012)	*Passer domesticus*	CORT	Medford and Somerville, Massachussets, USA
(Laursen *et al.* 2005)	*Anas acuta, Anas crecca, Anas penelope, Anas platyrhynchos, Branta bernicla, Calidris alpina, Charadrius hiaticula, Haematopus ostralegus, Larus canus, Larus ridibundus, Limosa lapponica, Numenius arquata, Pluvialis apricaria, Pluvialis squatarola, Recurvirostra avosetta, Tadorna tadorna, Tringa nebularia, Tringa totanus, Vanellus vanellus*	FID	Danish Wadden Sea, Denmark
(Leclaire *et al.* 2011)	*Rissa tridactyla*	CORT	Middleton Island, Gulf of Alaska
(Le Corre 2009)	*Anas crecca, Anas platyrhynchos, Branta bernicla, Calidris alpina, Egretta garzetta, Fulica atra, Haematopus ostralegus, Larus fuscus, Larus ridibundus, Limosa lapponica, Numenius arquata, Pluvialis squatarola, Recurvirostra avosetta, Tadorna tadorna, Tringa totanus*	FID	Bretagne, France
(Lendvai & Chastel 2008)	*Passer domesticus*	CORT	Centre d’Etudes Biologiques de Chize, France
(Lendvai *et al.* 2007)	*Passer domesticus*	CORT	Centre d’Etudes Biologiques de Chize, France
(Le Pape 2012)	*Rupicola rupicola*	FID	French Guiana
(Levey *et al.* 2009)	*Mimus polyglottos*	FID	Florida, USA
(Li *et al.* 2008)	*Passer domesticus, Passer montanus*	CORT	Phoenix, Arizona; Tibetan plateau
(Li *et al.* 2011)	*Passer montanus*	CORT	Qianjin village; Nanshijiazhuang village; Luancheng county
(Lin *et al.* 2012)	*Actitis hypoleucos, Anas crecca, Ardea alba, Ardea cinerea, Arenaria interpres, Calidris alpina, Calidris ferruginea, Calidris ruficollis, Calidris temminckii, Charadrius leschenaultii, Charadrius mongolus, Chlidonias hybrida, Larus ridibundus, Numenius arquata, Numenius phaeopus, Pluvialis fulva, Pluvialis squatarola, Recurvirostra avosetta, Sterna albifrons, Tringa nebularia, Tringa ochropus, Tringa stagnatilis, Tringa totanus, Xenus cinerea*	FID	Xiamen City, China
(Lindstrom *et al.* 2005)	*Carpodacus mexicanus*	CORT	Atlanta, Georgia; Ithaca, New York; Princeton, New Jersey, USA
(Long & Holberton 2004)	*Catharus guttatus*	CORT	Manomet, Massachusetts; Steuben, Maine, USA

(Lord *et al.* 2001)	*Charadrius obscurus*	FID	North Island, New Zealand
(Lormée 2001)	*Phaethon rubricauda*	CORT	Europa Island, Mozambique Channel, Western Indian Ocean
(Lunardi & Macedo 2013)	*Calidris pusilla*	FID	Bahia state, Brazil
(Lynn & Porter 2008)	*Passer domesticus*	CORT	Wooster, Ohio, USA
(Lynn *et al.* 2003)	*Calcarius ornatus*	CORT	Benton Lake National Wildlife Refuge, Montana, USA
(Mallory *et al.* 1998)	*Bucephala clangula, Lophodytes cucullatus*	FID	Ontario, Canada
(Malueg *et al.* 2009)	*Picoides borealis*	CORT	Marine Corps Base Camp Lejeune, North Carolina, USA
(Marra & Holberton 1998)	*Setophaga ruticilla*	CORT	Font Hill Nature Preserve, Jamaica
(Martin II *et al.* 2005)	*Passer domesticus*	CORT	Princeton, New Jersey, USA; Zona Libre, Colon, Panama
(Meddle *et al.* 2003)	*Calcarius pictus*	CORT	Toolik Lake, Alaska
(Miller *et al.* 2001)	*Pooecetes gramineus, Sturnella neglecta, Turdus migratorius*	FID	Colorado, USA
(Mizrahi *et al.* 2001)	*Calidris pusilla*	CORT	Thompsons Beach and Dennis Creek Marsh, Delaware Bay, USA
(Monie 2011)	*Cygnus atratus*	FID	Melbourne, Australia
(Møller & Tryjanowski 2014)	*Acrocephalus palustris, Alauda arvensis, Anas platyrhynchos, Ardea cinerea, Carduelis cannabina, Carduelis carduelis, Carduelis chloris, Certhia brachydactyla, Columba livia, Columba palumbus, Corvus cornix, Corvus corone, Corvus frugilegus, Corvus monedula, Cyanistes caeruleus, Delichon urbica, Dendrocopos major, Emberiza calandra, Emberiza citrinella, Erithacus rubecula, Fringilla coelebs, Galerida cristata, Gallinula chloropus, Garrulus glandarius, Hirundo rustica, Lanius collurio, Motacilla alba, Motacilla cinerea, Motacilla flava, Muscicapa striata, Parus major, Passer domesticus, Passer montanus, Phoenicurus ochruros, Phoenicurus phoenicurus, Phylloscopus collybita, Phylloscopus trochilus, Pica pica, Picus viridis, Prunella modularis, Serinus serinus, Sitta europaea, Streptopelia decaocto, Sturnus vulgaris, Sylvia atricapilla, Sylvia borin, Sylvia communis, Sylvia curruca, Troglodytes troglodytes, Turdus merula, Turdus philomelos, Turdus pilaris, Vanellus vanellus*	FID	Paris, France; Poznan, Poland
(O'Reilly & Wingfield 2001)	*Calidris melanotos, Calidris pusilla, Calidris pusilla, Calidris pusilla, Phalaropus fulicarius*	CORT	Barrow, Seward Peninsula, and Prudhoe Bay, Alaska
(O'Reilly & Wingfield 2003)	*Calidris mauri*	CORT	Nome, Alaska
(Paton *et al.* 2000)	*Recurvirostra novaehollandiae, Tringa nebularia*	FID	South Australia, Australia
(Payne *et al.* 2012)	*Cygnus atratus*	CORT	Albert Park Lake, Melbourne, Australia
(Pereyra & Wingfield 2003)	*Empidonax oberholseri*	CORT	Tioga Pass, California, USA

(Perfito *et al.* 2002)	*Histrionicus histrionicus*	CORT	Olympic Peninsula, Washington; Puget Sound, Protection Island, and Whidbey Island
(Perfito *et al.* 2007)	*Taeniopygia guttata*	CORT	Numurkah, Melbourne, Australia
(Pfeiffer 2005)	*Macronectes giganteus, Stercorarius antarcticus, Stercorarius maccormicki*	FID	King George Island, Antarctic
(Price 2003)	*Cracticus tibicen, Grallina cyanoleuca, Rhipidura leucophrys, Turdus merula*	FID	Victoria, Australia
(Quirici *et al.* 2014)	*Aphrastura spinicauda*	CORT	Fray Jorge National Park, Manquehue Hill, Williams Port in Navarino Island, Chile
(Remage-Healey & Romero 2001)	*Sturnus vulgaris*	CORT	Eastern Massachusetts, USA
(Reneerkens *et al.* 2002)	*Calidris canutus*	CORT	Ellesmere Island, Canada
(Riou *et al.* 2010)	*Puffinus puffinus*	CORT	Skomer Island, Wales
(Robinson 2008)	*Charadrius nivosus*	FID	California, USA
(Roby *et al.* 1981)	*Alle alle*	FID	Greenland
(Rodgers, Jr. & Smith 1995)	*Ardea alba, Ardea herodias, Egretta tricolor, Eudocimus albus, Mycteria americana, Nycticorax nycticorax, Pelecanus occidentalis, Phalacrocorax auritus, Rynchops niger, Sterna antillarum*	FID	Florida, USA
(Rodgers, Jr. & Smith 1997)	*Ardea alba, Ardea herodias, Calidris alba, Egretta caerulea, Egretta thula, Egretta tricolor, Larus delawarensis, Pelecanus occidentalis, Phalacrocorax auritus, Rynchops niger, Tringa semipalmata*	FID	Florida, USA
(Rodriguez-Prieto *et al.* 2009)	*Turdus merula*	FID	Madrid, Spain
(Rogers *et al.* 2010)	*Accipiter cooperii, Accipiter gentilis, Accipiter striatus*	CORT	Idaho Bird Observatory, USA
(Romero & Romero 2002)	*Calcarius lapponicus, Passer domesticus, Zonotrichia leucophrys*	CORT	Toolik Lake, Alaska; Albuquerque, New Mexico, USA
(Romero & Wingfield 2001)	*Columba livia*	CORT	University of Washington, USA
(Romero *et al.* 1997)	*Zonotrichia leucophrys*	CORT	Albuquerque, New Mexico; Phoenix, Arizona; Ellensburg, Washington; Fairbanks, Alaska; Sunnyside, Washington, USA
(Romero *et al.* 1998a)	*Plectrophenax nivalis*	CORT	Arctic Research Facility, Barrow, Alaska
(Romero *et al.* 1998b)	*Calcarius lappousnicus*	CORT	Near Toolik Lake and near Barrow, Alaska
(Romero *et al.* 1998c)	*Carduelis flammea*	CORT	Near Toolik Lake and near Barrow, Alaska
(Romero *et al.* 2009)	*Asio otus*	CORT	Western Montana, USA
(Michael Romero *et al.* 2006)	*Passer domesticus*	CORT	Albuquerque, New Mexico; Medford, Massachusetts
(Rouco *et al.* 2007)	*Actitis hypoleucos, Anas crecca, Anas platyrhynchos, Ardea cinerea, Calidris alpina, Calidris ferruginea, Charadrius dubius, Charadrius hiaticula, Egretta garzetta, Larus ridibundus, Podiceps cristatus, Vanellus vanellus*	FID	Salamanca, Spain

(Ruddock & Whitfield 2007)	*Accipiter gentilis, Accipiter gentilis, Aquila chrysaetos, Aquila chrysaetos, Asio flammeus, Asio flammeus, Asio otus, Asio otus, Bucephala clangula, Bucephala clangula, Caprimulgus europaeus, Caprimulgus europaeus, Circus aeruginosus, Circus aeruginosus, Circus cyaneus, Circus cyaneus, Falco columbarius, Falco columbarius, Falco peregrinus, Falco peregrinus, Gavia arctica, Gavia arctica, Gavia stellata, Gavia stellata, Haliaeetus albicilla, Haliaeetus albicilla, Loxia curvirostra, Loxia curvirostra, Melanitta nigra, Melanitta nigra, Milvus milvus, Milvus milvus, Pandion haliaeetus, Pandion haliaeetus, Parus cristatus, Parus cristatus, Podiceps auritus, Podiceps auritus, Tetrao tetrix, Tetrao urogallus, Tringa glareola, Tringa glareola, Turdus iliacus, Turdus iliacus, Turdus pilaris, Turdus pilaris, Tyto alba, Tyto alba*	FID	Scotland
(Rutherford 2012)	*Mimus polyglottos*	FID	South Carolina, USA
(Schmid *et al.* 2013)	*Upupa epops*	CORT	Rhone valley, Valais, Switzerland
(Schoech *et al.* 1997)	*Aphelocoma coerulescens*	CORT	Archbold Biological Station, Florida, USA
(Schoech *et al.* 1999)	*Junco hyemalis*	CORT	Mountain Lake Biological Station, Virginia, USA
(Schoech *et al.* 2007)	*Aphelocoma coerulescens*	CORT	Placid Lakes Estates and Archbold Biological Station, Florida, USA
(Schwabl *et al.* 1991)	*Sylvia borin*	CORT	Algerian sahara
(Seltmann *et al.* 2012)	*Somateria mollissima*	FID	Southern Finland
(Silverin 1997)	*Parus montanus*	CORT	30 km east of Göteborg, Sweden
(Silverin & Wingfield 1998)	*Ficedula hypoleuca*	CORT	Forest near Göteborg and Ammarnas, Sweden
(Silverin *et al.* 1997)	*Phylloscopus trochilus*	CORT	Forest near Göteborg and Ammarnas, Sweden
(Sims & Holberton 2000)	*Mimus polyglottos*	CORT	University of Mississippi campus, USA
(Skagen *et al.* 1991)	*Corvus brachyrhynchos, Haliaeetus leucocephalus, Larus glaucescens*	FID	Washington, USA
(Smith *et al.* 1994)	*Pelecanoides urinatrix*	CORT	South Georgia Islands
(Smith *et al.* 2007)	*Phalaropus fulicarius*	FID	Nunavut, Canada
(Stalmaster & Kaiser 1998)	*Haliaeetus leucocephalus*	FID	Washington, USA
Summers, R. personal communication	*Podiceps auritus*	FID	Scotland
(Tartu *et al.* 2015b)	*Pagodroma nivea*	CORT	Adélie land, Antarctica.
(Tartu *et al.* 2015a)	*Rissa tridactyla*	CORT	Storholmen, Kongsfjorden, Svalbard, Norway
Tensen & van Zoest 1983 in (Smit & Visser 1993)	*Haematopus ostralegus, Larus argentatus, Larus ridibundus, Limosa lapponica, Numenius arquata, Pluvialis apricaria, Tringa totanus*	FID	Dutch Wadden Islands, Nederlands
(Thiel *et al.* 2007)	*Tetrao urogallus*	FID	Black Forest, Germany; French Pyrenees
(Thomas *et al.* 2003)	*Calidris alba*	FID	California, USA

