OXFORD

Article

Anti-predator behavior along elevational and latitudinal gradients in dark-eyed juncos

Madelin ANDRADE and Daniel T. BLUMSTEIN*

Department of Ecology and Evolutionary Biology, University of California, 621 Young Drive South, Los Angeles, CA 90095-1606, USA

*Address correspondence to Daniel T. Blumstein. E-mail: marmots@ucla.edu.

Handling editor: Zhi-Yun Jia

Abstract

Flight-initiation distance (FID), the distance between an individual and experimenter when it begins to flee, can be used to quantify risk-assessment. Among other factors, prior studies have shown that latitude explains significant variation in avian FID: at lower latitudes, individuals and species have longer FIDs than those living at higher latitudes. No prior studies have focused on the effect of elevation on FID. Given the similar patterns of seasonality, climate, and potentially predator density, that covary between latitude and elevation, birds at higher elevations might tolerate closer approaches. We asked whether elevation or latitude would explain more variation in the FID of a common passerine bird species, dark-eyed juncos (*Junco hyemalis*). Juncos live in a variety of habitats along both latitudinal and elevational gradients. We found that statistical models containing elevation as a variable explained more of the variation in FID than did models containing latitude. We also found, unexpectedly, that birds at higher elevation fled at greater distances. While more predators were sighted per hour at higher elevations than at lower elevations, the frequency of predator sightings did not explain a significant amount of variation in FID. This result questions whether predator density is the main driver of risk perception along elevational gradients. Nonetheless, because elevation explains more variation in FID than latitude in at least one species, these findings have direct implications on how human impacts on birds are managed. Specifically, those designing set-back zones to reduce human impact on birds may consider modifying them based on both latitude and elevation.

Key words: antipredator behavior, FID, latitude, elevation, dark-eyed junco, *Junco hyemalis*

When approached by predators, animals flee and numerous factors have been shown to influence the decision to flee (Stankowich and Blumstein 2005; Blumstein 2006; Guay et al. 2013; Legagneux and Ducatez 2013; Samia et al. 2013; Møller 2014, 2015). Predator behavior that is associated with increased risk or danger should motivate animals to flee at longer distances. For example, certain species of birds flee at greater distances when 2 humans approach them as opposed to one (Geist et al. 2005). Flight-initiation distance (FID) is correlated with predator density; birds have greater FIDs when predator density is higher (Stankowich and Blumstein 2005; Møller et al. 2015). Additionally, a recent study has shown that breeding birds within 100 m of a raptor nest have larger FIDs than birds >500 m away (Møller et al. 2017). A prey's distance to refuge and predator approach speed is positively correlated with FID, with birds fleeing at greater distances when they are farther from their refuge or when they are approached at a greater speed (Stankowich and Blumstein 2005). Flock size has also been shown to affect FID, with a recent study showing that social species of birds in Europe have increased FID when their flock size is larger (Morelli et al. 2019). Characteristics of the prey itself can also affect FID; animals with armor or crypsis tolerate closer approaches, suggesting that they perceive themselves to be at a lower risk of predation

(Stankowich and Blumstein 2005; Møller et al. 2019); however, this shorter FID may also be attributed to the immobility that is required for an organism to be successfully camouflaged (Samia et al. 2015a).

There are geographic trends in antipredator behavior as well. Recent studies have shown that FID and pre-detection distance, the distance an observer travels before being detected by the focal organism, varies along a latitudinal gradient in birds (Díaz et al. 2013; Samia et al. 2017) and lizards (Samia et al. 2015b; Blumstein et al. 2016) whereby predators can approach individuals more closely at higher latitudes. This behavior may be explained by predation risk, because bird species experience a higher level of predation in the tropics than at higher latitudes (Schemske et al. 2009); however, the cause of this pattern remains poorly understood.

Given the many variables that vary similarly between latitude and elevation (e.g., temperature, precipitation, growing season length, species diversity, plant species composition, and possibly predation risk), we might expect to find patterns of anti-predator behavior along elevational gradients that mirror those found for latitude (e.g., see Camacho and Avilés 2019). In other words, we may expect that individuals of a species that are studied at higher elevations will respond similarly to those individuals in higher latitudes. However, a recent study over an elevation range of 981 m showed that an increased level of nest predation at higher elevations was associated with a reduction of avian clutch sizes at higher elevations (Dillon and Conway 2017). Another study, which compared low-elevation arctic and high-elevation alpine sites, found that nest predation was higher at high elevations than at low elevations (Sandercock et al. 2005), which is the opposite pattern of predator density that is reported for increasing latitude (Schemske et al. 2009; Díaz et al. 2013). So, it is an empirical question as to whether elevation mirrors latitude in terms of predation risk. We ask whether elevational patterns parallel those for latitude in terms of an individual's assessment of risk.

