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Publication Date

2019

Peer reviewed|Thesis/dissertation

UNIVERSITY OF CALIFORNIA

Los Angeles

Avian anti-predator behavior
along elevational and latitudinal gradients

A thesis submitted in partial satisfaction
of the requirements for the degree Master of Science
in Biology

by

Madelin Sue Andrade

2019

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ABSTRACT OF THE THESIS

Avian anti-predator behavior
along elevational and latitudinal gradients

by

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Master of Science in Biology

University of California, Los Angeles, 2019

Professor Daniel T. Blumstein, Chair

Flight-initiation distance (FID), the distance between an individual and experimenter when it begins to flee, can be used to quantify risk-assessment. Amongst 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, the Oregon form of 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, 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 have to modify them based on both latitude and elevation.

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

The thesis of Madelin Sue Andrade is approved.

Thomas Bates Smith

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Daniel T. Blumstein, Committee Chair

University of California, Los Angeles

2019

I dedicate this thesis to my mother, father, and older brother, for their unwavering love and support.

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Introduction

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; Møller 2015). Predator behavior that is associated with increased risk or danger should motivate animals to flee at larger distances. For example, certain species of birds flee at greater distances when two humans approach them as opposed to one (Geist et al. 2005). FID is correlated with predator density; birds have greater flight-initiation distances when predator density is higher (Stankowich and Blumstein 2005; Møller et al. 2015). A prey's distance to refuge and predator approach speed are 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). 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 flight initiation distance 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. While this may be explained by actual

predation risk, because bird species experience a higher level of predation in the tropics than at higher latitudes (Schemske et al. 2009), 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 that individuals of a species that are studied at higher altitudes will respond similarly to those individuals in higher latitudes. However, a recent study showed that an increased level of predation at higher elevations has driven birds to reduce their clutch sizes with increasing altitude (Dillon and Conway 2017), 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.

To mitigate these deleterious effects of humans, wildlife managers often create buffer zones—areas with restricted human access—to protect animals from human disturbance and they use FID to help create them (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 altitude, a species' buffer zone may have to be more dynamically managed. Our research identifies the degree to which the effect of altitude mimics that of latitude for a model avian species, the dark-eyed junco (*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 et al. 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. 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 flight initiation distances at seven 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), latitude (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 (Cooper and Blumstein 2015). Using binoculars, dark-eyed juncos were identified from afar. After a positive identification, we approached each bird by walking towards it in a straight line and at a constant speed (ca. 0.5 m/s). The distance at which we began to approach a bird was recorded as the Starting Distance (SD). The distance at which the bird first showed signs of being alarmed (i.e., the bird ruffled its feathers or oriented its body towards the observer) was recorded as the Alert Distance (AD), and the distance at which the bird began to flee was recorded as the Flight Initiation Distance (FID). While completing the flush, we dropped a flagged marker at each distance of interest and then placed a marker where the bird

was located before flushing. We 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 birds perched in trees, we determined the direct flight-initiation distance using the Pythagorean theorem where,

$FID_{\text{direct}} = \sqrt{(\text{indirect FID})^2 + (\text{height in tree})^2}$. We also determined the direct starting distance using a similar equation where, $SD_{\text{direct}} = \sqrt{(\text{indirect SD})^2 + (\text{height in tree})^2}$.

These values were used for all subsequent analyses. For each flush, observers recorded the wind speed using Beaufort Scale. Additionally, observers recorded the number of conspecifics within 10 m of the focal bird (group size), whether the focal bird was on the ground or in a tree, and the distance, in meters, from the focal bird to the nearest vegetation cover.

Observers ($n = 3$) 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 two weeks out of the field, or every six weeks otherwise. 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). We noted the weather and the windspeed on the Beaufort scale at the start of each experiment. For subsequent analyses, data were only included for times when it was not raining and when wind speed was ≤ 3 on the Beaufort scale.

In addition to FID data, we counted sightings of aerial and terrestrial predators while in the field collecting FID data. However, because only two ground predators were sighted, we limited

our statistical analyses to potential junco-eating raptors (Cooper's hawk *Accipiter cooperii*, red-tailed hawk *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 distribution.

