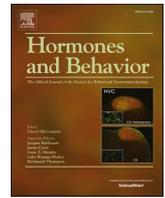




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## Factors modulating the behavioral and physiological stress responses: Do they modify the relationship between flight initiation distance and corticosterone reactivity?

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### 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 makes it 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.

### 1. 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.

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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.

## 2. Materials and methods

### 2.1. 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 min 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 built-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”, “post-breeding” (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.

## 2.2. 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 ( $\log(\text{FID}+0.1)$  and  $\log(\text{CORT})$ ), 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 min). 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 overparameterization.

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 to 90° 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 ( $V = 1$ ,  $\nu = 0.02$ ), 200,000 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 min; PPb), 2) stress levels (i.e. values at *sampling time* of 30 min, as measured by most authors; PP30), and 3) the increment in corticosterone levels from 1 to 30 min (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 the 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 ( $\log(\text{FID}+0.1)$ ) and CORT slope was square-rooted to fulfill 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, and burn-in than the previous two models. Consensus trees (for this

subset of species) were also obtained from [BirdTree.org](https://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.  $\log(\text{FID}+0.1)$  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, and found that both FID and CORT slope were highly repeatable within species, which supports the use of species averages for the correlation analysis ( $R_{\text{FID}} = 0.727$  [95% confidence interval: 0.597, 0.806],  $n = 261$  FID data;  $R_{\text{CORTSLOPE}} = 0.753$  [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.

### 3. 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 the 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 were available). Despite the lack of robust results (Table A.6, Fig. A.3), this multivariate model showed trends in agreement with the results observed in the separate phylogenetic linear mixed models (Figs. 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  $R_{\text{FID}} = 0.724$  [95% CI: 0.671, 0.769] and  $R_{\text{CORT}} = 0.494$  [0.376, 0.588], while the values after accounting for the modulating factors were  $R_{\text{FID}} = 0.751$  [0.706, 0.798] and  $R_{\text{CORT}} = 0.418$  [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 Appendix 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 Appendix Fig. 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; Figs. 1 and 2; Appendix Tables 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; Figs. 1 and 2; Appendix Tables 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 (Figs. 2a, b, e, f and 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; Figs. 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; Figs. 1b and 2b). Habitat type influenced FID, in 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; Figs. 1c and 2c).

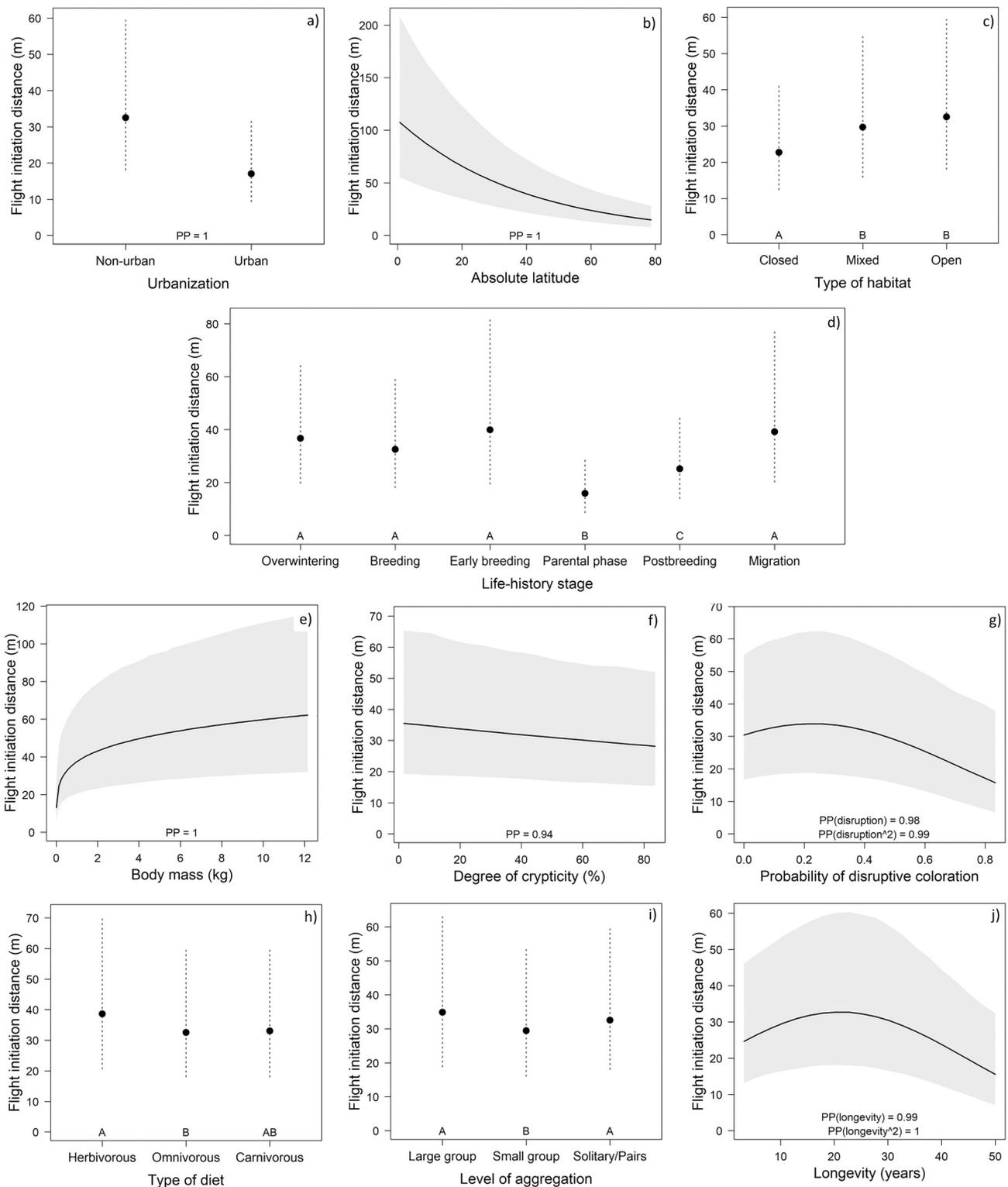
Regarding the temporal context, the behavioral and the physiological responses varied similarly across life-history stages. Birds had shorter FID and weaker CORT reactivity during the parental phases (i.e. incubation and chick rearing) and the molting period, while both FID and the CORT reactivity increased 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 (Figs. 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; Figs. 1 and 2). Birds with more disruptive color patterns tended to have a shorter FID and lower CORT reactivity (Figs. 1g and 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; Figs. 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; Figs. 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; Figs. 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; Figs. 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; Figs. 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; Figs. 1j and 2j).