(Touchton 2011)	*Gymnopithys leucaspis, Hylophylax naevioides*	CORT	Barro Colorado Island and Soberania National Park, Panama
(Triplet *et al.* 1998)	*Calidris alpina, Haematopus ostralegus, Larus argentatus, Larus canus, Larus ridibundus, Numenius phaeopus, Tadorna tadorna, Tringa totanus*	FID	Réserve Naturelle de la Baie de Somme, France
(Triplet *et al.* 2007)	*Anas acuta, Anas penelope, Anas platyrhynchos, Calidris alpina, Charadrius hiaticula, Egretta garzetta, Haematopus ostralegus, Larus argentatus, Larus ridibundus, Numenius arquata, Phalacrocorax carbo, Pluvialis squatarola, Tadorna tadorna, Tringa totanus*	FID	Réserve Naturelle de la Baie de Somme, France
(Trulio *et al.* 2011)	*Charadrius nivosus*	FID	California, USA
(Tsipoura *et al.* 1999)	*Calidris pusilla*	CORT	Manomet, Massachusetts; Moore's Beach, Fortescue, and Delaware Bay, New Jersey, USA
Tveraa, T. personal communication	*Pagodroma nivea*	FID	Dronning Maud Land, Antarctica
(Valcarcel & Fernández-Juricic 2009)	*Carpodacus mexicanus*	FID	California, USA
(Vázquez *et al.* 2011)	*Anas sibilatrix, Cygnus melancoryphus, Cygnus melancoryphus, Phoenicopterus chilensis*	FID	Patagonia, Argentina
(Verboven *et al.* 2010)	*Larus hyperboreus*	CORT	Bjørnøya, Svalbard
(Villanueva *et al.* 2012)	*Spheniscus magellanicus*	CORT	Estancia San Lorenzo, Peninsula Valdes, Argentina
(de Villiers *et al.* 2006)	*Macronectes halli*	FID	Marion Island
(Vos *et al.* 1985)	*Ardea herodias*	FID	Colorado, USA
(Walker *et al.* 2015)	*Calcarius lapponicus, Plectrophenax nivalis*	CORT	Thule Air Force Base, Thule, Greenland
(Wang *et al.* 2004)	*Motacilla alba, Paradoxornis webbianus, Parus major, Passer montanus, Streptopelia chinensis, Turdus merula*	FID	Hangzhou, China
(Washburn *et al.* 2002)	*Carduelis tristis, Passerina cyanea, Vireo olivaceus*	CORT	Near Rocheport and Current River Conservation Area, Missouri, USA
(Webb & Blumstein 2005)	*Larus occidentalis*	FID	California, USA
(Welcker *et al.* 2009)	*Alle alle*	CORT	Kongsfjorden: Svalbard
(Wheeler *et al.* 2009 & personal communication)	*Diomedea exulans*	FID	Marion Island
(Whitfield & Rae 2014)	*Tringa glareola*	FID	Kautokeino, Norway
(Wilson & Holberton 2004)	*Dendroica petechia*	CORT	Churchill River, Manitoba, Canada; Jennings Randolph Lake, Maryland and West Virginia, USA
(Wilson *et al.* 1991)	*Pygoscelis adeliae*	FID	Antarctica
(Wingfield *et al.* 1992)	*Amphispiza bilineata, Campylorhynchus brunneicapillus, Pipilo aberti, Scardafella inca, Toxostoma curvirostre*	CORT	Lower Sonoran desert, Arizona
(Wingfield *et al.* 1994a)	*Carduelis flammea*	CORT	Arctic Research Facility (Barrow), Toolik Lake and near Fairbanks, Alaska
(Wingfield *et al.* 1994b)	*Calcarius lapponicus, Plectrophenax nivalis*	CORT	Arctic Research Facility, Barrow, Alaska
(Wingfield *et al.* 1999)	*Sula nebouxii*	CORT	Isla Isabel: Pacific Ocean

(Yorio & Boersma 1992)	*Spheniscus magellanicus*	FID	Punta Tombo, Argentina

References

Ackerman, J.T., Takekawa, J.Y., Kruse, K.L., Orthmeyer, D.L., Yee, J.L., Ely, C.R., *et al.* (2004). Using radiotelemetry to monitor cardiac response of free-living Tule greater white-fronted geese (Anser albifrons elgasi) to human disturbance. *Wilson Bull.*, 116, 146–151.

Adams, N.J., Cockrem, J.F., Taylor, G.A., Candy, E.J. & Bridges, J. (2005). Corticosterone responses of grey-faced petrels (Pterodroma macroptera gouldi) are higher during incubation than during other breeding stages. *Physiol. Biochem. Zool.*, 78, 69–77.

Addison, B., Kitaysky, A. & Hipfner, J.M. (2008). Sex allocation in a monomorphic seabird with a single-egg clutch: test of the environment, mate quality, and female condition hypotheses. *Behav. Ecol. Sociobiol.*, 63, 135–141.

Albrecht, T. & Klvana, P. (2004). Nest Crypsis, Reproductive Value of a Clutch and Escape Decisions in Incubating Female Mallards Anas platyrhynchos. *Ethology*, 110, 603–613.

Alvarez, F., Braza, F. & Azcarate, T. (1984). Distancia de huida en aves. *Donana Acta Vertebr.*, 11.

Angelier, F., Moe, B., Blanc, S. & Chastel, O. (2009). What factors drive prolactin and corticosterone responses to stress in a long-lived bird species (snow petrel Pagodroma nivea)? *Physiol. Biochem. Zool.*, 82, 590–602.

Angelier, F., Moe, B., Weimerskirch, H. & Chastel, O. (2007). Age-specific reproductive success in a long-lived bird: do older parents resist stress better? *J. Anim. Ecol.*, 76, 1181–1191.

Angelier, F., Wingfield, J.C., Trouve, C., de Grissac, S. & Chastel, O. (2013). Modulation of the prolactin and the corticosterone stress responses: Do they tell the same story in a long-lived bird, the Cape petrel? *Gen. Comp. Endocrinol.*, 182, 7–15.

Astheimer, L.B., Buttemer, W.A. & Wingfield, J.C. (1994). Gender and Seasonal Differences in the Adrenocortical Response to ACTH Challenge in an Arctic Passerine, Zonotrichia leucophrys gambelii. *Gen. Comp. Endocrinol.*, 94, 33–43.

Astheimer, L.B., Buttemer, W.A. & Wingfield, J.C. (1995). Seasonal and Acute Changes in Adrenocortical Responsiveness in an Arctic-Breeding Bird. *Horm. Behav.*, 29, 442–457.

Astheimer, L.B., Buttemer, W.A. & Wingfield, J.C. (2000). Corticosterone treatment has no effect on reproductive hormones or aggressive behavior in free-living male Tree Sparrows, Spizella arborea. *Horm. Behav.*, 37, 31–39.

Atwell, J.W., Cardoso, G.C., Whittaker, D.J., Campbell-Nelson, S., Robertson, K.W. & Ketterson, E.D. (2012). Boldness behavior and stress physiology in a novel urban environment suggest rapid correlated evolutionary adaptation. *Behav. Ecol.*, 23, 960–969.

Baines, D. & Richardson, M. (2007). An experimental assessment of the potential effects of human disturbance on Black Grouse Tetrao tetrix in the North Pennines, England. *Ibis*, 149, 56–64.

Barron, D.G., Brawn, J.D., Butler, L.K., Romero, L.M. & Weatherhead, P.J. (2012). Effects of military activity on breeding birds. *J. Wildl. Manag.*, 76, 911–918.

Baudains, T.P. & Lloyd, P. (2007). Habituation and habitat changes can moderate the impacts of human disturbance on shorebird breeding performance. *Anim. Conserv.*, 10, 400–407.

Baugh, A.T., van Oers, K., Naguib, M. & Hau, M. (2013). Initial reactivity and magnitude of the acute stress response associated with personality in wild great tits (Parus major). *Gen. Comp. Endocrinol.*, 189, 96–104.

Beale, C.M. & Monaghan, P. (2004). Behavioural responses to human disturbance: a matter of choice? *Anim. Behav.*, 68, 1065–1069.

Bears, H., Smith, J.N. & Wingfield, J.C. (2003). Adrenocortical sensitivity to stress in Dark-eyed Juncos(Junco hyemalis oregonus) breeding in low and high elevation habitat. *Ecoscience*, 10, 127–133.

Bety, J. & Gauthier, G. (2001). Effects of nest visits on predator activity and predation rate in a greater snow goose colony. *J. Field Ornithol.*, 72, 573–586.

Blakney, A.H. (2004). Behavioural responses and habituation of the Hooded Plover, Thinornis rubricollis (Gmelin 1789), to disturbance stimuli. BSc(Hons) Thesis, University of Tasmania, Hobart.

Blumstein, D.T., Anthony, L.L., Harcourt, R. & Ross, G. (2003). Testing a key assumption of wildlife buffer zones: is flight initiation distance a species-specific trait? *Biol. Conserv.*, 110, 97–100.

de Boer, W.F. & Longamane, F.A. (1996). The exploitation of intertidal food resources in Inhaca Bay, Mozambique, by shorebirds and humans. *Biol. Conserv.*, 78, 295–303.

Bötsch, Y., Gugelmann, S., Tablado, Z. & Jenni, L. (2018). Effect of human recreation on bird anti-predatory response. *PeerJ*, 6:e5093; DOI 10.7717/peerj.5093.

Boughton, R.K., Atwell, J.W. & Schoech, S.J. (2006). An introduced generalist parasite, the sticktight flea (Echidnophaga gallinacea), and its pathology in the threatened Florida scrub-jay (Aphelocoma coerulescens). *J. Parasitol.*, 92, 941–948.
Bregnballe, T., Aaen, K. & Fox, A.D. (2009). Escape distances from human pedestrians by staging waterbirds in a Danish wetland. *Wildfowl*, 2, 115–130.
Breuner, C.W., Lynn, S.E., Julian, G.E., Cornelius, J.M., Heidinger, B.J., Love, O.P., *et al.* (2006). Plasma-binding globulins and acute stress response. *Horm. Metab. Res.*, 38, 260–268.
Breuner, C.W. & Orchinik, M. (2001). Seasonal Regulation of Membrane and Intracellular Corticosteroid Receptors in the House Sparrow Brain. *J. Neuroendocrinol.*, 13, 412–420.
Brooks, W.S. (1960). Songbird communities of the two marsh habitats. *Passeng. Pigeon*, 12, 111–125.
Burger, J. & Gochfeld, M. (1983). Behavioural responses to human intruders of herring gulls (Larus argentatus) and great black-backed gulls (L. marinus) with varying exposure to human disturbance. *Behav. Processes*, 8, 327–344.
Burger, J. & Gochfeld, M. (1991). Human Distance and Birds: Tolerance and Response Distances of Resident and Migrant Species in India. *Environ. Conserv.*, 18, 158–165.
Burhans, D.E. & Thompson, F.R., III. (2001). Relationship of songbird nest concealment to nest fate and flushing behavior of adults. *The Auk*, 118, 237–242.
Cárdenas, Y.L., Shen, B., Zung, L. & Blumstein, D.T. (2005). Evaluating temporal and spatial margins of safety in galahs. *Anim. Behav.*, 70, 1395–1399.
Chastel, O., Lacroix, A., Weimerskirch, H. & Gabrielsen, G.W. (2005). Modulation of prolactin but not corticosterone responses to stress in relation to parental effort in a long-lived bird. *Horm. Behav.*, 47, 459–466.
Clucas, B. & Marzluff, J.M. (2012). Attitudes and Actions Toward Birds in Urban Areas: Human Cultural Differences Influence Bird Behavior. *The Auk*, 129, 8–16.
Cockrem, J.F., Barrett, D.P., Candy, E.J. & Potter, M.A. (2009). Corticosterone responses in birds: Individual variation and repeatability in Adelie penguins (Pygoscelis adeliae) and other species, and the use of power analysis to determine sample sizes. *9th Int. Symp. Avian Endocrinol. Avian Endocrinol. 9th Int. Symp. Avian Endocrinol.*, 163, 158–168.
Cockrem, J.F., Potter, M.A., Barrett, D.P. & Candy, E.J. (2008). Corticosterone Responses to Capture and Restraint in Emperor and Adelie Penguins in Antarctica. *Zoolog. Sci.*, 25, 291–298.
Cockrem, J.F., Potter, M.A. & Candy, E.J. (2006). Corticosterone in relation to body mass in Adelie penguins (Pygoscelis adeliae) affected by unusual sea ice conditions at Ross Island, Antarctica. *Gen. Comp. Endocrinol.*, 149, 244–252.
Cooke, A.S. (1980). Observations on how close certain passerine species will tolerate an approaching human in rural and suburban areas. *Biol. Conserv.*, 18, 85–88.
Cornelius, J.M., Breuner, C.W. & Hahn, T.P. (2012). Coping with the extremes: stress physiology varies between winter and summer in breeding opportunists. *Biol. Lett.*, 8, 312–315.
Diaz, M., Møller, A.P., Flensted-Jensen, E., Grim, T., Ibañez-Alamo, J.D., Jokimäki, J., *et al.* (2013). The Geography of Fear: A Latitudinal Gradient in Anti-Predator Escape Distances of Birds across Europe. *PLoS ONE*, 8, e64634.
Douglas, H., Kitaysky, A., Kitaiskaia, E., Maccormick, A. & Kelly, A. (2009). Size of ornament is negatively correlated with baseline corticosterone in males of a socially monogamous colonial seabird. *J. Comp. Physiol. B*, 179, 297–304.
Dwyer, R.G. (2010). Ecological and anthropogenic constraints on waterbirds of the Forth Estuary: population and behavioural responses to disturbance. PhD thesis, University of Exeter. UK.
Eason, P.K., Sherman, P.T., Rankin, O. & Coleman, B. (2006). Factors affecting flight initiation distance in American robins. *J. Wildl. Manag.*, 70, 1796–1800.
Ellenberg, U., Setiawan, A.N., Cree, A., Houston, D.M. & Seddon, P.J. (2007). Elevated hormonal stress response and reduced reproductive output in Yellow-eyed penguins exposed to unregulated tourism. *Gen. Comp. Endocrinol.*, 152, 54–63.
Erwin, R.M. (1989). Responses to human intruders by birds nesting in colonies: experimental results and management guidelines. *Colon. Waterbirds*, 104–108.
Falsone, K., Jenni-Eiermann, S. & Jenni, L. (2009). Corticosterone in migrating songbirds during endurance flight. *Horm. Behav.*, 56, 548–556.
Fernandez-Juricic, E., Jimenez, M.D. & Lucas, E. (2001). Alert distance as an alternative measure of bird tolerance to human disturbance: implications for park design. *Environ. Conserv.*, 28, 263–269.
Fernandez-Juricic, E., Vaca, R. & Schroeder, N. (2004). Spatial and temporal responses of forest birds to human approaches in a protected area and implications for two management strategies. *Biol. Conserv.*, 117, 407–416.

