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Individual variation and population-level changes in escape behavior across urban and non-urban dark-eyed juncos (*Junco hyemalis*) in southern California

A thesis submitted in partial satisfaction of the requirements

for the degree Master of Science in Biology

by

Hayley Stansell

2018

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ABSTRACT OF THE THESIS

Individual variation and population-level changes in escape behavior across urban and non-urban dark-eyed juncos (*Junco hyemalis*) in southern California

by

Hayley Stansell

Master of Science in Biology

University of California, Los Angeles, 2018

Professor Peter Nicholas Nonacs, Co-Chair

Professor Pamela J Yeh, Co-Chair

An important goal of ecology is to examine what differentiates urban-adapted populations from their non-urban ancestors and urban-intolerant species. A major stressor in urban environments is direct disturbance by human activity, and the key to success may be to be sufficiently plastic so as to tolerate those interactions. By studying escape behavior we can ask how wildlife respond to threats and many species view humans as threats. But most studies of escape behavior do not track individuals and thus cannot study individual plasticity. We compared flight-initiation distance and distance fled from approaching humans across urban and non-urban populations of individually-marked dark-eyed juncos (*Junco hyemalis*) in southern California. Both urban and non-urban juncos primarily use information about proximity of an approaching threat to

determine escape decisions. We compared approaches towards marked birds and found evidence for overall urban habituation to people on a population level, evidenced by attenuated flight initiation distances and distances fled relative to non-urban birds. As a population, we found that urban juncos do not consistently either habituate or sensitize to humans when repeatedly tested within or across days. At an individual level, however, urban juncos do exhibit variability in habituated or sensitized responses. What factors explain this behavioral variability, whether there is an urban-rural gradient in within-population variation, and whether or not this individual variability has fitness consequences for reproductive success needs further study.

The thesis of Hayley Stansell is approved.

Daniel T Blumstein

Peter Nicholas Nonacs, Committee Co-Chair

Pamela J Yeh, Committee Co-Chair

University of California, Los Angeles

2018

To my many academic mentors over the years which encouraged me in my studies, including Mrs. Grace Coan and Dr. Rob Dunn. I also wish to dedicate this to my peers and friends who have been tremendously supportive - my success would not have been possible without you.

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design and theory, facilitated data collection for the study, and also contributed to the editing of the manuscript. Lastly, Peter Nonacs also offered guidance in study design, facilitated data collection for the study, and contributed to editing of the manuscript.

Introduction

Urbanization poses a rapidly-growing threat to wildlife worldwide, including native birds. Depending on the species, urban habitat may contain more or less food, reduced or altered predation pressure, and present an overall change in habitat quality (Chace and Walsh 2006, Partecke et al. 2006, Møller and Ibáñez-Álamo 2012). Furthermore, urban settings contain stressful and generally detrimental stimuli that include noise, pollution, and human activity. Nevertheless, some species prosper in the urban environment while others suffer or are pushed out entirely (Chace and Walsh 2006; Schlesinger et al. 2008; Møller 2010). Understanding how species adapt and change to survive in the city can inform conservation and urban planning decisions to support the maintenance of native biodiversity in proximity to human activity (Fernández-Juricic et al. 2001a, Chace and Walsh 2006, McKinney 2006, Sih et al. 2011, Aronson et al. 2014).

Previous research suggests that direct disturbance by human activity may be one of the primary stressors faced by urban birds (Partecke et al. 2006, Strasser and Heath 2013). Exposure to vehicle traffic, noise, domestic animals and pedestrians can limit fitness and quality of life for urban birds (Partecke et al. 2006, Strasser and Heath 2013), to the degree that some species are wholly excluded. Schlesinger et al. (2008) found that intensity of human activity strongly influences species richness among urban birds at a local scale, more strongly than habitat loss or alteration. To understand why, it is important to look at behavioral responses to human activity.