FID is often used to help wildlife managers create buffer zones—areas with restricted human access—to protect animals from human disturbance (Holmes et al. 1993; Rodgers and Smith 1995). The logic is that humans should be kept back some multiple of the average FID (Blumstein et al. 2003; Glover et al. 2011; Livezey et al. 2016). But, if FIDs systematically vary with both latitude and elevation, a species' buffer zone may have to be more dynamically managed. Our research identifies the degree to which the effect of elevation mimics that of latitude for a model avian species, the Oregon form of dark-eyed juncos (*Junco hyemalis*), which we studied along both elevational and altitudinal gradients. Juncos are ideally suited for this study because they are common in California and are found across a wide range of latitudes and elevations. In addition, research has shown that juncos have considerable phenotypic plasticity (Yeh and Price 2004) and have remained or become abundant in urbanized areas (Marzluff et al. 2016), suggesting that they are able to successfully adapt to a range of environments with changes in life history and behavior (Møller and Díaz 2017). If elevational patterns of perceived risk parallel those for latitude, then we predict that higher elevation birds will respond similarly to higher latitude birds, whereby individuals will tolerate relatively closer approaches.

Materials and Methods

Between April and September 2018, we estimated dark-eyed junco FIDs at 7 University of California Natural Reserve System (UCNRS) field sites spanning the elevational and latitudinal range of California: Angelo Coast Range Reserve, Blue Oak Ranch Reserve, Hastings Natural History Reservation, James San Jacinto Mountains Reserve, Sagehen Creek Field Station, Sedgwick Reserve, and White Mountain Research Center. We report elevation range (3012 m), latitudinal range (5.9° N), and average annual 2018 temperatures (Dendra ND) along with the number of days juncos were studied at each site in Table 1.

Data were gathered following a standard protocol (Blumstein 2006) and using standard terminology of starting distance (SD), alert distance (AD), and FID (Cooper and Blumstein 2015). Using binoculars, observers identified dark-eyed juncos from afar. After a positive identification, the observer approached each bird by walking toward it in a straight line and at a constant speed (ca. 0.5 m/s). The distance at which the observer began to approach a bird was recorded as the SD. The distance at which the bird first showed signs of being alarmed (i.e., the bird ruffled its feathers or oriented its body toward the observer) was recorded as the AD, and the distance at which the bird began to flee, or "flush," was recorded as the FID. While completing the flush, the observer dropped a flagged marker at each distance of interest and then placed a marker where the bird was located before flushing. The observer then used a meter tape to measure the distances from the bird's position to each marker. Individuals who already seemed to be engaged in alarmed behaviors (e.g., ruffling feathers) were not approached. For each flush, observers recorded the wind speed using Beaufort Scale. Additionally, because of their potential effect on FID (Stankowich and Blumstein 2005; Møller et al. 2017), observers recorded the number of conspecifics within 10 m of the focal bird (group size) and the distance, in meters, from the focal bird to the nearest vegetation cover. Observers also recorded whether the bird was on the ground or in a tree and the bird's height in tree, if applicable. Age and sex of the focal bird was not always readily determined in the field, so these variables were excluded from subsequent analyses (see Table A2 for a defined list of variables collected). For birds perched in trees, their height off the ground was measured using proportions. At a distance, the height of the bird in tree was measured, proportionately, using a pencil. This proportional distance was then rotated 90° and the distance was measured along the ground (Blumstein et al. 2004). To avoid pseudoreplication, the observer moved at least 30 m away after completing a flush.

Observers ($n = 2$) were carefully trained to walk at a constant speed of 0.5 m/s before beginning data collection. To ensure that the observers had a consistent stride length, the trainer set up a 30-m tape in a straight line and had the observers walk along the tape repeatedly, until they walked 30 m in a repeatable and consistent number of steps. Then, observers timed their walks until they consistently walked the 30 m in 60 s (i.e., 0.5 m/s). For consistency, observers were retrained if they spent more than 2 weeks out of the field, or every 6 weeks otherwise. Before recording data, observers trained in the field to ensure a standardized methodology and consistently recorded data. In addition, observers wore similar drab clothing across all trials to control for confounding effects of observer appearance on FID data (Gutzwiller and Marcum 1993; Altenau et al. 2004; Putman et al. 2017). For subsequent analyses, data were only included for times when it was not raining and when wind speed was ≤3 on the Beaufort scale.