Fernandez-Juricic, E., Zahn, E., Parker, T. & Stankowich, T. (2009). California's Endangered Belding's Savannah Sparrow (Passerculus sandwichensis beldingi): Tolerance of Pedestrian Disturbance. *Avian Conserv. Ecol.*, 4.

Ferrari, S.N., Albrieu, C., Bernardos, J. & Mercuri, C. (2012). Turismo y aves playeras migratorias en la Patagonia Austral (Santa Cruz, Argentina): lineamientos para minimizar el disturbio humano y ordenar la actividad. *TURyDES Tur. Desarro. Local Málaga Esp. 16 Pp*.

Forbes, M.R.L., Clark, R.G., Weatherhead, P.J. & Armstrong, T. (1994). Risk-Taking by Female Ducks: Intra- and Interspecific Tests of Nest Defense Theory. *Behav. Ecol. Sociobiol.*, 34, 79–85.

Fowler, G.S. (1999). Behavioral and hormonal responses of Magellanic penguins (Spheniscus magellanicus) to tourism and nest site visitation. *Biol. Conserv.*, 90, 143–149.

Fraser, J.D., Frenzel, L.D. & Mathisen, J.E. (1985). The impact of human activities on breeding bald eagles in north-central Minnesota. *J. Wildl. Manag.*, 585–592.

Galeotti, P., Tavecchia, G. & Bonetti, A. (2000). Parental defence in Long-eared Owls Asio otus: effects of breeding stage, parent sex and human persecution. *J. Avian Biol.*, 31, 431–440.

Geist, C., Liao, J., Libby, S. & Blumstein, D. (2005). Does intruder group size and orientation affect flight initiation distance in birds? *Anim. Biodivers. Conserv.*, 28, 69–73.

Glover, H.K., Weston, M.A., Maguire, G.S., Miller, K.K. & Christie, B.A. (2011). Towards ecologically meaningful and socially acceptable buffers: response distances of shorebirds in Victoria, Australia, to human disturbance. *Landsc. Urban Plan.*, 103, 326–334.

Goutte, A., Antoine, E., Weimerskirch, H. & Chastel, O. (2010). Age and the timing of breeding in a long-lived bird: a role for stress hormones? *Funct. Ecol.*, 24, 1007–1016.

Guay, P.J., Lorenz, R.D.A., Robinson, R.W., Symonds, M.R.E. & Weston, M.A. (2013). Distance from Water, Sex and Approach Direction Influence Flight Distances Among Habituated Black Swans. *Ethology*, 119, 552–558.

Gulbransen, D., Segrist, T., Del Castillo, P. & Blumstein, D.T. (2006). The Fixed Slope Rule: An Inter-Specific Study. *Ethology*, 112, 1056–1061.

Gutzwiller, K.J. & Marcum, H.A. (1997). Bird Reactions to Observer Clothing Color: Implications for Distance-Sampling Techniques. *J. Wildl. Manag.*, 61, 935–947.

Gutzwiller, K.J., Marcum, H.A., Harvey, H.B., Roth, J.D. & Anderson, S.H. (1998). Bird tolerance to human intrusion in Wyoming montane forests. *Condor*, 519–527.

Heidinger, B.J., Chastel, O., Nisbet, I.C.T. & Ketterson, E.D. (2010). Mellowing with age: older parents are less responsive to a stressor in a long-lived seabird. *Funct. Ecol.*, 24, 1037–1044.

Holberton, R.L. & Able, K.P. (2000). Differential migration and an endocrine response to stress in wintering dark-eyed juncos (Junco hyemalis). *Proc. R. Soc. Lond. B Biol. Sci.*, 267, 1889–1896.

Holberton, R.L., Helmuth, B. & Wingfield, J.C. (1996a). The Corticosterone Stress Response in Gentoo and King Penguins during the Non-Fasting Period. *The Condor*, 98, 850–854.

Holberton, R.L., Parrish, J.D. & Wingfield, J.C. (1996b). Modulation of the Adrenocortical Stress Response in Neotropical Migrants during Autumn Migration. *The Auk*, 113, 558–564.

Holberton, R.L. & Wingfield, J.C. (2003). Modulating the corticosterone stress response: a mechanism for balancing individual risk and reproductive success in arctic-breeding sparrows? *The Auk*, 120, 1140–1150.

Holmes, N.D. (2007). Comparing king, gentoo, and royal penguin responses to pedestrian visitation. *J. Wildl. Manag.*, 71, 2575–2582.

Holmes, T.L., Knight, R.L., Stegall, L. & Craig, G.R. (1993). Responses of wintering grassland raptors to human disturbance. *Wildl. Soc. Bull.*, 21, 461–468.

Hood, L.C., Boersma, P.D. & Wingfield, J.C. (1998). The adrenocortical response to stress in incubating Magellanic Penguins (Spheniscus magellanicus). *The Auk*, 115, 76–84.

Hope, D.D., Lank, D.B. & Ydenberg, R.C. (2014). Mortality-minimizing sandpipers vary stopover behavior dependent on age and geographic proximity to migrating predators. *Behav. Ecol. Sociobiol.*, 68, 827–838.

Horton, B.M. & Holberton, R.L. (2010). Morph-Specific Variation in Baseline Corticosterone and the Adrenocortical Response in Breeding White-Throated Sparrows (Zonotrichia albicollis). *The Auk*, 127, 540–548.

Humphrey, P.S., Livezey, B.C. & Siegel-Causey, D. (1987). Tameness of Birds of the Falkland Islands: An Index and Preliminary Results. *Bird Behav.*, 7, 67–72.

Ikuta, L.A. & Blumstein, D.T. (2003). Do fences protect birds from human disturbance? *Biol. Conserv.*, 112, 447–452.

Jungius, H. & Hirsch, U. (1979). Herzfrequenzänderungen bei Brutvögeln in Galapagos als Folge von Störungen durch Besucher. *J. Ornithol.*, 120, 299–310.

Kight, C.R. & Swaddle, J.P. (2007). Associations of anthropogenic activity and disturbance with fitness metrics of eastern bluebirds (< i> Sialia sialis). *Biol. Conserv.*, 138, 189–197.

Kitaysky, A.S., Wingfield, J.C. & Piatt, J.F. (1999). Dynamics of food availability, body condition and physiological stress response in breeding Black-legged Kittiwakes. *Funct. Ecol.*, 13, 577–584.

Kitchen, K., Lill, A. & Price, M. (2011). Tolerance of human disturbance by urban magpie-larks. *Aust. Field Ornithol.*, 28, 1.
Koch, S.L. & Paton, P.W. (2014). Assessing anthropogenic disturbances to develop buffer zones for shorebirds using a stopover site. *J. Wildl. Manag.*, 78, 58–67.
Kosztolanyi, A., Kupper, C., Chastel, O., Parenteau, C., Yilmaz, K.T., Miklosi, A., *et al.* (2012). Prolactin stress response does not predict brood desertion in a polyandrous shorebird. *Horm. Behav.*, 61, 734–740.
Landys-Ciannelli, M.M., Ramenofsky, M., Piersma, T., Jukema, J., Group, C.R. & Wingfield, J.C. (2002). Baseline and stress-induced plasma corticosterone during long-distance migration in the bar-tailed godwit, Limosa lapponica. *Physiol. Biochem. Zool.*, 75, 101–110.
Lattin, C.R., Bauer, C.M., de Bruijn, R. & Michael Romero, L. (2012). Hypothalamus-pituitary-adrenal axis activity and the subsequent response to chronic stress differ depending upon life history stage. *Gen. Comp. Endocrinol.*, 178, 494–501.
Laursen, K., Kahlert, J. & Frikke, J. (2005). Factors affecting escape distances of staging waterbirds. *Wildl. Biol.*, 11, 13–19.
Le Corre, N. (2009). Le derangement de l'avifaune sur les sites naturels proteges de Bretagne: Etat des lieux, enjeux et reflexions autour d'un outil d'etude des interactions hommes/oiseaux. PhD thesis. Universite de Bretagne occidentale-Brest.
Le Pape, A. (2012). Etude de la biologie et de l'écologie du Coq-de-roche (Rupicola rupicola) et propositions de mesures conservatoires pour l'espèce et son habitat. MSc thesis. Université des Antilles et de la Guyane.
Leclaire, S., Bourret, V., Wagner, R.H., Hatch, S.A., Helfenstein, F., Chastel, O., *et al.* (2011). Behavioral and physiological responses to male handicap in chick-rearing black-legged kittiwakes. *Behav. Ecol.*, 22, 1156–1165.
Lendvai, A.Z. & Chastel, O. (2008). Experimental mate-removal increases the stress response of female house sparrows: The effects of offspring value? *Horm. Behav.*, 53, 395–401.
Lendvai, A.Z., Giraudeau, M. & Chastel, O. (2007). Reproduction and modulation of the stress response: an experimental test in the house sparrow. *Proc. R. Soc. B Biol. Sci.*, 274, 391–397.
Levey, D.J., Londono, G.A., Ungvari-Martin, J., Hiersoux, M.R., Jankowski, J.E., Poulsen, J.R., *et al.* (2009). Urban mockingbirds quickly learn to identify individual humans. *Proc. Natl. Acad. Sci.*, 106, 8959–8962.
Li, D., Wang, G., Wingfield, J.C., Zhang, Z., Ding, C. & Lei, F. (2008). Seasonal changes in adrenocortical responses to acute stress in Eurasian tree sparrow (Passer montanus) on the Tibetan Plateau: Comparison with house sparrow (P. domesticus) in North America and with the migratory P. domesticus in Qinghai Province. *Gen. Comp. Endocrinol.*, 158, 47–53.
Li, D., Wu, J., Zhang, X., Ma, X., Wingfield, J.C., Lei, F., *et al.* (2011). Comparison of adrenocortical responses to acute stress in lowland and highland Eurasian tree sparrows (Passer montanus): similar patterns during the breeding, but different during the prebasic molt. *J. Exp. Zool. Part Ecol. Genet. Physiol.*, 315, 512–519.
Lin, T., Coppack, T., Lin, Q. xian, Kulemeyer, C., Schmidt, A., Behm, H., *et al.* (2012). Does avian flight initiation distance indicate tolerance towards urban disturbance? *Ecol. Indic.*, 15, 30–35.
Lindstrom, K.M., Hawley, D.M., Davis, A.K. & Wikelski, M. (2005). Stress responses and disease in three wintering house finch (Carpodacus mexicanus) populations along a latitudinal gradient. *Gen. Comp. Endocrinol.*, 143, 231–239.
Long, J.A. & Holberton, R.L. (2004). Corticosterone secretion, energetic condition, and a test of the migration modulation hypothesis in the hermit thrush (Catharus guttatus), a short-distance migrant. *The Auk*, 121, 1094–1102.
Lord, A., Waas, J.R., Innes, J. & Whittingham, M.J. (2001). Effects of human approaches to nests of northern New Zealand dotterels. *Biol. Conserv.*, 98, 233–240.
Lormée, H. (2001). Hormones, soins parentaux et dimorphisme sexuel chez les oiseaux marins tropicaux: soins parentaux. Thése de Doctorat, Biologie du Comportement, Université Paris 13.
Lunardi, V.O. & Macedo, R.H. (2013). Shorebirds can adopt foraging strategies that take advantage of human fishing practices. *Emu*, 114(1), 50–60.
Lynn, S.E., Hunt, K.E. & Wingfield, J.C. (2003). Ecological factors affecting the adrenocortical response to stress in chestnut-collared and McCown's longspurs (Calcarius ornatus, Calcarius mccownii). *Physiol. Biochem. Zool.*, 76, 566–576.
Lynn, S.E. & Porter, A.J. (2008). Trapping initiates stress response in breeding and non-breeding house sparrows Passer domesticus: implications for using unmonitored traps in field studies. *J. Avian Biol.*, 39, 87–94.
Mallory, M.L., McNicol, D.K., Walton, R.A. & Wayland, M. (1998). Risk-Taking by Incubating Common Goldeneyes and Hooded Mergansers. *The Condor*, 100, 694–701.