Escape behavior is one way to understand the cost of human disturbance on wildlife based on the premise that wildlife perceive humans as a predation risk (Fernández-Juricic et al. 2001a, Frid and Dill 2002, Blumstein 2013). Escape decisions should reflect the balance between

the cost of fleeing versus the risk of staying in place (Ydenberg and Dill 1986, Blumstein 2003, Cooper and Blumstein 2015). Decisions may vary depending on the economics of escaping, lost opportunity cost, and perceived risk of predation. All of these factors vary between urban and non-urban populations of birds and indeed, there is abundant literature illustrating large and consistent differences in escape behavior between urban and non-urban birds (Møller 2008, Mikula 2014, Samia et al. 2017).

However, to date most of these studies focus only on population-level differences. Variation within and between individual birds is worth studying because the composition of personalities present in different populations can reflect ecological and evolutionary forces which maintain variation and drive adaptation to new environments (reviewed in Réale et al. 2007). Only a few studies have sought to measure individual variation in the field, and fewer still have gotten series of repeated samples of marked individuals. Territory fidelity is sometimes used as a substitute for banding birds (Carrete and Tella 2010), but the limitation there is that this restricts study to species with very high fidelity. Those few which have sampled marked individuals in the field have collected few repeated measures (2-6 measures, Garamszegi et al. 2015; approx. 2-4 measures, Carrete and Tella 2013) per individual or sampled few individuals (9 individuals, Runyan and Blumstein 2004; however see also Petelle et al. 2013). Carrete and Tella (2010, 2013) have sampled FID in burrowing owls (*Athene cunicularia*) over short and long time scales, and are one of the few studies to do so to date (see also Petelle et al. 2013). They found high individual consistency among both urban and non-urban owls and evidence for inter-individual variation in mean FID in both populations. Repeated samples allowed them to detect a possible sensitization response in non-urban birds over the adult lifespan, and suggest no evidence for habituation in either population either within or across years. This study, therefore,

is novel in using free-living individually-marked juncos to gather many repeated samples of FID over very short time intervals (within-day) and longer intervals (across-days), with up to 16 samples collected per individual.

Dark-eyed juncos (*Junco hyemalis*) are an ideal species for research into personality with respect to adaptation to urban environments; widespread across North America and successful in cities, they are easy subjects for FID studies as they both forage and nest on the ground (Nolan Jr et al. 2002). Their long history as a model species (Nolan Jr et al. 2002) is coupled to a rich body of work on a population which recently colonized the campus of the University of California, San Diego. These studies illustrate rapid evolutionary and behavioral changes in physiology, morphology, and behavior occurring over the course of a few decades (e.g., Rasner et al. 2004a; Yeh 2004; Yeh and Price 2004; Newman et al. 2006; Atwell et al. 2012; Atwell et al. 2014). This study builds on this body of work by contributing data from another Southern California population of juncos which are abundant across the campus of the University of California, Los Angeles.

We had two goals. First, to examine whether urban and non-urban dark-eyed juncos (*Junco hyemalis*) vary either qualitatively or quantitatively in response to human activity as measured through flight-initiation distance (hereafter FID) and distance fled (DF). It is possible that urban populations may essentially be human-tolerant subsets of individuals from non-urban ancestor populations (Carrete and Tella 2010, 2011; Møller 2010). Given this, we would hypothesize that urban and non-urban birds' escape decisions should be predicted by the same factors. Second, to collect repeated data on individual urban and non-urban birds to map the variability of behavioral responses between a successfully-breeding urban population and a non-

urban population. Doing so would shed light on whether the explanation proposed by Carrete and Tella (2011) is supported, or whether an alternative explanation is appropriate. It is possible that urban birds have been selected to be disturbance tolerant (Møller 2008, Carrete et al. 2016) or have habituated through repeated exposure to human activity (Fernández-Juricic et al. 2001b, Stankowich and Blumstein 2005, Rodriguez-Prieto et al. 2009, Blumstein 2016). However, we ultimately focus on individual variation among urban birds, because it was not possible to collect repeated samples with the much warier non-urban population. By differentiating between inter-individual variation and within-individual plasticity, we can identify the roles each play in adaptation to the urban environment (Møller 2010, Carrete and Tella 2011).