Because SD and FID values were measured along the ground, this value was an indirect measurement of SD and FID for birds perched in trees, who perceived our distance from a height. For birds perched in trees, we determined the direct FID using the Pythagorean theorem,

Table 1. Field station latitude, average elevation of flushes, average annual temperature, number of days each UCNRS site was visited, and the number of FID measurements taken at each site (*N*)

UCNRS site	Average elevation (m)	Latitude	Average annual temperature (°C)	Days visited	N
James San Jacinto Mountains Reserve	1,645	33°48′32.7″	12.1	16	38
Sedgwick Reserve	105	34°41′35.0″	15.5	20	22
Hastings Natural History Reservation	525	36°22′46.6″	13.5	16	65
Blue Oak Ranch Reserve	571	37°22′52.8″	13.6	26	28
White Mountain Research Center	3117	37°29′59.1″	3.28	10	12
Sagehen Creek Field Station	1936	39°25′56.2″	−0.66	13	31
Angelo Coast Range Reserve	439	39°43′06.1″	11.5	12	22

where $FID_{direct} = \sqrt{(\text{indirect FID})^2 + (\text{height in tree})^2}$. We also determined the direct SD using a similar equation, where $SD_{direct} = \sqrt{(\text{indirect SD})^2 + (\text{height in tree})^2}$. These values were used for all subsequent analyses.

In addition to FID data, we counted sightings of aerial and terrestrial predators while in the field collecting FID data. However, because only 2 ground predators were sighted, we limited our statistical analyses to potential junco-eating raptors (Cooper's hawks *Accipiter cooperii* and red-tailed hawks *Buteo jamaicensis*). Using these sightings, we calculated predator use per site by dividing the total number of raptors detected by the total time we were in the field collecting data at each site. We used this predator per hour (PPH) data as a proxy for the predation pressure that juncos faced at different elevations and latitudes.

Statistical analysis

We calculated the direct FID and SD for birds that were perched in trees according to the FID_{direct} and SD_{direct} equations listed above. We then log-10 transformed the direct FID and SD, as well as the elevation data in order to reduce skew in the distributions.

We fitted 2 sets of general linear mixed effects models in R (R Core Team 2018) using the lme4 package (Bates et al. 2015) to explain variation in FID: FID ~ SD + elevation + SD * elevation + (1 | Site), and FID ~ SD + latitude + SD * latitude + (1 | Site). Because each site had its unique elevation and latitude (i.e., they do not vary independently), we could not include both variables in the same model. Thus, we compared models that included either latitude or elevation, and determined which explained more variation. We added site as a random effect to control for repeated sampling of birds within a site. In addition, we fitted the junco data to models including PPH to test for the effect of predator sightings on FID across both elevational and latitudinal gradients: FID ~ SD + elevation + SD * elevation + PPH + (1 | Site), and FID ~ SD + latitude + SD * latitude + PPH + (1 | Site). R^2 is an appropriate criterion for comparison because the models have the same number of parameters. We compared the conditional R^2 and marginal R^2 values in order to evaluate the effect of site on each model. We included the interaction terms because if an interaction term was significant, the effect of SD on FID likely changes with varying elevation (or latitude) (Blumstein et al. 2015). We plotted frequency distributions of residuals and used q–q plots to confirm that residuals were approximately normally distributed.

We tested to see if other covariates could confound the interpretation of our models in 2 ways. First, we fitted ANOVAs to test if site explained variation in group size and distance to vegetation cover. We fitted a chi-square to test if there was an association between site and whether the bird was on the ground or in a tree. Because these variables varied by site, we then included these as

covariates in our main models to see if their inclusion explained more of the variation in FID. We fitted our main model with all 3 covariates, with each covariate individually, and with pairwise groups (see Appendix A1a–g). To test for the possible effect of observer on FID, we added observer as a variable in our best-fit model. In addition, we obtained visitation data from each UCNRS site and averaged the number of people that visited the site over a 5-year period. We correlated human visitation rate with elevation to see if this could be a potential confounding factor.