Malueg, A.L., Walters, J.R. & Moore, I.T. (2009). Do stress hormones suppress helper reproduction in the cooperatively breeding red-cockaded woodpecker (Picoides borealis)? *Behav. Ecol. Sociobiol.*, 63, 687–698.
Marra, P.P. & Holberton, R.L. (1998). Corticosterone Levels as Indicators of Habitat Quality: Effects of Habitat Segregation in a Migratory Bird during the Non-Breeding Season. *Oecologia*, 116, 284–292.
Martin II, L.B., Gilliam, J., Han, P., Lee, K. & Wikelski, M. (2005). Corticosterone suppresses cutaneous immune function in temperate but not tropical House Sparrows, Passer domesticus. *Gen. Comp. Endocrinol.*, 140, 126–135.
Meddle, S.L., Owen-Ashley, N.T., Richardson, M.I. & Wingfield, J.C. (2003). Modulation of the hypothalamic-pituitary-adrenal axis of an Arctic–breeding polygynandrous songbird, the Smith's longspur, Calcarius pictus. *Proc. R. Soc. LondonSeries B Biol. Sci.*, 270, 1849–1856.
Michael Romero, L., Cyr, N.E. & Romero, R.C. (2006). Corticosterone responses change seasonally in free-living house sparrows (Passer domesticus). *Gen. Comp. Endocrinol.*, 149, 58–65.
Miller, S.G., Knight, R.L. & Clinton, K.M. (2001). Wildlife Responses to Pedestrians and Dogs. *Wildl. Soc. Bull.*, 29, 124–132.
Mizrahi, D.S., Holberton, R.L. & Gauthreaux, J. (2001). Patterns of corticosterone secretion in migrating semipalmated sandpipers at a major spring stopover site. *The Auk*, 118, 79–91.
Møller, A.P. & Tryjanowski, P. (2014). Direction of approach by predators and flight initiation distance of urban and rural populations of birds. *Behav. Ecol.*, aru073.
Monie, L. (2011). Factors affecting alert distance and flight-initiation distance in Black Swans (Cygnus atratus) at Albert Park Lake, Victoria, Australia. B. Sc. Thesis, Victoria University, Australia.
O'Reilly, K.M. & Wingfield, J.C. (2001). Ecological Factors Underlying the Adrenocortical Response to Capture Stress in Arctic-Breeding Shorebirds. *Gen. Comp. Endocrinol.*, 124, 1–11.
O'Reilly, K.M. & Wingfield, J.C. (2003). Seasonal, age, and sex differences in weight, fat reserves, and plasma corticosterone in Western Sandpipers. *The Condor*, 105, 13–26.
Paton, D.C., Ziembicki, M.R., Owen, P. & Heddle, C.B. (2000). Disturbance distances for water birds and the management of human recreation with special reference to the Coorong region of South Australia. Final report for the Migratory Waterbird component of the National Wetlands Program. May 2000.
Payne, C.J., Jessop, T.S., Guay, P.J., Johnstone, M., Feore, M. & Mulder, R.A. (2012). Population, behavioural and physiological responses of an urban population of black swans to an intense annual noise event. *PLoS ONE*, 7, e45014.
Pereyra, M.E. & Wingfield, J.C. (2003). Changes in plasma corticosterone and adrenocortical response to stress during the breeding cycle in high altitude flycatchers. *Gen. Comp. Endocrinol.*, 130, 222–231.
Perfito, N., Schirato, G., Brown, M. & Wingfield, J.C. (2002). Response to acute stress in the Harlequin Duck (Histrionicus histrionicus) during the breeding season and moult: relationships to gender, condition, and life-history stage. *Can. J. Zool.*, 80, 1334–1343.
Perfito, N., Zann, R.A., Bentley, G.E. & Hau, M. (2007). Opportunism at work: habitat predictability affects reproductive readiness in free-living zebra finches. *Funct. Ecol.*, 21, 291–301.
Pfeiffer, S. (2005). Effects of human activities of southern giant petrels and skuas in the Antarctic. PhD thesis, University of Jena, Jena.
Price, M. (2003). Tolerance of a human observer by four ground-foraging bird species in urban and rural areas. B. Sc.(Hons) Thesis, Monash University, Melbourne.
Quirici, V., Venegas, C.I., Gonzalez-Gomez, P.L., Castaño-Villa, G.J., Wingfield, J.C. & Vasquez, R.A. (2014). Baseline corticosterone and stress response in the Thorn-tailed Rayadito (< i> Aphrastura spinicauda) along a latitudinal gradient. *Gen. Comp. Endocrinol.*, 198, 39–46.
Remage-Healey, L. & Romero, L.M. (2001). Corticosterone and insulin interact to regulate glucose and triglyceride levels during stress in a bird. *Am. J. Physiol. - Regul. Integr. Comp. Physiol.*, 281, R994–R1003.
Reneerkens, J., Morrison, R.G., Ramenofsky, M., Piersma, T. & Wingfield, J.C. (2002). Baseline and stress-induced levels of corticosterone during different life cycle substages in a shorebird on the high arctic breeding grounds. *Physiol. Biochem. Zool.*, 75, 200–208.
Riou, S., Chastel, O., Lacroix, A. & Hamer, K.C. (2010). Stress and parental care: Prolactin responses to acute stress throughout the breeding cycle in a long-lived bird. *Gen. Comp. Endocrinol.*, 168, 8–13.
Robinson, C.W. (2008). Western snowy plover use of managed salt ponds at Eden Landing, Hayward, CA. MSc thesis, San Jose State University, California.
Roby, D.D., Brink, K.L. & Nettleship, D.N. (1981). Measurements, chick meals and breeding distribution of dovekies (Alle alle) in northwest Greenland. *Arctic*, 34, 241–248.

Rodgers, Jr., J.A. & Smith, H.T. (1995). Set-Back Distances to Protect Nesting Bird Colonies from Human Disturbance in Florida Distancia de alejamiento para proteger de las perturbaciones humanas a las colonias de aves nidificadoras en Florida. *Conserv. Biol.*, 9, 89–99.
Rodgers, Jr., J.A. & Smith, H.T. (1997). Buffer zone distances to protect foraging and loafing waterbirds from human disturbance in Florida. *Wildl. Soc. Bull.*, 25, 139–145.
Rodriguez-Prieto, I., Fernandez-Juricic, E., Martin, J. & Regis, Y. (2009). Antipredator behavior in blackbirds: habituation complements risk allocation. *Behav. Ecol.*, 20, 371–377.
Rogers, H.M., Bechard, M.J., Kaltenecker, G.S. & Dufty Jr, A.M. (2010). The adrenocortical stress response in three North American accipiters during fall migration. *J. Raptor Res.*, 44, 113–119.
Romero, L.M., Holt, D.W. & Petersen, J.L. (2009). Flushing Effects and Seasonal Changes on Corticosterone Levels in Adult Long-Eared Owls Asio otus. *Ardea*, 97, 603–608.
Romero, L.M., Ramenofsky, M. & Wingfield, J.C. (1997). Season and Migration Alters the Corticosterone Response to Capture and Handling in an Arctic Migrant, the White-Crowned Sparrow (Zonotrichia leucophrys gambelii). *Comp. Biochem. Physiol. C Pharmacol. Toxicol. Endocrinol.*, 116, 171–177.
Romero, L.M. & Romero, R.C. (2002). Corticosterone responses in wild birds: the importance of rapid initial sampling. *The Condor*, 104, 129–135.
Romero, L.M., Soma, K.K. & Wingfield, J.C. (1998a). Changes in pituitary and adrenal sensitivities allow the snow bunting (Plectrophenax nivalis), an Arctic-breeding song bird, to modulate corticosterone release seasonally. *J. Comp. Physiol. B*, 168, 353–358.
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. - Regul. Integr. Comp. Physiol.*, 274, R1338–R1344.
Romero, L.M., Soma, K.K. & Wingfield, J.C. (1998c). The Hypothalamus and Adrenal Regulate Modulation of Corticosterone Release in Redpolls (Carduelis flammea—An Arctic-Breeding Song Bird). *Gen. Comp. Endocrinol.*, 109, 347–355.
Romero, L.M. & Wingfield, J.C. (2001). Regulation of the hypothalamic-pituitary-adrenal axis in free-living pigeons. *J. Comp. Physiol. B*, 171, 231–235.
Rouco, M., Ceballos, A., García, P., López, V., González, A., Hernández, G., *et al.* (2007). Análisis preliminar del impacto humano sobre las aves acuáticas en el azud de Riolobos (Salamanca) durante el paso migratorio post-nupcial de 2005. *Anu. Ornitológico Prov. Salamanca2004-2006SEO-Salamanca*.
Ruddock, M. & Whitfield, D.P. (2007). *A Review of Disturbance Distances in Selected Bird Species*. Report from Natural Research (Projects) Ltd. to Scottish Natural Heritage. Natural Research, Banchory, UK.
Rutherford, J. (2012). Quantifying acclimation levels of the northern mockingbird Mimus polyglottos in the presence of people. BSc Thesis, Coastal Carolina University, USA.
Schmid, B., Tam-Dafond, L., Jenni-Eiermann, S., Arlettaz, R., Schaub, M. & Jenni, L. (2013). Modulation of the adrenocortical response to acute stress with respect to brood value, reproductive success and survival in the Eurasian hoopoe. *Oecologia*, 173, 33–44.
Schoech, S.J., Bowman, R., Bridge, E.S. & Boughton, R.K. (2007). Baseline and acute levels of corticosterone in Florida Scrub-Jays (Aphelocoma coerulescens): Effects of food supplementation, suburban habitat, and year. *Gen. Comp. Endocrinol.*, 154, 150–160.
Schoech, S.J., Ketterson, E.D. & Nolan, V., Jr. (1999). Exogenous Testosterone and the Adrenocortical Response in Dark-Eyed Juncos. *The Auk*, 116, 64–72.
Schoech, S.J., Mumme, R.L. & Wingfield, J.C. (1997). Corticosterone, Reproductive Status, and Body Mass in a Cooperative Breeder, the Florida Scrub-Jay (Aphelocoma coerulescens). *Physiol. Zool.*, 70, 68–73.
Schwabl, H., Bairlein, F. & Gwinner, E. (1991). Basal and stress-induced corticosterone levels of garden warblers, Sylvia borin, during migration. *J. Comp. Physiol. B*, 161, 576–580.
Seltmann, M.W., Öst, M., Jaatinen, K., Atkinson, S., Mashburn, K. & Hollmén, T. (2012). Stress responsiveness, age and body condition interactively affect flight initiation distance in breeding female eiders. *Anim. Behav.*, 84, 889–896.
Silverin, B. (1997). The stress response and autumn dispersal behaviour in willow tits. *Anim. Behav.*, 53, 451–459.
Silverin, B., Arvidsson, B. & Wingfield, J. (1997). The adrenocortical responses to stress in breeding willow warblers Phylloscopus trochilus in Sweden: effects of latitude and gender. *Funct. Ecol.*, 11, 376–384.
Silverin, B. & Wingfield, J.C. (1998). Adrenocortical Responses to Stress in Breeding Pied Flycatchers Ficedula hypoleuca: Relation to Latitude, Sex and Mating Status. *J. Avian Biol.*, 29, 228–234.
Sims, C.G. & Holberton, R.L. (2000). Development of the Corticosterone Stress Response in Young Northern Mockingbirds (Mimus polyglottos). *Gen. Comp. Endocrinol.*, 119, 193–201.
Skagen, S.K., Knight, R.L. & Orians, G.H. (1991). Human disturbance of an avian scavenging guild. *Ecol. Appl.*, 215–225.