Methods

Study sites

One observer (H. Stansell) collected escape behavior data for individuals within an urban (the UCLA campus) and non-urban population (UC James San Jacinto Mountains Reserve and surroundings) of dark-eyed juncos (*Junco hyemalis*). UCLA is located in the northwest portion of the Los Angeles Basin (34° 4' 10" N, 118° 26' 43" W) at approximately 100 to 150 meters elevation. Summers are hot and dry, with rainfall occurring mostly during a cool winter (average temp. 14-22 °C over the year, 44.5 cm average annual precipitation). With a student body of over 45,000 (UCLA Office of Academic Planning and Budget 2017), there is abundant human activity across the campus throughout most of the year. Pedestrian activity fluctuates throughout the day in accordance with class schedules. The largely urban 170 hectare campus contains a mix of largely non-native plant species popular to southern California such as eucalyptus (*Eucalyptus*

spp.) and Moreton Bay fig (*Ficus macrophylla*), planted around large patches of lawn. The James Reserve (33° 48'30" N, 116° 46'40" W) is located in the San Jacinto Mountains around 300 km east of UCLA campus. The reserve elevation is approximately 1650 meters. Compared with UCLA, the James and adjacent areas have a cooler and wetter climate (4-19 °C average annual temperature range, 66 cm average annual precipitation) and has much lower pedestrian activity. All together, the study population was sampled in 20 hectares of habitat including montane riparian forest and mixed conifer and hardwood forest with open understory consisting of gravel roads, parking areas and grassy meadows.

Color-banding individuals

Prior to collecting behavioral data, birds were individually marked at each site (74 at UCLA, 29 at James) with USGS aluminum bands, and a unique set of color bands. At each site, the observer avoided collecting behavioral data a given junco until approximately one week after that individual was banded. Furthermore, in the case that both individuals of a mated pair were sampled, we avoided sampling the two simultaneously and allowed a week rest period between each.

Sampling methodology

Initially, our goal was to collect repeated measures on individuals on both a short time scale (within a day) and on a longer time scale (over a 4 day period). Unfortunately, a combination of factors at the James prohibited effective repeated sampling. The overall terrain was more heterogeneous with many areas of an individual's territory precluding controlled approaches. Individual birds often could not be found or approached within or across days and overall were comparatively more flighty than those on UCLA campus; they tended to move more often and further within their territories, regardless of being approached or not. Thus, we focused

our repeated sampling on the urban population. In total, we collected 278 individual approaches across 23 individuals at UCLA from February to July of 2017, and 35 approaches across 20 individuals at the James Reserve through June and July of 2017. At both sites, the majority of data were collected between 08:00 and 13:00 h.

Relaxed (foraging or looking but not alarm calling) adult juncos that were on the ground were flushed following the Blumstein (2006) protocol commonly used to study FID (Martín et al. 2008, Møller 2010). Given the goal to sample individuals consecutively, we elected to use markers to track SD and FID (different colored markers for different iterations), and visually estimate DF to avoid the need to approach the individual and risk unintentionally eliciting escape behavior. Birds were always approached when on the ground and exposed from vegetation, with no obstacles or other juncos between the observer and the focal bird. This ensured consistent, readily-detectable approaches to each individual (Frid and Dill 2002, Fernández-Juricic et al. 2004, Samia et al. 2016, Tätté et al. 2018). The observer approached a focal individual in a straight line, dropping a colored marker at the location where the experimental approach began, a colored marker at the observer location when the focal subject fled, and a colored marker at the location from where the focal subject fled. It was important to mark the location from which the bird fled to avoid FID being confounded by incidental movement of the focal bird, given that the majority of individuals were actively foraging during observer approach. This meant that the initial location of an individual at the start of approach was rarely the same as the location from which an individual fled. Starting distance (SD) and flight initiation distance (FID) were measured based on these distances by converting the paces between these markers to meters. We also recorded estimated the distance fled (DF) for each interaction when possible by visually estimating the horizontal and vertical distance travelled in meters, then converting to a Euclidian