Results

We conducted 218 FID measurements on dark-eyed juncos across 7 sites with an average of 31 ± 17 FID measurements at each site. The conditional R^2 was greatest for the model with elevation ($R^2 = 0.439$) and we found that both elevation [$P = 0.0409$; Table 2, panel (a)] and the interaction between elevation and SD [$P = 0.016$; Table 2, panel (a)] explained significant variation in FID. FID also increased with increasing SD, but this relationship was less steep as elevation increased (Table 2 and Figure 1). The model containing latitude had a conditional R^2 value of 0.426 [Table 2, panel (b)]. PPH explained a statistically significant amount of variation in FID ($P = 0.034$; Table 2, panel (b)) and FID increased with increasing predator sightings per hour. However, no statistically significant variation in FID was explained by either latitude ($P = 0.577$; Table 2, panel (b)) or by the interaction between latitude and SD [$P = 0.358$; Table 2, panel (b)]. Additionally, the model including only latitude, SD, and their interaction term explained less variation in FID [conditional $R^2 = 0.408$; Table 2, panel (d)] than the model that included only elevation, SD, and their interaction term [conditional $R^2 = 0.430$; Table 2, panel (c)]. Taken together, these results suggest that elevation was a stronger predictor of FID than latitude over the range of latitudes we studied.

Predators detected per hour were not statistically significant in our best-fit model; there were fewer predator sightings per hour at higher elevations when compared with lower elevations ($r = -0.566$, $P = 0.184$). Furthermore, there was no relationship between human visitation rate and elevation ($r = -0.274$, $P = 0.552$), suggesting that differences in human activity likely did not influence the pattern of FID found along the elevational gradient.

However, PPH was statistically significant in the model containing latitude [$P = 0.034$; Table 2, panel (b)], with FID increasing as PPH increased. There were fewer predator sightings per hour at higher latitudes when compared with lower latitudes ($r = -0.289$, $P < 0.001$). These results are consistent with prior reports of predator detections along a latitudinal gradient (e.g., Díaz et al. 2013).

The ANOVA showed a significant difference in the focal bird's group size ($P < 0.001$) and distance to nearest vegetation

($P < 0.001$) between study sites. The difference in group size was driven by 2 sites (Blue Oak Range Reserve and Angelo Coast Range Reserve) and the difference in distance to vegetation was driven by one site (James San Jacinto Mountains Reserve). In addition, the Pearson's chi-squared test showed that there was a significant difference between sites in the proportion of birds found in trees and on

Table 2. Results from mixed models explaining variation in dark-eyed junco flight initiation distance (FID)

Parameter	B	Standard error	P-value
(a) Parameter values for the linear mixed model			
FID $\sim$ SD+elevation+SD * elevation+PPH+(1 | site)[a]			
Intercept	−1.44	0.743	0.055
SD	2.15	0.620	<0.001
Elevation	0.522	0.253	0.041
SD * elevation	−0.512	0.212	0.016
PPH	0.097	0.089	0.338
(b) Parameter values for the linear mixed model			
FID $\sim$ SD+latitude+SD * latitude+PPH+(1 | site)[b]			
Intercept	0.856	1.466	0.560
SD	−0.466	1.224	0.704
Latitude	−0.022	0.040	0.577
SD * latitude	0.031	0.033	0.358
PPH	0.222	0.065	0.034
(c) Parameter values for the linear mixed model			
FID $\sim$ SD+elevation+SD * elevation+(1 | site)[c]			
Intercept	−1.438	0.745	0.055
SD	2.283	0.607	<0.001
Elevation	0.525	0.254	0.040
SD * elevation	−0.554	0.208	0.008
(d) Parameter values for the linear mixed model			
FID $\sim$ SD+latitude+SD * latitude+(1 | site)[d]			
Intercept	1.555	1.527	0.31
SD	−0.682	1.240	0.538
Latitude	−0.040	0.041	0.336
SD * latitude	0.037	0.034	0.273

[a] Marginal R^2: 0.424, conditional R^2: 0.439, $N = 218$.
[b] Marginal R^2: 0.419, conditional R^2: 0.426, $N = 218$.
[c] Marginal R^2: 0.414, conditional R^2: 0.430, $N = 218$.
[d] Marginal R^2: 0.335, conditional R^2: 0.408, $N = 218$.

the ground ($P = 0.036$), which was driven by one site (White Mountain Research Center). When observer was added as a variable in our best-fit model, it explained less of the variation in FID (conditional $R^2 = 0.440$), suggesting that the identity of the observer did not influence our results.

When we added these covariates to our main models (see Appendix A1a–g), the best-fit model [conditional $R^2 = 0.441$; Table A1, panel (e)] included the proportion of juncos found in trees and on the ground and group size; however, neither of these variables were statistically significant [see Appendix Table A1, panel (e)] and their addition explained <1% of the variation in FID. Therefore, the additional covariates did not change our interpretation of the main results and we focus on interpreting models without these covariates.