Smit, C.J. & Visser, G.J. (1993). Effects of disturbance on shorebirds: a summary of existing knowledge from the Dutch Wadden Sea and Delta. *Wader Study Croup Bull. Numéro Spec.*, 68, 6–19.
Smith, G.T., Wingfield, J.C. & Veit, R.R. (1994). Adrenocortical response to stress in the common diving petrel, Pelecanoides urinatrix. *Physiol. Zool.*, 526–537.
Smith, P.A., Gilchrist, H.G., Smith, J.N., Nol, E. & Lank, D.B. (2007). Annual variation in the benefits of a nesting association between Red Phalaropes (Phalaropus fulicarius) and Sabine's Gulls (Xema sabini). *The Auk*, 124, 276–290.
Stalmaster, M.V. & Kaiser, J.L. (1998). Effects of recreational activity on wintering bald eagles. *Wildl. Monogr.*, 3–46.
Tartu, S., Angelier, F., Bustnes, J.O., Moe, B., Hanssen, S.A., Herzke, D., *et al.* (2015a). Polychlorinated biphenyl exposure and corticosterone levels in seven polar seabird species. *Environ. Pollut.*, 197, 173–180.
Tartu, S., Angelier, F., Wingfield, J.C., Bustamante, P., Labadie, P., Budzinski, H., *et al.* (2015b). Corticosterone, prolactin and egg neglect behavior in relation to mercury and legacy POPs in a long-lived Antarctic bird. *Sci. Total Environ.*, 505, 180–188.
Thiel, D., Menoni, E., Brenot, J. & Jenni, L. (2007). Effects of recreation and hunting on flushing distance of capercaillie. *J. Wildl. Manag.*, 71, 1784–1792.
Thomas, K., Kvitek, R.G. & Bretz, C. (2003). Effects of human activity on the foraging behavior of sanderlings Calidris alba. *Biol. Conserv.*, 109, 67–71.
Touchton, J.M. (2011). The emergence of an alternative phenotype following species loss: Ecological, behavioral, and physiological evidence from spotted antbirds. PhD Thesis. Princeton University, USA.
Triplet, P., Bacquet, S., Morand, M.-E. & Lahilaire, L. (1998). La distance d'envol, un indicateur de dérangements: L'exemple de quelques espèces d'oiseaux en milieu estuarien. *Alauda*, 66, 199–206.
Triplet, P., Mequin, N. & Sueur, F. (2007). Prendre en compte la distance d'envol n'est pas suffisant pour assurer la quiétude des oiseaux en milieu littoral. *Alauda*, 75, 237–242.
Trulio, L.A., Robinson-Nilsen, C., Sokale, J. & Lafferty, K.D. (2011). *Report on nesting snowy plover response to new trail use in the South Bay Salt Pond Restoration Project.*
Tsipoura, N., Scanes, C.G. & Burger, J. (1999). Corticosterone and growth hormone levels in shorebirds during spring and fall migration stopover. *J. Exp. Zool.*, 284, 645–651.
Valcarcel, A. & Fernández-Juricic, E. (2009). Antipredator strategies of house finches: are urban habitats safe spots from predators even when humans are around? *Behav. Ecol. Sociobiol.*, 63, 673.
Vázquez, M.V., Encabo, M.E. & Paz Barreto, D. (2011). Aviturismo y su ordenamiento en conservación. Presented at the Encuentro Internacional de Turismo., Mar del Plata, Argentina.
Verboven, N., Verreault, J., Letcher, R.J., Gabrielsen, G.W. & Evans, N.P. (2010). Adrenocortical function of Arctic-breeding glaucous gulls in relation to persistent organic pollutants. *Gen. Comp. Endocrinol.*, 166, 25–32.
Villanueva, C., Walker, B.G. & Bertellotti, M. (2012). A matter of history: effects of tourism on physiology, behaviour and breeding parameters in Magellanic Penguins (Spheniscus magellanicus) at two colonies in Argentina. *J. Ornithol.*, 153, 219–228.
de Villiers, M., Bause, M., Giese, M. & Fourie, A. (2006). Hardly hard-hearted: heart rate responses of incubating Northern Giant Petrels (Macronectes halli) to human disturbance on sub-Antarctic Marion Island. *Polar Biol.*, 29, 717–720.
Vos, D.K., Ryder, R.A. & Graul, W.D. (1985). Response of Breeding Great Blue Herons to Human Disturbance in Northcentral Colorado. *Colon. Waterbirds*, 8, 13–22.
Walker, B.G., Meddle, S.L., Romero, L.M., Landys, M.M., Reneerkens, J. & Wingfield, J.C. (2015). Breeding on the extreme edge: modulation of the adrenocortical response to acute stress in two High Arctic passerines. *J. Exp. Zool. Part Ecol. Genet. Physiol.*, 323, 266–275.
Wang, Y., Chen, S. & Ding, P. (2004). Flush distance: bird tolerance to human intrusion in Hangzhou. *Zool. Res.*, 25, 214–220.
Washburn, B.E., Morris, D.L., Millspaugh, J.J., Faaborg, J. & Schulz, J.H. (2002). Using a commercially available radioimmunoassay to quantify corticosterone in avian plasma. *The Condor*, 104, 558–563.
Webb, N.V. & Blumstein, D.T. (2005). Variation in human disturbance differentially affects predation risk assessment in western gulls. *The Condor*, 107, 178–181.
Welcker, J., Harding, A.M.A., Kitaysky, A.S., Speakman, J.R. & Gabrielsen, G.W. (2009). Daily energy expenditure increases in response to low nutritional stress in an Arctic-breeding seabird with no effect on mortality. *Funct. Ecol.*, 23, 1081–1090.
Wheeler, M., Villiers, M. & Majiedt, P. (2009). The effect of frequency and nature of pedestrian approaches on the behaviour of wandering albatrosses at sub-Antarctic Marion Island. *Polar Biol.*, 32, 197–205.

Whitfield, D.P. & Rae, R. (2014). Human disturbance of breeding Wood Sandpipers Tringa glareola: implications for “alert distances” in prescribing protective buffer zones. *Ornis Fenn.*, in Press.
Wilson, C.M. & Holberton, R.L. (2004). Individual risk versus immediate reproductive success: a basis for latitudinal differences in the adrenocortical response to stress in yellow warblers (Dendroica petechia). *The Auk*, 121, 1238–1249.
Wilson, R.P., Culik, B., Danfeld, R. & Adelung, D. (1991). People in Antarctica: how much do Adelie Penguins Pygoscelis adeliae care? *Polar Biol.*, 11, 363–370.
Wingfield, J.C., Deviche, P., Sharbaugh, S., Astheimer, L.B., Holberton, R., Suydam, R., *et al.* (1994a). Seasonal changes of the adrenocortical responses to stress in redpolls, Acanthis flammea, in Alaska. *J. Exp. Zool.*, 270, 372–380.
Wingfield, J.C., Ramos-Fernandez, G., Nuñez-de la Mora, A. & Drummond, H. (1999). The Effects of an “El Niño” Southern Oscillation Event on Reproduction in Male and Female Blue-Footed Boobies,Sula nebouxii. *Gen. Comp. Endocrinol.*, 114, 163–172.
Wingfield, J.C., Suydam, R. & Hunt, K. (1994b). The adrenocortical responses to stress in snow buntings (Plectrophenax nivalis) and Lapland longspurs (Calcarius lapponicus) at Barrow, Alaska. *Comp. Biochem. Physiol. C Pharmacol. Toxicol. Endocrinol.*, 108, 299–306.
Wingfield, J.C., Vleck, C.M. & Moore, M.C. (1992). Seasonal changes of the adrenocortical response to stress in birds of the Sonoran Desert. *J. Exp. Zool.*, 264, 419–428.
Yorio, P. & Boersma, P.D. (1992). The effects of human disturbance on Magellanic penguin Spheniscus magellanicus behaviour and breeding success. *Bird Conserv. Int.*, 2, 161–173.

Appendix B: Additional sources of species-specific characteristics, such as body mass, habitat type, level of aggregation, diet and longevity.

1. Handbook of the Birds of the World (https://www.hbw.com/)
2. The complete birds of the western Palearctic on CD-ROM. Oxford, UK: Oxford University Press (Cramp S. 1998)
3. Birds of North America (https://birdsna.org/Species-Account/bna/home)
4. All about birds (from the Cornell Lab of Ornithology; https://www.allaboutbirds.org/guide/search/)
5. New Zealand Birds Online (http://nzbirdsonline.org.nz/)
6. Neotropical Birds Online (https://neotropical.birds.cornell.edu/Species-Account/nb/species)
7. Handbook of Australian, New Zealand and Antarctic Birds. Oxford University Press, Melbourne. ISBN 0-19-553244-9.
8. Species Profile and Threats Database of The Australian Government Department of the Environment (http://www.environment.gov.au/cgi-bin/sprat/public/sprat.pl)
9. AnAge Database of Animal Ageing and Longevity (http://genomics.senescence.info/species/)
10. Euring databases (https://euring.org/)
11. Vital Rates of North American Landbirds (http://www.vitalratesofnorthamericanlandbirds.org/)
12. Australian Bird and Bat Banding Scheme (ABBBS) (http://www.environment.gov.au/topics/science-and-research/bird-and-bat-banding/banding-data/search-abbbs-database)
13. Longevity Records Of North American Birds (https://www.pwrc.usgs.gov/BBL/longevity/Longevity_main.cfm)
14. Longevity Records: Life Spans of Mammals, Birds, Amphibians, Reptiles, and Fish (Carey, J. R. and Judge, D. S. (2008); http://www.demogr.mpg.de/longevityrecords/)
15. Life history traits databases (The Fagan lab; http://www.clfs.umd.edu/biology/faganlab/life_history/index.html)
16. Animal Diversity Web (http://animaldiversity.org/)
17. Encyclopedia of life (http://eol.org/)
18. Oiseaux.net (http://www.oiseaux.net/)
19. Oiseaux-birds.com (http://www.oiseaux-birds.com/home-page.html)
20. Arkive (http://www.arkive.org/explore/species)
21. BTO BirdFacts (https://www.bto.org/about-birds/birdfacts)
22. BirdLife International Data Zone (http://datazone.birdlife.org/species/search)
23. The IUCN Red List of Threatened Species (http://www.iucnredlist.org/search)
24. Yamashina Institute for Ornithology (http://www.yamashina.or.jp/hp/english/banding/birds_rings.html)
25. Istituto Veneto di Scienze Lettere ed Arti (http://www.istitutoveneto.org/venezia/divulgazione/pirelli/pirelli_2005_en/Banca_Dati_Ambientale/192.168.10.66/pirelli_new/divulgazione/valli/specie.html)
26. Birds of Kazakhstan (http://birds.kz/)
27. Norwegian Polar Institute (http://www.npolar.no/en/species)
28. OGATT: The Online Guide to the Animals of Trinidad and Tobago (https://sta.uwi.edu/fst/lifesciences/birds)
29. ZipcodeZoo (http://zipcodezoo.com/index.php/Main_Page)
30. Threatened Species Nomination Form for the 2013–2014 Assessment Period (http://birdlife.org.au/documents/BNB-nomination-form-species-Hooded_Plover_eastern.pdf)

31. Guide technique pour la prise en compte du Coq-de-roche dans les projets d'aménagement (https://lifecapdom.org/IMG/pdf/20150724_guidetech_c2r_freng_web.pdf)
32. Agüero, M. L., P. García Borboroglu and D. Esler. (2012). Distribution and abundance of Chubut Steamerducks: an endemic species to Central Patagonia, Argentina. Bird Conservation International, 22(3): 307-315.
33. Bianchi, G., Carpenter, K. E., Roux, J-P., Molloy, F. J., Boyer, D., Boyer, H. J. (1999) Field guide to the living marine resources of Namibia. FAO, Rome, p 265.
34. BirdLife International. (2011). The Illustrated Encyclopedia of Birds. Dorling Kindersley Ltd, London.
35. Bornschein, M. R., Pizo, M. A., Sobotka, D. D., Belmonte-Lopes, R., Golec, C., Machado-de-Souza, T., Pie, M. R. and Reinert, B. L., (2015). Longevity records and signs of aging in Marsh Antwren Formicivora acutirostris (Thamnophilidae). Wilson Journal of Ornithology, 127(1): 98-102.
36. Boto, A., Galimberti, A., and Bonser, R. (2009). The parrotbills in Lombardy, Italy. Birding World, 22.
37. Cherel, Y., Bocher, P., De Broyer, C., and Hobson, K. A. (2002). Food and feeding ecology of the sympatric thin-billed Pachyptila belcheri and Antarctic P. desolata prions at Iles Kerguelen, Southern Indian Ocean. Marine Ecology Progress Series, 228, 263-281.
38. Copeland, K. E. (2008) Concerted small-group foraging behavior in gentoo penguins Pygoscelis papua. Marine Ornithology 36: 193-194.
39. Cook, T. R. (2008). Ecologie des oiseaux plongeurs (Phalacrocorax spp.): réponses écophysiologiques, comportementales et sexuelles aux variations de l'environnement (Doctoral dissertation, Université de La Rochelle).
40. Gibbs, J. P., and Kinkel, L. K. (1997). Determinants of the size and location of Great Blue Heron colonies. Colonial Waterbirds, Jan 1: 1-7
41. Hansen, B. D., Minton, C. D., Harrison, A. E., and Jessop, R. (2014). Conservation assessment of the Sooty Oystercatcher Haematopus fuliginosus. The Conservation Status of Oystercatchers around the World: 161-172.
42. Hickling, R. A. O. (1954) The Wintering of Gulls in Britain, Bird Study, 1(4): 129-148.
43. Holberton, R. L., Helmuth, B., and Wingfield, J. C. (1996). The corticosterone stress response in gentoo and king penguins during the non-fasting period. The Condor, 98(4): 850-854.
44. James, D.A. and J.C. Neal. (1986). Arkansas birds: their distribution and abundance. Univ. Arkansas Press, Fayetteville, AR U.S.A.
45. Jiménez, J., Wynia, A., Rijal, R., and Rozzi, R. (2015). How long do birds in the southernmost forests of the world live? Maximum longevity estimates. Ecological Society of America annual meeting, Baltimore, MD, August 2015.
46. Koenig, W. D., & Dickinson, J. L. (Eds.). (2016). Cooperative breeding in vertebrates: studies of ecology, evolution, and behavior. Cambridge University Press.
47. Kylin, H., Louette, M., Herroelen, P., and Bouwman, H. (2010). Nominate Lesser Black-backed Gulls (Larus fuscus fuscus) winter in the Congo basin. Ornis Fennica, 87(3): 106.
48. Ledwoń, M., Neubauer, G., and Betleja, J. (2013). Adult and pre-breeding survival estimates of the Whiskered Tern Chlidonias hybrida breeding in southern Poland. Journal of ornithology, 154(3): 633-643.
49. Lendvai, Á. Z., Bókony, V., Angelier, F., Chastel, O., and Sol, D. (2013). Do smart birds stress less? An interspecific relationship between brain size and corticosterone levels. Proceedings of the Royal Society of London B: Biological Sciences, 280(1770): 20131734.