We fitted two sets of general linear models to explain variation in FID: $FD \sim SD + \text{elevation} + SD * \text{elevation}$, and $FD \sim SD + \text{latitude} + SD * \text{latitude}$. 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. In addition, we fitted the junco data to additional models to test for an effect of PPH on FID: $FD \sim SD + \text{elevation} + SD * \text{elevation} + \text{PPH}$, $FD \sim SD + \text{latitude} + SD * \text{latitude} + \text{PPH}$ and $FD \sim SD + \text{PPH} + SD * \text{PPH}$. R^2 is an appropriate criterion for comparison because the models have the same number of parameters. We included the interaction terms because if the interaction term were significant, the effect of SD on FID likely changes with varying elevation (or latitude) (Blumstein et al. 2015). We used partial eta squared to evaluate the effect size of each variable. 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 two 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. In addition, we obtained visitation data from each UCNRS site and averaged the number of people that visited the site over a five-year period. We correlated 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 seven sites with an average of 31 ± 17 FID measurements at each site and found that both elevation and the interaction between elevation and SD had a significant effect on FID. The results are summarized in table 2.

After controlling for SD, a significant amount of the variation in FID was explained by both elevation ($P = 0.034$; Table 2a) and the interaction between elevation and SD ($P = 0.006$; Table 2a). FID increased as elevation increased. FID also increased with increasing SD, but this relationship was less steep as elevation increased.

When controlling for SD, no significant variation in FID was explained by either latitude ($P = 0.297$; Table 2b) or by the interaction between latitude and SD ($P = 0.219$). Additionally, the model including latitude and latitude*SD explained less variation in FID (adjusted $R^2 = 0.374$; Table 2b) than the model that included elevation and elevation*SD (adjusted $R^2 = 0.423$; Table 2a).

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 two 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 the ground ($P = 0.036$), which was driven by one site (White Mountain Research Center).

When we added the covariates to our main models, three of them led to slightly larger adjusted R^2 than that in our main model (see Appendix Table A1a-c). However, in no case were the individual covariates significant and their addition explained less than one percent of the variation in FID. Therefore, the covariates did not change our interpretation of the main results and we focus on interpreting models without these covariates.

After controlling for SD, predator sightings per hour did not explain any significant variation in our FID measurements. Therefore, the frequency of predator sightings likely did not confound our evaluation of the effects of elevation and latitude. While not significant, there were fewer predator sightings per hour at higher elevations when compared to lower elevations ($r = 0.566$, $P = 0.184$). Finally, there was no relationship between 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.

Discussion

This study has begun to uncover the effects of elevation on risk assessment in birds. Our study found that elevation explained a significant amount of variation in FID, with FID *increasing* as elevation increased. Thus, elevation and latitude appear to have opposite effects on FID, based on previous studies on birds that have found that FID decreases with increasing latitude (Díaz et al. 2013; Blumstein et al. 2016; Samia et al. 2017). These results are not an artifact of juncos living in urban areas at lower altitudes and rural areas at higher altitudes because all FID data was collected at protected research reserves and where 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 between elevational and latitudinal gradients within our study area. 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 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). If the number of predators detected was not representative of actual predation pressure at higher elevations, this could explain why PPH could not explain any significant variation in our study. Further research is needed to understand how predation pressure precisely changes along elevational gradients.

In addition to elevation being a significant main effect, it also had a significant interaction with SD. At lower elevations, FID increased with increasing SD. At higher elevations, FID also increased with increasing SD, but less so. Therefore, elevation influences the relationship between SD and FID. It is possible that birds have more environmental stressors at high elevations (decreased food abundance, decreased food quality, etc.), such that it may be more costly to flee an approaching threat, and thus 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 (Zuberogitia 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. To evaluate this, 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 three coastal cities (Santa Barbara, CA; Portland, OR; Woodinville, WA), obtained from the National Centers for Environmental Information. The cities have an elevational range of 3.3m, 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 three inland cities (Bishop, CA; Bend, OR; 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 explains more variation in FID than latitude, these findings may have direct implications on how natural areas are managed; those designing setback zones to reduce human impact on birds 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.