Discussion

We found that elevation explained a statistically significant ($P = 0.041$) amount of variation in FID, with FID *increasing* as elevation increased [Table 2, panel (a)]. Previous studies on birds have found that FID decreases with increasing latitude (Díaz et al. 2013; Blumstein et al. 2016; Samia et al. 2017). Thus, elevation and latitude appear to have opposite effects on FID. These results are not an artifact of juncos living in urban areas at lower elevations and rural areas at higher elevations because all FID data were collected at protected research reserves and where human visitation rates did not vary significantly as a function of elevation. This apparent reversal of anti-predator behavior patterns from latitudinal patterns could be due to a difference in predation risk for dark-eyed juncos between elevational and latitudinal gradients within our study area.

However, PPH did not explain a statistically significant ($P = 0.338$) amount of variation in FID in our main model, which included elevation [Table 2, panel (a)]. It is possible that our predator counts were not an accurate proxy for predation pressure along elevational gradients. For example, a recent study has shown that predation risk for red-faced warblers *Cardellina rubrifrons* was higher at higher elevations (Dillon and Conway 2017), and we know that predation pressure affects FID (Díaz et al. 2013; Møller et al. 2017). Further research is needed to understand how predation pressure precisely changes along elevational gradients. If the number
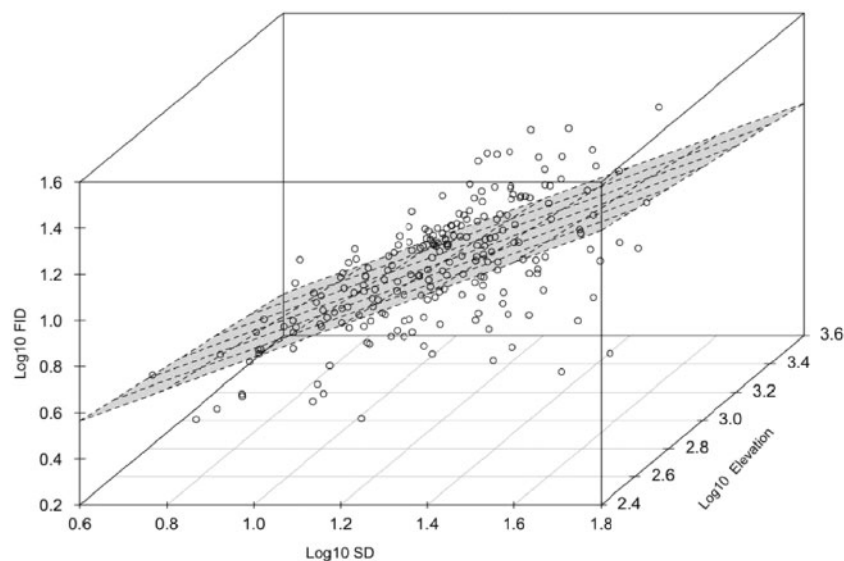
Figure 1. The relationship between elevation and SD in explaining FID in dark-eyed juncos.

of predators detected was not representative of actual predation pressure at higher elevations, this would be a possible reason for why PPH was unable to explain any significant variation in FID along our study's elevational range.

In addition to elevation having a significant main effect ($P = 0.041$), it also had a significant interaction with SD [$P = 0.016$; Table 2, panel (a)]. At lower elevations, FID increased with increasing SD. At higher elevations, FID also increased with increasing SD, but less so. Therefore, elevation is associated with the relationship between SD and FID. It is possible that dark-eyed juncos have more environmental stressors at high elevations (decreased food abundance, decreased food quality, decreased partial pressure of oxygen, etc.), such that it may be more costly to flee an approaching threat. Thus, these birds would tolerate closer approaches for any given SD at higher elevations because the benefit of foraging would outweigh the cost of fleeing—a response seen in food-deprived vultures (Zuberogoitia et al. 2010).

While our study did not find latitude to be a significant predictor of FID, this could be due to the limited range of latitude in our study, along with our relatively small sample size ($N = 218$). We used average change in temperature to compare our study system's latitudinal and elevational ranges. Using the average adiabatic lapse rate in California of 1.833°C per 304.8 m, our elevational range covered a change of 18.1°C. To find the lapse rate for latitude, we compared the average annual temperature of 3 coastal cities (Santa Barbara, CA; Portland, OR; and Woodinville, WA), obtained from the National Centers for Environmental Information. The cities have an elevational range of 3.3 m, temperature range of 4.61°C, and a degrees latitude range of 13.3°, yielding a lapse rate of 0.346°C per latitude degree North. In addition, we compared the average annual temperature of 3 inland cities (Bishop, CA; Bend, OR; and Barkerville, BC), obtained from the National Centers for Environmental Information. The cities have an elevational range of 527 m, a temperature range of 11.61°C, and a degrees latitude range of 15.7°, yielding a lapse rate of 0.739°C per latitude degree North. Therefore, our study covered an elevational range that was approximately 4.1–8.9 times larger than its latitudinal range—at least as quantified by average temperature. Subsequent research with larger latitudinal range will be needed to better understand the precise relationship between elevation and latitude on FID.