**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 Tables A.1 and A.2 for the full model output).

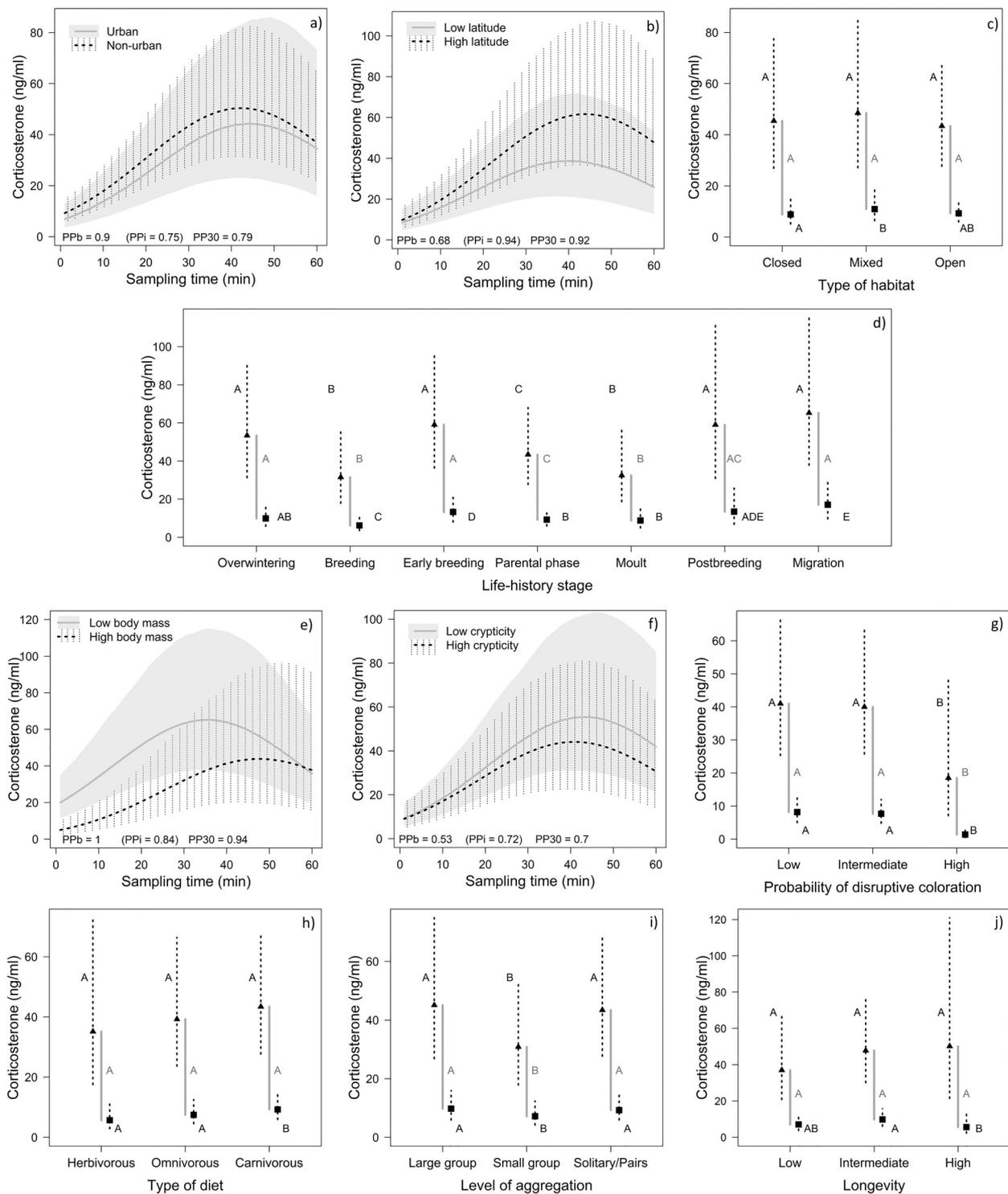
Modulating factor	Stress response	
	FID	CORT reactivity
Urbanization	Non-urban > urban	Non-urban > urban
Absolute latitude	Low > high	High > low
Type of habitat	Mixed, open > closed	Closed ~ mixed ~ open
Life-history stage	Migration, overwintering and early breeding > parental phase	Migration, overwintering and early breeding > parental phase and molt
Body mass	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