50. Liker, A., Freckleton, R. P., Remeš, V., and Székely, T. (2015). Sex differences in parental care: gametic investment, sexual selection, and social environment. Evolution, 69(11): 2862-2875.
51. Markula, A., Hannan-Jones, M., and Csurhes, S. (2009). Pest animal risk assessment: Indian myna, Acridotheres tristis. Pest animal risk assessment: Indian myna, Acridotheres tristis., (PR09-4413).
52. McCrie, N., and Noske, R. (2015). Birds of the Darwin region. CSIRO PUBLISHING.
53. Mirville, M. O., Kelley, J. L., and Ridley, A. R. (2016). Group size and associative learning in the Australian magpie (Cracticus tibicen dorsalis). Behavioral ecology and sociobiology, 70(3): 417-427.
54. Møller, A. P. (2006). Sociality, age at first reproduction and senescence: comparative analyses of birds. Journal of evolutionary biology, 19(3): 682-689.
55. Murton, R. K., Coombs, C. F. B., and Thearle, R. J. P. (1972). Ecological studies of the feral pigeon Columba livia var. II. Flock behaviour and social organization. Journal of Applied Ecology, Dec 1: 875-889.
56. Navedo, J.G. and Masero, J.A. (2008). Effects of traditional clam harvesting on the foraging ecology of migrating curlews (Numenius arquata). Journal of Experimental Marine Biology and Ecology, 355(1): 59-65.
57. Petraitis A., Uznyte R. 2010. Abundance and seasonal migration of gulls (Laridae) on the Lithuanian Baltic sea coast. Acta Biol. Univ. Daugavp., 10(2): 147 – 164.
58. Samia, D. S., Nakagawa, S., Nomura, F., Rangel, T. F., and Blumstein, D. T. (2015). Increased tolerance to humans among disturbed wildlife. Nature communications, 6: 8877.
59. Seeliger, Ulrich, Clarisse Odebrecht, and Jorge P. Castello, eds. (2012). Subtropical convergence environments: the coast and sea in the southwestern Atlantic. Springer Science & Business Media.
60. Sibly, R. M., Witt, C. C., Wright, N. A., Venditti, C., Jetz, W., and Brown, J. H. (2012). Energetics, lifestyle, and reproduction in birds. Proceedings of the National Academy of Sciences, 109(27): 10937-10941.
61. Sol, D., Maspons, J., Vall-Llosera, M., Bartomeus, I., García-Peña, G. E., Piñol, J., and Freckleton, R. P. (2012). Unraveling the life history of successful invaders. Science, 337(6094): 580-583.
62. Tan, H. J. (2011). Habitat use and population dynamics of the Azure-winged Magpie, Cyanopica cyanus, and their response to fire in Northern Mongolia (Master of International Nature Conservation, Lincoln University).
63. Taylor, I.R., Newman, O.M.G., Park, P., Hansen, B., Minton, C.D.T., Harrison, A. and Jessop, R. (2014). Conservation assessment of the Australian Pied Oystercatcher Haematopus longirostris. International Wader Studies 20: 116–128.
64. Vuilleumier, F. (1994). Status of the Ruddy-headed Goose Chloephaga rubidiceps (Aves, Anatidae): a species in serious danger of extinction in Fuego-Patagonia. Revista Chilena de Historia Natural, 67: 341-349.
65. Woods, R. W. (2014). Conservation assessment of the Blackish Oystercatcher Haematopus ater. International Wader Studies, 20: 109-115.

Table A.1: Results of the linear mixed model exploring the factors explaining flight initiation distance (i.e. escape response) across bird species when approached by humans. Represented are the posterior means of the effect of each variable with its corresponding 95% credible interval (CrI). Posterior means are the non-transformed estimates referring to the log-transformed FID values.

Effects	Posterior mean	CrI 95%
Intercept	4.489	3.744; 5.208
Urbanization		
Non-urban	/	/
Urban	-0.652	-0.728; -0.569
Latitude (absolute values; º)	-0.025	-0.030; -0.019
Habitat		
Closed	/	/
Mixed	0.265	0.096; 0.426
Open	0.333	0.127; 0.526
Life-history stage		
Overwintering	/	/
Breeding	-0.137	-0.539; 0.230
Early breeding	0.010	-0.652; 0.686
Parental phase	-0.974	-1.470; -0.456
Postbreeding	-0.419	-0.854; -0.032
Migration	0.148	-0.283; 0.563
ln (Body mass; kg)	0.226	0.139; 0.316
Degree of crypticity (%)	-0.003	-0.007; 0.0002
Probability of disruptive coloration	0.783	-0.048; 1.715
Probability of disruptive coloration^2	-1.812	-3.480; -0.165
Diet		
Herbivores	/	/
Omnivores	-0.158	-0.381; 0.089
Carnivores	-0.136	-0.402; 0.147
Level of aggregation		
Large group	/	/
Small group	-0.161	-0.299; -0.002
Solitary/pairs	-0.067	-0.242; 0.101
Longevity (years)	0.036	0.005; 0.066
Longevity (years)^2	-0.001	-0.002; -0.0003
FID-measurement technique		
Direct measurement	/	/
Expert communication	-1.864	-2.717; -0.913

/ = Reference category (included in the Intercept)

Random factors(+variance component estimates) = study(1.22)+ phylogeny(0.29)+ species(0.02) (+ residual variance (0.19))

Phylogenetic signal: λ = 0.17

N = 878. Note that this is the total raw sample size, but in mixed models effective sample sizes lie somewhere between the total sample size and the number of clusters defined by the random factors (Snijders & Bosker 2012)

Table A.2: Results (posterior means ± 95% credible intervals) of the linear mixed model investigating the factors modulating corticosterone levels across bird species. Posterior means are the non-transformed estimates refering to the log-transformed CORT concentrations.

Effects	Posterior mean	CrI 95%
Intercept	0.191	-0.950; 1.423
Sampling time	0.191	0.096; 0.145
Sampling time^2	-0.0010	-0.0011; -0.0009
Urbanization		
Non-urban	/	/
Urban	-0.297	-0.720; 0.155
Urban × Sampling time	0.004	-0.006; 0.014
Latitude (absolute values; º)	0.002	-0.006; 0.009
Latitude (absolute values; º) × Sampling time	0.0001	-0.00004; 0.0003
Habitat		
Closed	/	/
Mixed	0.227	-0.076; 0.562
Open	0.057	-0.306; 0.469
Mixed × Sampling time	-0.005	-0.011; 0.001
Open × Sampling time	-0.003	-0.009; 0.003
Life-history stage		
Overwintering	/	/
Breeding	-0.461	-0.847; -0.097
Early breeding	0.300	-0.051; 0.640
Parental phase	-0.056	-0.393; 0.276
Moult	-0.087	-0.483; 0.318
Postbreeding	0.318	-0.234; 0.832
Migration	0.537	0.151; 0.955
Breeding × Sampling time	-0.002	-0.011; 0.007
Early breeding × Sampling time	-0.007	-0.015; 0.0003
Parental phase × Sampling time	-0.005	-0.013; 0.002
Moult × Sampling time	-0.013	-0.022; -0.004
Postbreeding × Sampling time	-0.008	-0.021; 0.004
Migration × Sampling time	-0.012	-0.020; -0.004
ln (Body mass; kg)	-0.194	-0.314; -0.075
ln (Body mass; kg) × Sampling time	0.003	0.001; 0.006
Degree of crypticity (%)	-0.00006	-0.009; 0.009
Degree of crypticity (%) × Sampling time	-0.00006	-0.0002; 0.00009
Probability of disruptive coloration	1.67	-0.011; 3.508
Probability of disruptive coloration^2	-4.916	-7.749; -1.721
Probability of disruptive coloration × Sampling time	-0.031	-0.070; 0.005
Probability of disruptive coloration^2 × Sampling time	0.091	0.018; 0.169
Diet		
Herbivores	/	/
Omnivores	0.282	-0.306; 0.886
Carnivores	0.501	-0.070; 1.125
Omnivores × Sampling time	-0.006	-0.016; 0.006
Carnivores × Sampling time	-0.010	-0.022; 0.002
Level of aggregation		
Large group	/	/
Small group	-0.299	-0.649; 0.053
Solitary/pairs	-0.053	-0.384; 0.279
Small group × Sampling time	-0.002	-0.010; 0.006
Solitary/pairs × Sampling time	0.0006	-0.008; 0.008
Longevity (years)	0.040	-0.006; 0.092
Longevity (years)^2	-0.0008	-0.0017; 0.0001
Longevity (years) × Sampling time	-0.0007	-0.0017; 0.0002
Longevity (years)^2 × Sampling time	0.00002	0.000002; 0.00004
CORT-measurement assay		
EIA	/	/
RIA	0.453	-0.030; 0.957
RIA × Sampling time	-0.011	-0.020; -0.0008
Bird capture method		
Positive	/	/
Mixed	-0.137	-0.544; 0.310
Neutral	0.278	-0.122; 0.720
Negative	0.175	-0.294; 0.598
Mixed × Sampling time	0.003	-0.004; 0.010
Neutral × Sampling time	0.001	-0.006; 0.009
Negative × Sampling time	0.0005	-0.008; 0.009

/ = Reference category (included in the Intercept)

Random factors(+variance component estimates) = study(0.03)+ laboratory(0.08)+ phylogeny(0.09)+ species(0.02) +ID(0.09) (+ residual variance (0.17))
Phylogenetic signal: λ = 0.17
N = 574. Note that this represents the total raw sample size, but in mixed models effective sample sizes lie somewhere between the total sample size and the number of clusters defined by the random factors (Snijders & Bosker 2012)

Figure A.1: Methodological factors influencing FID or CORT levels. Effect (estimate ± 95% credible intervals) of the technique used to determine FID (a), of *CORT-measurement assay* used in the lab (b) and of the capture method for blood sampling (c & d*). The latter (c & d*) show different representations of the same data, first (c) the variation in CORT levels across the entire sampling-time range, and second (d*) only CORT levels at baseline (around 1 min; black squares) and around 30 min after capture (black triangles) with their credible intervals (dashed line) for each category, as well as the increase in CORT between both sampling times (solid black line). This latter representation allows for more straighforward comparison among capture methods, since the overlapping curves make inference difficult. PPs are the posterior probabilities that FID or CORT levels differ among categories of a given factor (PP used for differences between FID means, PPb for differences between baseline CORT levels, PP30 for differences between CORT levels at 30 minutes, and PPi for differences between increments from CORT at 1 min to CORT at 30 min). The higher this probability (from 0.5 to 1), the more likely the difference. For factors with more than two categories, for reference the categories differing with a PP over 0.9 are labelled with different letters (pairwise PPs are shown in the table Table A.4).