distance. DF was later binned into distances of under ("near") and over 2 meters ("far") in order to account for poorer estimation ability with longer distances fled, some of which took the bird out of sight of the observer (see Analysis). For each approach, a set of predictor variable data were collected - time of day, number of conspecifics and heterospecifics within a 5 m radius of the focal bird, distance to nearest cover, pedestrian density (high or low), and manner of escape (hopping, flying, or hopping followed by flight). Pedestrian density was recorded categorically as high or low where low was defined as < 5 people per minute crossing a 10 meter sample transect in the immediate vicinity of the approach (see Appendix: Pedestrian Analysis) and high was defined as ≥ 5 people/min.

Analysis

We conducted all statistical analyses using R version 3.4.2 (R Core Team 2017). Escape behaviors (FID and DF) and their predictor variables (e.g., starting distance, distance to cover) were compared between urban and non-urban juncos using t-tests and linear regression. Given the difficulty collecting repeated samples on non-urban birds, these between-site analyses only incorporated the first encounter per individual. We compared mean and variation in mean FID using Welch's t-test and the F-test for equality of variances, respectively. We then used variable-appropriate tests to examine whether contextual variables influence FID. We fitted linear models to assess the relationship between starting distance and FID, and in addition, employed the Phi Index (Φ , Samia and Blumstein 2014) to test the relationship a second way. The Phi Index, similar to Pearson's chi-square test, tests the relative deviance of the SD:FID relationship from a 1:1 test relationship, better encapsulating the nature of escape distance data. For remaining contextual variables, we used Welch's t-tests to examine between-site differences in continuous

variables, and for differences in categorical and ordinal predictors of FID within-site, while continuous relationships were tested via linear regression. This process was repeated to analyze distance fled between sites.

We used linear (FID) and logistic (DF) mixed-effects models to study individuals' responses to repeated approaches on the UCLA campus. Models were fitted using the R package "lme4" v1.1-14 (Bates et al. 2015) (supporting package "car" v2.1-6 (Fox and Weisberg 2011)). We elected to use logistic models for DF given the that some individuals flew too far away to reliably estimate DF on continuous scale. We began by generating a null model containing individual ID as a random intercept, then iteratively incorporated fixed effects (contextual variables) into the model, manually conducting stepwise selection to find the combination of fixed effects which generated the lowest AIC value for the model. Each predictor variable was added to the model with AIC recorded for each stepwise addition, then variables were selectively removed depending on their effect on AIC relative to that of the null model. In cases where a fixed effect resulted in only a minor decrease in AIC, we conducted likelihood ratio tests using "lmerTest" v2.0-33 (Kuznetsova et al. 2016) to test for significance of that fixed effect. If this test indicated that the fixed effect offered no significant improvement in the model, we discarded that effect. After selecting a model via this process, we conducted a likelihood ratio test to determine whether inclusion of fixed effects improved explanatory power over the null intercept-only model. We again employed the likelihood ratio test to evaluate whether either the inclusion of trial iteration as a fixed effect or as a random slope significantly improved the explanatory power of the model over the model containing contextual predictor variables and the random intercept. Finally, we compared best mixed-models against their fixed effects-only counterparts via likelihood ratio test using "RLRsim" v3.1-3 (Scheipl et al. 2008) (supporting packages

"MASS" v7.3-47 (Venables and Ripley 2002) and "arm" v1.9-3 (Gelman and Su 2016)) to determine whether individual differences among birds explained a significant portion of the variation in observed behavior. Where individual was a significant random effect in models, adjusted repeatability was calculated using code provided by Jean-Nicolas Audet (pers. comm.), modified from "rptR" v0.9.21 (Stoffel et al. 2017). This repeatability value provides the approximate amount of variation explained by individual effect in the model. Assumptions for selected models were evaluated by plotting residuals versus fitted values, and examining normality of residuals. Lastly, linear regressions tested for individual consistency of reaction norms across long and short sampling intervals. Figures shown were plotted using ggplot2 v2.2.1 (Wickham 2009) and lattice 0.20-35 (Sarkar 2008).