Because elevation is a stronger predictor of FID within our study area, these findings may have direct implications on how natural areas are managed. Assuming other birds have similar elevational relationships as the juncos we studied, we suggest that those designing setback zones to reduce human impact on birds (e.g., Guay et al. 2016) may have to modify them based on both latitude and elevation. Given that California has the greatest elevational gradient and latitudinal range in the lower 48 states, this work should be directly useful for California wildlife managers. Additionally, it is essential to understand the impacts of elevation on antipredator behavior because upland reserves, under stress from climate change, may also experience disproportionate disturbance from people, who may be attracted there in a warming climate.

Acknowledgments

Funding

References

Altenau B, Blumstein DT, Green L, Gould ML, 2004. A study of the species—confidence hypothesis with spiny-cheeked honeyeaters *Acanthagenys rufogularis*. *Emu* 104:267–271.

Bates D, Maechler M, Bolker B, Walker S, 2015. Fitting linear mixed-effects models using lme4. *J Stat Soft* 67:1–48.

Blumstein DT, Anthony LL, 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.

Blumstein DT, 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 DT, Fernández-Juricic E, LeDee O, Larsen E, Rodriguez-Prieto I et al., 2004. Avian risk assessment: effects of perching height and detectability. *Ethology* 110:273–285.

Blumstein DT, Samia DS, Cooper WE, 2016. Escape behavior: dynamic decisions and a growing consensus. *Curr Opin Behav Sci* 12:24–29.

Blumstein DT, Samia DS, Stankowich T, Cooper WE, 2015. Best practice for the study of escape behavior. In: Cooper WE, Blumstein DT, editors. *Escaping from Predators: An Integrative View of Escape Decisions*. UK: Cambridge University Press, 413–416.

Camacho LF, Avilés L, 2019. Decreasing predator density and activity explains declining predation of insect prey along elevational gradients. *Am Nat* 194:334–343.

Cooper WE, Blumstein DT, 2015. Escape behavior: importance, scope, and variables. In: Cooper WE, Blumstein DT, editors. *Escaping from Predators: An Integrative View of Escape Decisions*. UK: Cambridge University Press, 9–10.

Dendra, ND. Dendra Sensor Observatory Curation. Available at: https://ucnrs.dendra.science/#/ (10 April 2019).

Díaz M, Møller AP, Flensted-Jensen E, Grim T, Ibáñez-Álamo JD et al., 2013. The geography of fear: a latitudinal gradient in anti-predator escape distances of birds across Europe. *PLoS ONE* 8:e64634.

Dillon KG, Conway CJ, 2017. Nest predation risk explains variation in avian clutch size. *Behav Ecol* 29:301–311.

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

Glover HK, Weston MA, Maguire GS, Miller KK, Christie BA, 2011. Towards ecologically meaningful and socially acceptable buffers: response distances of shorebirds in Victoria, Australia, to human disturbance. *Landsc Urban Plan* 103:326–334.

Guay P, Lorenz RD, Robinson RW, Symonds MR, Weston MA, 2013. Distance from water, sex and approach direction influence flight distances among habituated black swans. *Ethology* 119:552–558.

Guay PJ, van Dongen WF, Robinson RW, Blumstein DT, Weston MA, 2016. AvianBuffer: an interactive tool for characterising and managing wildlife fear responses. *AMBIO* 45:841–851.

Gutzwiller KJ, Marcum HA, 1993. Avian responses to observer clothing color: caveats from winter point counts. *Wilson Bull* 105:628.

Holmes TL, Knight RL, Stegall L, Craig GR, 1993. Responses of wintering grassland raptors to human disturbance. *Wildl Soc Bull* 21:461–468.

Legagneux P, Ducatez S, 2013. European birds adjust their flight initiation distance to road speed limits. *Biol Lett* **9**:20130788.