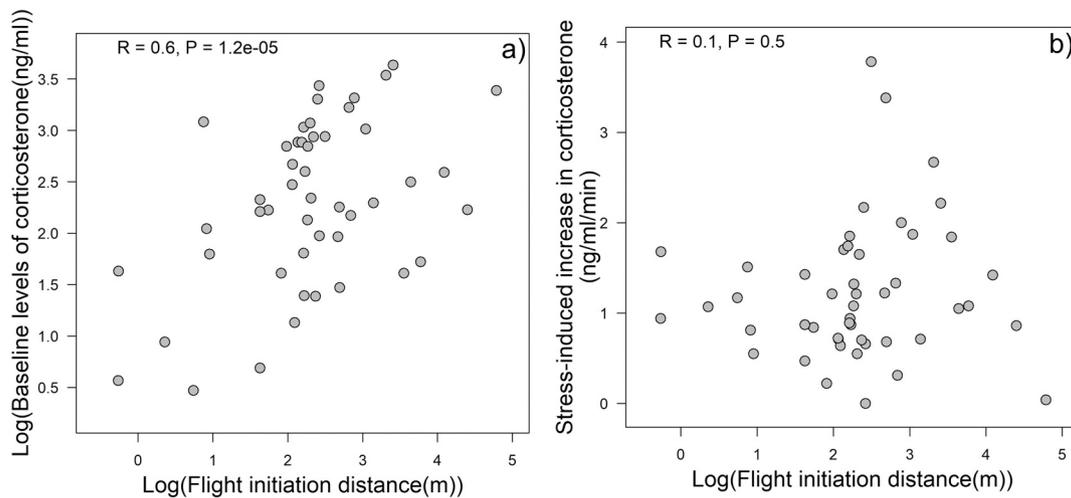
**Fig. 1.** Graphical presentation of effect sizes for factors influencing flight initiation distance (estimated means  $\pm$  95% credible intervals) derived from the model presented in Appendix Table A.1. Posterior probabilities (PP ranging from 0.5 to 1) represent the strength of the support for a 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.

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; Fig. 3a), stress-

induced increases in CORT (CORT slope/reactivity) did not show a clear association with FID (correlation coefficient = 0.1; p-value = 0.5; Fig. 3b).



**Fig. 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 ( $\pm 95\%$  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 Fig. 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 Appendix Table A.4. Note the differences in the y-axes.



**Fig. 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.

#### 4. 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 across-species 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 antipredator 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, in probabilities of detection or of being detected and attacked, and thus in 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.

#### CRediT authorship contribution statement

Z.T. participated in the study design, collected and analyzed 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.

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#### Data availability

The datasets generated and analyzed during the current study will be available from the Swiss Ornithological Institute (<https://zenodo.org/communities/vora?page=1&size=20>), if this manuscript will be accepted for publication.

#### Appendices. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.yhbeh.2021.104979>.

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