Results

Comparison of Urban and Non-urban Populations

In the analysis that used only the first flushes, urban juncos had significantly shorter flight initiation distances (Fig. 1a; $p < 0.001$, Welch's t-test, $t = 6.56$, $df = 23.35$) than non-urban juncos (urban mean = 3.25 m, non-urban mean = 10.35 m). In addition, variation in observed FID was smaller at the urban site (Fig. 1a; urban SD = 1.63 m, non-urban SD = 4.48 m; $F = 7.88_{19,21}$, $p < 0.001$, F-test for equality of variances). FID among non-urban juncos at the James Reserve was strongly influenced by starting distance (Fig. 2a: $p < 0.001$, adj. $R^2 = 0.47$, linear regression), whereas among urban juncos, FID seemed to be less strongly related to starting distance (Fig. 2b; $p = 0.328$ linear regression, however see Repeated Sampling for urban population). This result is corroborated by the Phi Index (Samia and Blumstein 2014), where

non-urban $\Phi = 0.64$ ($p = 0.012$, $n = 20$), and urban $\Phi = 0.41$ ($p = 0.94$, $n = 22$). Urban juncos had much shorter starting distances ($p < 0.001$, Welch's t-test, urban mean = 8.20 m, SD 1.77, non-urban mean = 16.11 m, SD 6.47). Furthermore, there was a significant difference in how closely urban or non-urban birds foraged beside sources of cover. Birds at UCLA foraged much more closely to cover than their non-urban counterparts ($p < 0.001$, Welch's t-test; urban mean = 1.81 m, SD 1.78, non-urban mean = 4.2 m, SD 2.12); however, distance to cover did not explain any variation in FID at either site ($p = 0.41$ urban, $p = 0.36$ non-urban; linear regression). Other predictor variables tested failed to significantly predict FID. The presence of nearby conspecifics (urban $p = 0.092$, non-urban $p = 0.74$, Welch's t-test; urban $n = 22$, non-urban $n = 20$) did not predict FID, nor did pedestrian density (urban $p = 0.10$, Welch's t-test; no variation to test for non-urban). Test values for number of heterospecifics, sex of the focal birds, distance to cover, and manner of escape were all non-significant ($p \geq 0.20$).

Comparing distances fled among first flushes, urban juncos responded by travelling much shorter distances on average than non-urban juncos (Fig. 1b; urban mean = 5.2 m, non-urban mean = 14.6 m; $p < 0.0054$, Welch's t-test. DF was \log_{10} transformed only for between-site comparison of DF). Most first responses were to fly (81% urban, 89% non-urban), so manner of escape does not explain the difference between sites in distances travelled. The lack of significant predictor variables for DF could be due to the low number of unique individuals observed at each site (urban $n = 22$, non-urban $n = 20$ individuals). Distance to cover did not predict distance fled in any regressions ($p = 0.75$ urban, $p = 0.63$ non-urban; linear regression), nor did starting distance or other contextual variables tested, including FID, number of conspecifics, number of heterospecifics, and sex of the focal bird.

Individual Variation - Urban Population

For within-day mixed effects models of FID ($n = 22$ birds, 72 observations) we selected a mixed model with SD as a fixed effect (Table 1). Starting distance was also the only fixed effect retained in mixed models for across-days data ($n = 23$ birds, 72 observations; Table 1).

Increasing starting distance was associated with an increase in FID. Distance fled was predicted by FID on both time scales (within-day $n = 12$ birds, 53 observations; across-days ($n = 23$ birds, 61 observations), with an increase in FID associated with an increase in DF (Table 2). Distance to cover was also retained as a fixed effect in the model for across days, but was not associated with a change in DF over short time scales (Table 2 & A4).

After controlling for fixed effects, we found that trial number explained no significant variation in FID (Tables A1&2) or DF (Tables A3&4) over either sample period. When models containing trial number as either a fixed effect or a random slope were compared to a random-intercept only model, trial failed to significantly improve model fit. These results tell us that repeated flushes were not associated with a predictable change in FID or DF dependent on initial FID or DF of an individual bird. Therefore, we found no evidence for habituation or sensitization for the sample population as a whole.