Livezey KB, Fernández-Juricic E, Blumstein DT, 2016. Database of bird flight initiation distances to assist in estimating effects from human disturbance and delineating buffer areas. *J Fish Wildl Manage* **7**:181–191.

Marzluff JM, Clucas B, Oleyar MD, DeLap J, 2016. The causal response of avian communities to suburban development: a quasi-experimental, longitudinal study. *Urban Ecosyst* **19**:1597–1621.

Møller AP, 2014. Life history, predation and flight initiation distance in a migratory bird. *J Evol Biol* **27**:1105–1113.

Møller AP, 2015. Birds. In: Cooper WE, Blumstein DT, editors. *Escaping from Predators: An Integrative View of Escape Decisions*. UK: Cambridge University Press, 88–107.

Møller AP, Stokke BG, Samia DS, 2015. Hawk models, hawk mimics, and antipredator behavior of prey. *Behav Ecol* **26**:1039–1044.

Møller AP, Díaz M, 2017. Avian preference for close proximity to human habitation and its ecological consequences. *Curr Zool* **64**:623–630.

Møller AP, Kwiecinski Z, Tryjanowski P, 2017. Prey reduce risk-taking and abundance in the proximity of predators. *Curr Zool* **63**:591–598.

Møller AP, Liang W, Samia DS, 2019. Flight initiation distance, color and camouflage. *Curr Zool* **65**. doi: 10.1093/cz/zoz005.

Morelli F, Benedetti Y, Díaz M, Grim T, Ibáñez-Álamo JD et al., 2019. Contagious fear: escape behavior increases with flock size in European gregarious birds. *Ecol Evol* **9**:6096

National Centers for Environmental Information, ND. *Climate Data Online Search*. Available at: https://www.ncdc.noaa.gov/cdo-web/search (23 Setpember 2019).

Putman BJ, Drury JP, Blumstein DT, Pauly GB, 2017. Fear no colors? Observer clothing color influences lizard escape behavior. *PLoS ONE* **12**:e0182146.

R Core Team, 2018. *R: A Language and Environment for Statistical Computing*. R Vienna: Foundation for Statistical Computing. Available at: https://www.r-project.org/ (23 September 2019).

Rodgers JA, Smith HT, 1995. Set-back distances to protect nesting bird colonies from human disturbance in Florida. *Conserv Biol* **9**:89–99.

Samia DS, Nomura F, Blumstein DT, 2013. Do animals generally flush early and avoid the rush? A meta-analysis. *Biol Lett* **9**:20130016.

Samia DS, Blumstein DT, Stankowich T, Cooper WE, 2015a. Fifty years of chasing lizards: new insights advance optimal escape theory. *Biol Rev* **91**: 349–366.

Samia DS, Moller AP, Blumstein DT, Stankowich T, Cooper WE, 2015b. Sex differences in lizard escape decisions vary with latitude, but not sexual dimorphism. *Proc Biol Sci Biol* **282**:20150050.

Samia DSM, Blumstein DT, Díaz M, Grim T, Ibáñez-Álamo JD et al., 2017. Rural–urban differences in escape behavior of European birds across a latitudinal gradient. *Front Ecol Evol* **5**:66.

Sandercock BK, Martin K, Hannon SJ, 2005. Life history strategies in extreme environments: comparative demography of arctic and alpine ptarmigan. *Ecology* **86**:2176–2186.

Schemske DW, Mittelbach GG, Cornell HV, Sobel JM, Roy K, 2009. Is there a latitudinal gradient in the importance of biotic interactions? *Annu Rev Ecol Evol Syst* **40**:245–269.

Stankowich T, Blumstein DT, 2005. Fear in animals: a meta-analysis and review of risk assessment. *Proc Biol Sci* **272**:2627–2634.

Yeh PJ, Price TD, 2004. Adaptive phenotypic plasticity and the successful colonization of a novel environment. *Am Nat* **164**:531–542.

Zuberogoitia I, Martínez JE, Margalida A, Gómez I, Azkona A et al., 2010. Reduced food availability induces behavioural changes in Griffon Vulture *Gyps fulvus*. *Ornis Fenn* **87**:52.