Acknowledgements

We thank the following UC Natural Reserve System sites for permission to conduct our field work: Sedgwick Reserve, James San Jacinto Mountains Reserve, Hastings Natural History Reservation, Blue Oak Ranch Reserve, White Mountain Research Center, Sagehen Creek Field Station, and Angelo Coast Range Reserve. We also thank their respective Reserve Directors for their assistance: Kate McCurdy, Jennifer Gee and Andrea Campanella, Vincent Voegeli, Zac Harlow, Glenn MacDonald, Jeff Brown, and Peter A. Steele. This work was generously supported by grants to M.A. from: the Pasadena Audubon Society, the UCLA Department of Ecology and Evolutionary Biology, and the White Mountain Research Center. In addition, D.T.B is supported by the US National Science Foundation. Birds were studied under UCLA IUCAC # 2000-147. We thank Ani Antaramian and Ghislene Adjaoute for assistance in the field, as well as Dan Cooper and members of the Blumstein lab for advice and constructive comments on previous drafts.

APPENDIX

Table A1: Results from linear models explaining variation in dark-eyed junco flight initiation distance with covariates included.

(a) Parameter values for the linear model $FD \sim \text{elevation} + SD + \text{elevation} * SD + \text{distance to veg cover} + \text{ground} + \text{group size}$

Parameter	B	Std. Error	P-value	partial η^2
Intercept	-1.28	0.843	0.131	
Elevation	0.476	0.288	0.010	0.053
SD	2.20	0.681	0.001	0.339
Dist. to veg	-0.006	0.005	0.200	0.009
On ground	-0.030	0.036	0.410	0.004
(0/1)				
Group size	0.015	0.010	0.113	0.013
SD*elevation	-0.525	0.235	0.027	0.026

Adjusted R²: 0.402

N=194

(b) Parameter values for the linear model $FD \sim \text{elevation} + SD + \text{elevation} * SD + \text{on ground}$

Parameter	B	Std. Error	P-value	partial η^2
Intercept	-1.24	0.741	0.097	
Elevation	0.456	0.253	0.073	0.061
SD	2.20	0.605	<0.001	0.370

On ground (0/1)	-0.048	0.031	0.121	0.113
SD*Elevation	-0.514	0.209	0.015	0.028

Adjusted R²: 0.426

N=218

(c) Parameter values for the linear model $FD \sim \text{elevation} + SD + \text{elevation} * SD + \text{group size}$

Parameter	B	Std. Error	P-value	partial η^2
Intercept	-1.56	0.736	0.036	
Elevation	0.561	0.251	0.027	0.050
SD	2.39	0.604	<0.001	0.356
Group size	0.017	0.009	0.069	0.016
SD*elevation	-0.592	0.208	0.005	0.037

Adjusted R²: 0.426

N=214

Table 1: Field station latitude, average elevation of flushes, average annual temperature and number of days each UCNRS site was visited.

UCNRS Site	Average Elevation (m)	Latitude	Average Annual Temperature (°C)	Days Visited
James San Jacinto Mountains Reserve	1645	33°48'32.7"	12.1	16
Sedgwick Reserve	105	34°41'35.0"	15.5	20
Hastings Natural History Reservation	525	36°22'46.6"	13.5	16
Blue Oak Ranch Reserve	571	37°22'52.8"	13.6	26
White Mountain Research Center	3117	37°29'59.1"	3.28	10
Sagehen Creek Field Station	1936	39°25'56.2"	-0.66	13
Angelo Coast Range Reserve	439	39°43'06.1"	11.5	12

Table 2: Results from linear models explaining variation in dark-eyed junco flight initiation distance.

(a) Parameter values for the linear model $FID \sim SD + Elevation + SD*Elevation$.

Parameter	B	Std. Error	P-value	Partial η^2
Intercept	-1.460	0.729	0.046	
SD	2.340	0.599	<0.001	0.360
Elevation	0.531	0.249	0.034	0.057
SD*Elevation	-0.573	0.206	0.006	0.035

Adjusted R²: 0.423

N=218

(b) Parameter values for the linear model $FID \sim SD + Latitude + SD*Latitude$.

Parameter	B	Std. Error	P-value	Partial η^2
Intercept	1.56	1.490	0.296	
SD	-0.808	1.260	0.522	0.377
Latitude	-0.042	0.040	0.297	0.005
SD*Latitude	0.042	0.034	0.219	0.007

Adjusted R²: 0.374

N=218

(c) Parameter values for the linear model $FID \sim SD + PPH + SD*PPH$

Parameter	B	Std. Error	P-value	Partial η^2
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Intercept	0.226	0.119	0.057	
SD	0.504	0.101	<0.001	0.311
PPH	-0.410	0.337	0.224	0.062
SD*PPH	0.503	0.271	0.065	0.016

Adjusted R²: 0.415

N=218

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