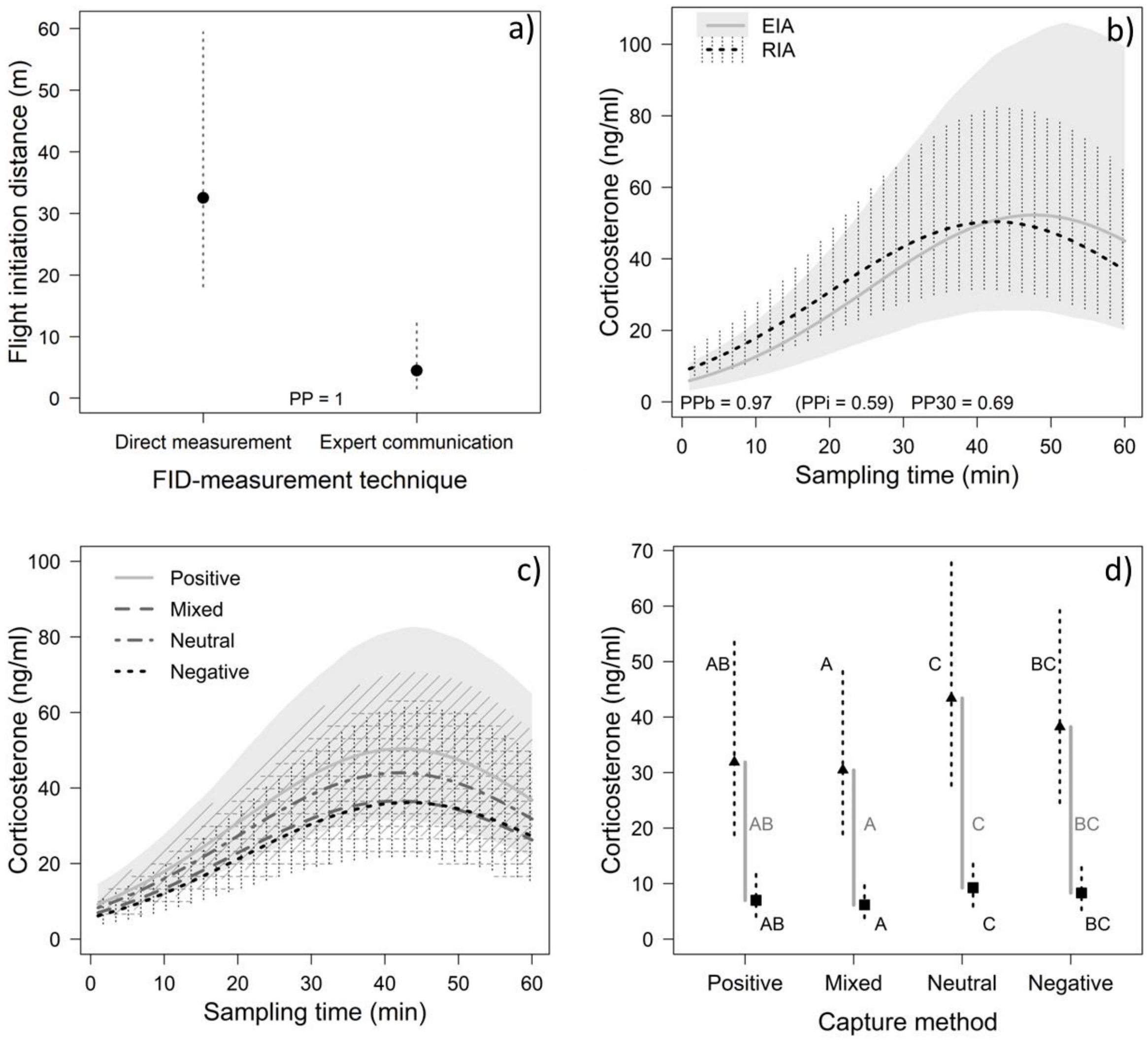


Table A.3: Posterior probabilities that estimated FID means differ between pairs of categories in factors with more than 2 categories. The higher this probability (from 0.5 to 1), the stronger the support for the difference.

PP (Type of habitat)			
	Closed	Mixed	Open
Closed	NA	1	1
Mixed	1	NA	0.78
Open	1	0.78	NA

PP (Life-history stage)						
	Overwintering	Breeding	Early breeding	Parental phase	Postbreeding	Migration
Overwintering	NA	0.75	0.52	1	0.98	0.76
Breeding	0.75	NA	0.68	1	0.94	0.84
Early breeding	0.52	0.68	NA	1	0.92	0.63
Parental phase	1	1	1	NA	0.99	1
Postbreeding	0.98	0.94	0.92	0.99	NA	0.98
Migration	0.76	0.84	0.63	1	0.98	NA

PP (Type of diet)			
	Herbivores	Omnivores	Carnivores
Herbivores	NA	0.90	0.84
Omnivores	0.84	NA	0.60
Carnivores	0.90	0.60	NA

PP (Level of aggregation)			
	Large group	Small group	Solitary/Pairs
Large group	NA	0.98	0.78
Small group	0.98	NA	0.91
Solitary/Pairs	0.78	0.91	NA

Table A.4: Posterior probabilities that CORT levels and CORT reactivity differ between pairs of categories in factors with more than 2 categories (PPb represents differences between baseline CORT levels, PP30 differences among CORT levels at 30 minutes, and PPi differences between increments from CORT at 1 min to CORT at 30 min). The higher this probability (from 0.5 to 1), the more likely the differences.

PPb / PPi / PP30 (Type of habitat; Figure A.2a)

	Closed	Mixed	Open
Closed	NA/ NA/ NA	0.91/ 0.59/ 0.68	0.59/ 0.65/ 0.60
Mixed	0.91/ 0.59/ 0.68	NA/ NA/ NA	0.81/ 0.70/ 0.74
Open	0.59/ 0.65/ 0.60	0.81/ 0.70/ 0.74	NA/ NA/ NA

PPb / PPi / PP30 (Life-history stage; Figure A.2b)

	Overwintering	Breeding	Early breeding	Parental phase	Molt	Postbreeding	Migration
Overwintering	NA/ NA/ NA	0.99/ 1/ 1	0.95/ 0.61/ 0.64	0.65/ 0.92/ 0.91	0.69/ 1/ 0.99	0.87/ 0.55/ 0.63	1/ 0.69/ 0.82
Breeding	0.99/ 1/ 1	NA/ NA/ NA	1/ 1/ 1	0.98/ 0.94/ 0.94	0.92/ 0.61/ 0.59	0.99/ 0.98/ 0.98	1/ 0.99/ 1
Early breeding	0.95/ 0.61/ 0.64	1/ 1/ 1	NA/ NA/ NA	1/ 1/ 1	0.98/ 1/ 0.99	0.52/ 0.51/ 0.55	0.90/ 0.58/ 0.72
Parental phase	0.65/ 0.92/ 0.91	0.98/ 0.94/ 0.94	1/ 1/ 1	NA/ NA/ NA	0.59/ 0.97/ 0.87	0.92/ 0.87/ 0.90	1/ 0.95/ 0.98
Molt	0.69/ 1/ 0.99	0.92/ 0.61/ 0.59	0.98/ 1/ 0.99	0.59/ 0.97/ 0.87	NA/ NA/ NA	0.93/ 0.99/ 0.98	1/1/1
Postbreeding	0.87/ 0.55/ 0.63	0.99/ 0.98/ 0.98	0.52/ 0.51/ 0.55	0.92/ 0.87/ 0.90	0.93/ 0.99/ 0.98	NA/ NA/ NA	0.80/ 0.59/ 0.63
Migration	1/ 0.69/ 0.82	1/ 0.99/ 1	0.90/ 0.58/ 0.72	1/ 0.95/ 0.98	1/1/1	0.80/ 0.59/ 0.63	NA/ NA/ NA

PPb / PPi / PP30 (Degree of disruptive coloration; Figure A.2c)

	Low	Intermediate	High
Low	NA/ NA/ NA	0.65/ 0.54/ 0.57	1/ 0.91/ 0.95
Intermediate	0.65/ 0.54/ 0.57	NA/ NA/ NA	1/ 0.92/ 0.96
High	1/ 0.91/ 0.95	1/ 0.92/ 0.96	NA/ NA/ NA

PPb / PPi / PP30 (Type of diet; Figure A.2d)

	Herbivores	Omnivores	Carnivores
Herbivores	NA/ NA/ NA	0.85/ 0.61/ 0.66	0.95/ 0.70/ 0.78
Omnivores	0.85/ 0.61/ 0.66	NA/ NA/ NA	0.94/ 0.69/ 0.76
Carnivores	0.95/ 0.70/ 0.78	0.94/ 0.69/ 0.76	NA/ NA/ NA

PPb / PPi / PP30 (Level of aggregation; Figure A.2e)

	Large group	Small group	Solitary/Pairs
Large group	NA/ NA/ NA	0.95/ 0.98/ 0.98	0.65/ 0.59/ 0.62
Small group	0.95/ 0.98/ 0.98	NA/ NA/ NA	0.95/ 0.99/ 0.99
Solitary/Pairs	0.65/ 0.59/ 0.62	0.95/ 0.99/ 0.99	NA/ NA/ NA

PPb / PPi / PP30 (Longevity; Figure A.2f)

	Low	Intermediate	High
Low	NA/ NA/ NA	0.87/ 0.79/ 0.82	0.70/ 0.84/ 0.78
Intermediate	0.87/ 0.79/ 0.82	NA/ NA/ NA	0.93/ 0.69/ 0.57
High	0.70/ 0.84/ 0.78	0.93/ 0.69/ 0.57	NA/ NA/ NA

PPb / PPi / PP30 (Bird capture method; Figure A.1c,d)

	Positive	Mixed	Neutral	Negative
Positive	NA/ NA/ NA	0.74/ 0.55/ 0.60	0.91/ 0.93/ 0.93	0.76/ 0.79/ 0.79
Mixed	0.74/ 0.55/ 0.60	NA/ NA/ NA	0.99/0.98/0.98	0.94/ 0.88/ 0.91
Neutral	0.91/ 0.93/ 0.93	0.99/0.98/0.98	NA/ NA/ NA	0.76/ 0.81/ 0.81
Negative	0.76/ 0.79/ 0.79	0.94/0.88/ 0.91	0.76/ 0.81/ 0.81	NA/ NA/ NA

Figure A.2: Variation in CORT levels across the whole sampling-time range for the categorical variables. These figures represent a visual support to the PPb/PPi/PP30 of Table A.4, and to the Figure 3 in the main text, since the overlap of their multiple curves impedes the inference of the results directly from these figures.

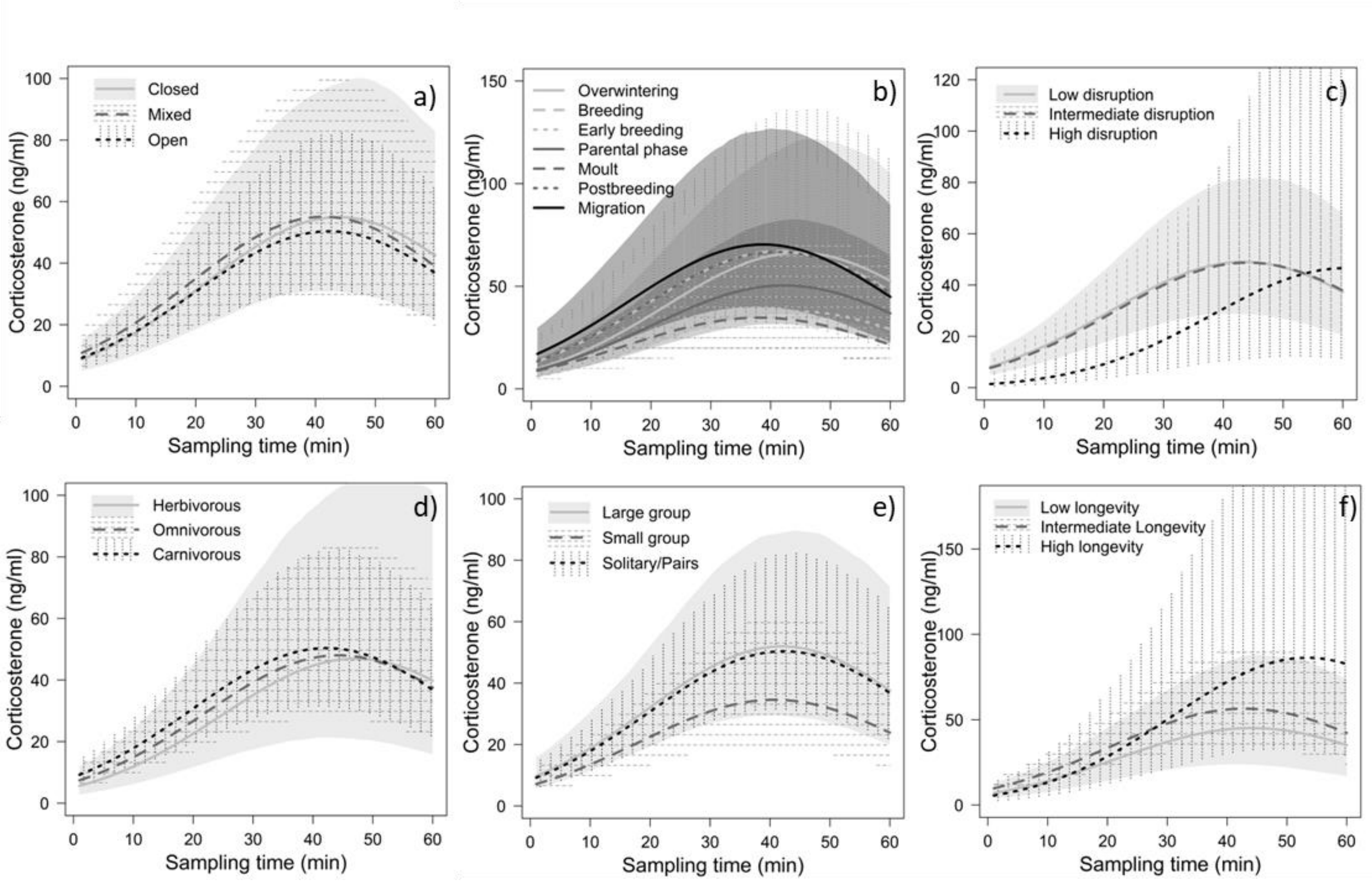


Table A.5: Table showing, for each modulating factor, the variation available in the database used in the FID model, in the CORT model and in the multivariate model. For continuous variables, the variation is expressed with the mean and the range of values. In the case of categorical variables the percentage of data belonging to each category is presented.