Appendix

Table A1. Results from mixed models explaining variation in dark-eyed junco FID with covariates included

Parameter	B	Standard error	P-value
(a) Parameter values for the linear mixed model FID ~ elevation+SD+elevation * SD+PPH+distance to veg cover+on ground+group size+(1 | site)			
Intercept	−1.05	0.854	0.220
Elevation	0.401	0.291	0.170
SD	1.85	0.716	0.010
PPH	0.127	0.083	0.127
Dist. to veg	−0.006	0.005	0.260
On ground (0/1)	−0.031	0.036	0.390
Group size	0.016	0.010	0.096
SD * elevation	−0.419	0.244	0.088
(b) Parameter values for the linear mixed model FID ~ elevation+SD+elevation * SD+PPH+on ground+(1 | site)			
Intercept	−1.219	0.751	0.107
Elevation	0.450	0.256	0.081
SD	2.02	0.624	0.001
PPH	0.089	0.083	0.346
On ground (0/1)	−0.043	0.031	0.163
SD * Elevation	−0.462	0.214	0.032
(c) Parameter values for the linear mixed model FID ~ elevation+SD+elevation * SD+PPH+group size+(1 | site)[c]			
Intercept	−1.48	0.737	0.047
Elevation	0.533	0.252	0.035
SD	2.15	0.621	<0.001
PPH	0.117	0.076	0.204
Group size	0.0175	0.009	0.058
SD * elevation	−0.518	0.212	0.016

(continued)

Table A1. (continued)

Parameter	B	Standard error	P-value
(d) Parameter values for the linear mixed model FID ~ elevation+SD+elevation * SD+PPH+distance to veg cover+(1 | site)			
Intercept	−1.15	0.831	0.168
Elevation	0.434	0.284	0.128
SD	1.96	0.705	0.006
PPH	0.105	0.082	0.200
Dist. to veg	−0.007	0.005	0.174
SD * elevation	−0.454	0.240	0.060
(e) Parameter values for the linear mixed model FID ~ elevation+SD+elevation * SD+PPH+group size+on ground+(1 | site)			
Intercept	−1.29	0.749	0.088
Elevation	0.471	0.256	0.067
SD	2.04	0.626	0.001
PPH	0.109	0.073	0.140
Group size	0.016	0.009	0.072
On ground	−0.038	0.031	0.220
SD * elevation	−0.474	0.215	0.028
(f) Parameter values for the linear mixed model FID ~ elevation+SD+elevation * SD+PPH+on ground+distance to veg cover+(1 | site)[f]			
Intercept	−0.963	0.846	0.256
Elevation	0.374	0.288	0.196
SD	1.84	0.711	0.010
PPH	0.108	0.082	0.186
On ground (0/1)	−0.041	0.035	0.248
Dist. to veg	−0.006	0.005	0.232
SD * Elevation	−0.411	0.243	0.092

(continued)

Table A1. (continued)

Parameter	B	Standard error	P-value
(g) Parameter values for the linear mixed model FID ~ elevation+SD+elevation * SD+PPH+distance to veg cover-group size+(1 | site)			
Intercept	−1.20	0.835	0.152
Elevation	0.449	0.285	0.117
SD	1.94	0.709	0.007
PPH	0.125	0.083	0.132
Dist. to veg	−0.006	0.005	0.212
Group size	0.017	0.009	0.067
SD * Elevation	−0.453	0.241	0.062

[a] Marginal R^2: 0.418, conditional R^2: 0.418, $N = 194$,
[b] Marginal R^2: 0.430, conditional R^2: 0.439, $N = 218$,
[c] Marginal R^2: 0.437, conditional R^2: 0.439, $N = 214$,
[d] Marginal R^2: 0.410, conditional R^2: 0.410, $N = 198$,
[e] Marginal R^2: 0.441, conditional R^2: 0.441, $N = 214$,
[f] Marginal R^2: 0.412, conditional R^2: 0.412, $N = 198$,
[g] Marginal R^2: 0.417, conditional R^2: 0.417, $N = 194$.

Table A2. Variables collected in the field and their definitions

Variable	Definition
SD	The distance (m) between the observer and the focal bird when the observer began to approach the bird
AD	The distance (m) between the observer and the focal bird when the bird first showed signs of being alarmed (e.g., fluffing feathers)
FID	The distance (m) between the observer and the focal bird when the bird began to flee
Elevation	The elevation (m) at the site of the flush
Latitude	The latitude at the site of the flush
Wind speed	The wind speed at the time of the flush, measured using the Beaufort wind scale
On ground or in tree (0/1)	The observer recorded a 0 if the bird was on the ground, or a 1 if the bird was perched in a tree at the time of the flush
Height in tree	For birds perched in trees, the observer recorded the height off the ground (m) that the bird was located at the time of the flush
Group size	The number of conspecifics within 10 m of the focal bird at the time of the flush
Distance to vegetation cover	The distance (m) between the focal bird and the nearest vegetation (shrub, grass, tree) at the time of the flush