Variables	FID model	CORT model	Multivariate model
Latitude (absolute values; º)	47.8 (0.7-78.6)	50.1 (9.2-82.5)	50.0 (9.2-82.5)
Body mass (kg)	0.5 (0.006-12.2)	0.5 (0.008-12.2)	0.4 (0.008-12.2)
Degree of crypticity (%)	32.5 (1.7-78.8)	39.7 (7.5-85.8)	33.0 (7.5-76.7)
Probability of disruptive coloration	0.1 (0-0.8)	0.1 (0-0.8)	0.1 (0-0.8)
Longevity (years)	18.5 (3.2-50.0)	15.8 (4.0-50.9)	16.7 (6.1-46.0)
Urbanization			
Non-urban	72.4%	90.7%	65.5%
Urban	27.6%	9.3%	34.5%
Life-history stage			
Overwintering	11.8%	13.6%	8.6%
Breeding	56.7%	7.1%	42.6%
Early breeding	3.0%	21.9%	8.6%
Parental phase	13.1%	36.7%	22.6%
Moult		4.9%	
Postbreeding	10.3%	3.0%	9.2%
Migration	5.1%	12.8%	6.7%
Diet			
Herbivorous	14.8%	4.1%	20.9%
Omnivorous	48.9%	46.5%	51.0%
Carnivorous	36.3%	49.4%	28.1%
Level of aggregation			
Large group	15.5%	22.3%	21.7%
Small group	23.6%	20.8%	32.0%
Solitary/pairs	60.9%	56.9%	46.2%
Habitat			
Closed	19.7%	30.7%	30.1%
Mixed	36.8%	23.0%	41.5%
Open	43.5%	46.3%	28.4%

Table A.6: Results (posterior means ± 95% credible intervals) of the multivariate mixed model explaining the relationship of modulating factors simultaneously with flight initiation distance (i.e. escape response) and with CORT reactivity across bird species. Posterior means are the non-transformed estimates refering to the log-transformed FID values and to the square-root of corticosterone increases from baseline to stress values (i.e. square-root of corticosterone slope).

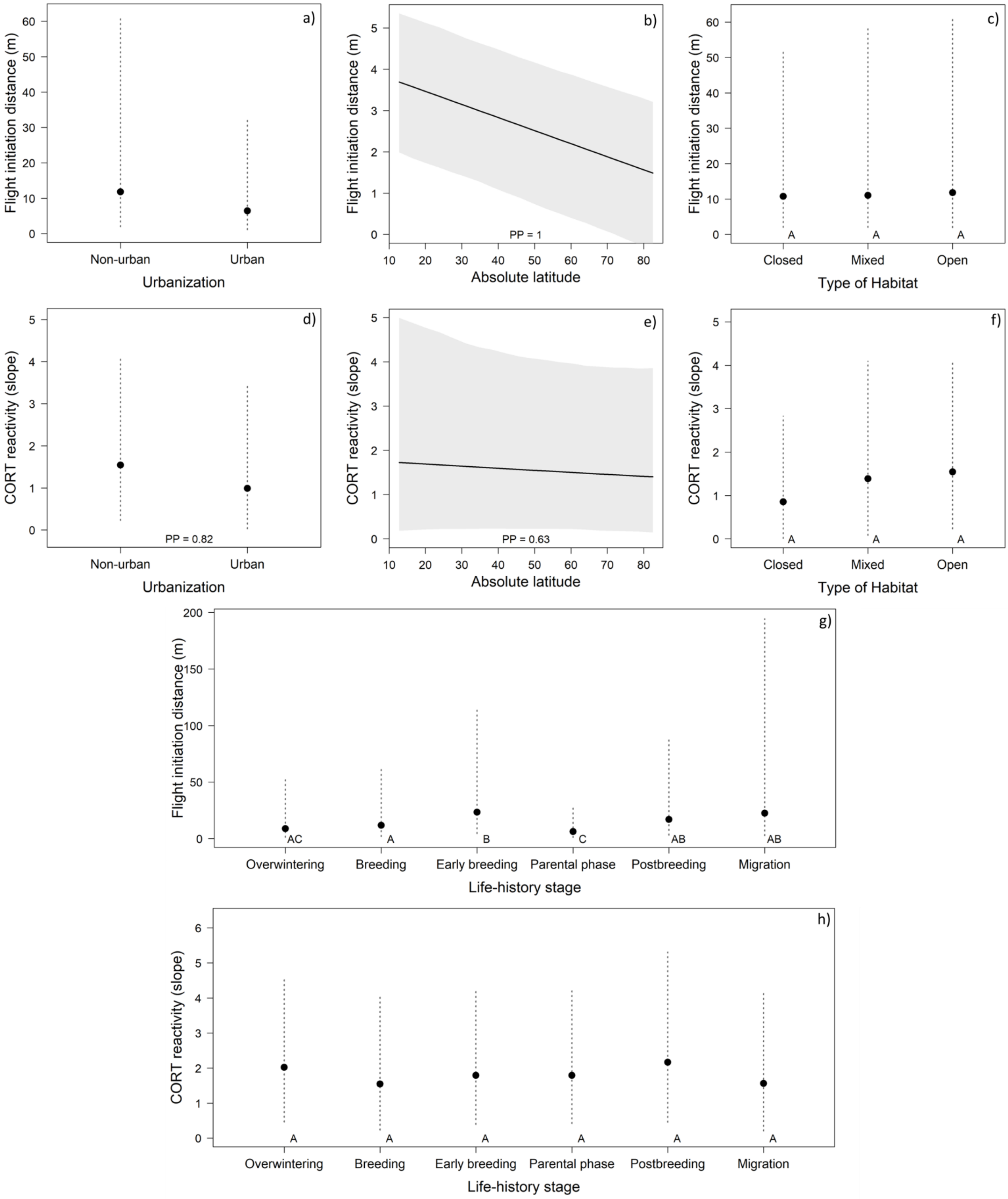
	FID		**CORT reactivity**	
Effects	Posterior mean	CrI 95%	Posterior mean	CrI 95%
Intercept	2.347	0.002; 5.124	0.384	-1.310; 2.103
Urbanization				
Non-urban	/	/	/	/
Urban	-0.606	-0.777; -0.423	-0.236	-0.799; 0.262
Latitude (absolute values; º)	-0.032	-0.045; -0.019	-0.002	-0.013; 0.008
Habitat				
Closed	/	/	/	/
Mixed	0.041	-0.816; 1.009	0.25	-0.260; 0.725
Open	0.115	-0.963; 1.291	0.31	-0.309; 0.903
Life-history stage				
Breeding	/	/	/	/
Overwintering	-0.281	-1.444; 0.924	0.181	-0.200; 0.570
Early breeding	0.714	-0.282; 1.634	0.102	-0.305; 0.488
Parental phase	-0.629	-1.386; -0.007	0.102	-0.252; 0.522
Postbreeding	0.375	-0.695; 1.501	0.227	-0.272; 0.819
Migration	0.65	-0.888; 2.243	0.013	-0.574; 0.597
ln (body mass; kg)	-0.108	-0.444; 0.252	-0.036	-0.213; 0.126
Degree of crypticity (%)	0.001	-0.022; 0.024	0.002	-0.013; 0.018
Probability of disruptive coloration	0.458	-4.197; 4.704	0.699	-1.585; 3.254
Probability of disruptive coloration^2	-3.063	-11.140; 4.007	-1.398	-5.040; 2.221
Diet				
Hervibores	/	/	/	/
Omnivores	-0.437	-1.891; 1.088	0.135	-0.554; 0.956
Carnivores	0.356	-0.986; 1.615	-0.093	-0.950; 0.728
Level of aggregation				
Small group	/	/	/	/
Large group	-0.084	-0.658; 0.574	0.093	-0.217; 0.362
Solitary/pairs	0.145	-0.357; 0.680	0.086	-0.159; 0.349
Longevity (years)	0.165	0.006; 0.325	0.019	-0.074; 0.110
Longevity (years)^2	-0.004	-0.007; -0.0004	-0.0002	-0.002; 0.002

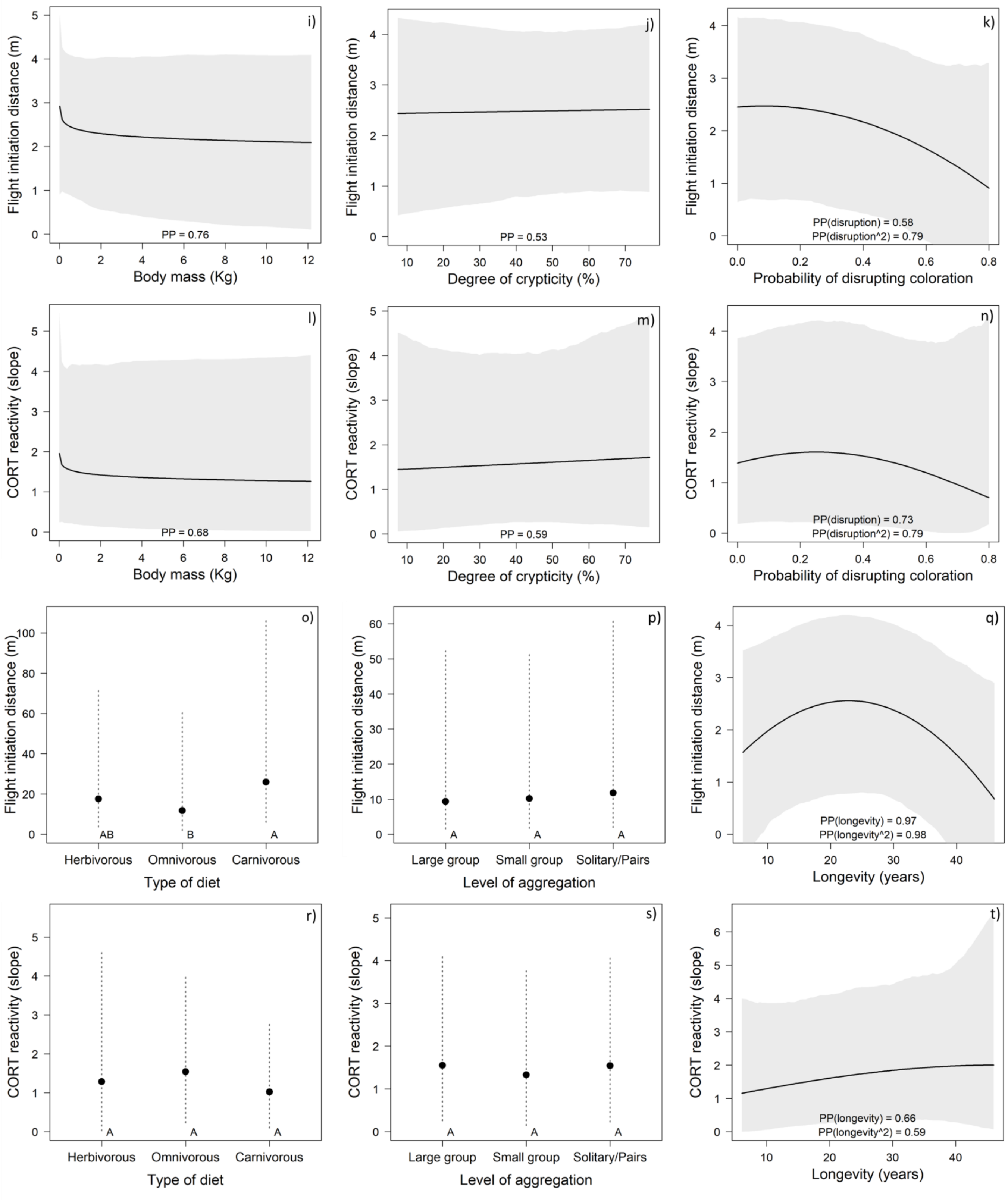
/ = Reference category (included in the Intercept)

Distribution = log-normal; link = identity; random factors = study+phylogeny+species

N = 261. Note that this is the total raw sample size, but in mixed models effective sample sizes lie somewhere between the total sample size and the number of clusters defined by the random factors (Snijders & Bosker 2012)

Figure A.3: Estimates obtained from the multivariate mixed model (Table A.6) for the association of modulating factors with flight initiation distance and CORT reactivity (estimated means ± 95% credible intervals). Posterior probabilities (PP = 0.5 - 1) represent the strength of the support for a given effect. For factors with more than two categories, as a reference different letters represent categories differing with a PP above 0.9.




i)
Flight initiation distance (m)
PP = 0.76
Body mass (Kg)
j)
Flight initiation distance (m)
PP = 0.53
Degree of crypticity (%)
k)
Flight initiation distance (m)
PP(disruption) = 0.58
PP(disruption^2) = 0.79
Probability of disrupting coloration
l)
CORT reactivity (slope)
PP = 0.68
Body mass (Kg)
m)
CORT reactivity (slope)
PP = 0.59
Degree of crypticity (%)
n)
CORT reactivity (slope)
PP(disruption) = 0.73
PP(disruption^2) = 0.79
Probability of disrupting coloration
o)
Flight initiation distance (m)
AB
B
A
Herbivorous
Omnivorous
Carnivorous
Type of diet
p)
Flight initiation distance (m)
A
A
A
Large group
Small group
Solitary/Pairs
Level of aggregation
q)
Flight initiation distance (m)
PP(longevity) = 0.97
PP(longevity^2) = 0.98
Longevity (years)
r)
CORT reactivity (slope)
A
A
A
Herbivorous
Omnivorous
Carnivorous
Type of diet
s)
CORT reactivity (slope)
A
A
A
Large group
Small group
Solitary/Pairs
Level of aggregation
t)
CORT reactivity (slope)
PP(longevity) = 0.66
PP(longevity^2) = 0.59
Longevity (years)