We did, however, find evidence for significant variation in between-individual responses, and some evidence for individual consistency. Likelihood ratio tests comparing mixed models against linear models indicated a strong individual effect ($p < 0.01$ for both time scales) on FID. Similarly, adjusted repeatability tests suggest a large proportion of the variation in FID was explained by individual bird after controlling for fixed effects ($R = 0.46$ within-day, $R = 0.43$ across-days, Table 1). Surprisingly, we found no evidence for an individual effect on DF (Tables

A3 & A4). Thus, we selected a simple binary logistic regression with no random effects to model variation in DF (Table 2).

Behavioral reaction norms of individual birds appear to be consistent across the temporal scales sampled. Slopes of each individual's reaction norms for FID within one day and across days are significantly correlated with one another (Fig. 3a; adj. $R^2 = 0.24$, $p = 0.0256$, linear regression). Slopes for distances fled also appear correlated across both time scales (Fig. 3b; adj. $R^2 = 0.45$, $p = 0.00180$, linear regression). However, reaction norm slopes for individual FID do not predict the reaction norms for individual DF (adj. $R^2 = 0.006$, $p = 0.312$, linear within-day; adj. $R^2 = -0.05$, $p = 0.641$ across-days). Individual behavioral responses varied widely, with some birds exhibiting slopes consistent with habituation while others showed slopes suggesting sensitization (Fig. 4a,b). This reflects results from mixed models analyses of FID and DF, indicating urban population of juncos did not consistently habituate or sensitize at the population level.

Discussion

Overall, this study illustrates that urban and non-urban juncos significantly differ in their escape behavior. Urban juncos have strongly attenuated flight initiation distances and distances fled when compared with non-urban juncos. In addition, their range of behavioral response is more limited, with less variation in FID and DF. Escape decisions do not appear to be strongly driven by cues from the surrounding environment. Rather, both FID and DF seem most strongly driven by the distances that precede them (starting distance for FID, and FID for DF). We also found that individual urban juncos were both consistent in their behavior and variable from one

another, and find that these individual differences are a significant determinant of FID, but not DF.

In both populations sampled, the primary drivers of FID and DF appear to be distances between the observer and individual bird. Starting distance has a linear, positive relationship with FID in non-urban juncos, and while not observed with unrepeated data, starting distance is the strongest predictor variable for FID in mixed models of urban junco behavior. The difference in average starting distances between populations is likely a large determinant of the observed differences in FID (Blumstein 2003). Starting distance is often positively associated with FID because monitoring potential threats requires attention (Samia and Blumstein 2015), so if a bird is able to identify a threat earlier, it should likewise flee sooner. A large SD also affords individuals more time to assess, and therefore vary, their escape decisions (Cooper 2006). Together, these concepts may explain the reduced mean and variation in FID observed among urban juncos. The lack of a relationship between SD and FID at UCLA could also be due to urban birds having a relatively low D_{\max} (Blumstein 2003), a distance beyond which they do not respond to approaching threats, because the abundant pedestrian activity on campus would otherwise demand too much attention too often (Samia et al. 2017, Tatte et al. 2018). The observer was frequently the only person in the vicinity when approaching non-urban juncos, whereas on the UCLA campus, the observer was one person among a regular flow of pedestrians. Thus, urban juncos may not have assessed the observer as approaching them until they were relatively close (Samia et al. 2017). Tatte et al. (2018) found similar results in their study of escape behavior of over 700 individuals across 17 species of birds. They suggested that the lack of relationship between SD and FID in urban birds is due to having a lower "zone of awareness" (Ydenberg and Dill 1986, Blumstein 2003, Samia et al. 2017).

The strongest predictor for distance fled was FID, with an increase in FID associated with an increase in DF. However, this relationship was only detected in the analysis of repeated samples of urban birds, suggesting DF may also be influenced by other factors. Escape behavior theory suggests DF and FID should be related as both decisions incur a cost (Ydenberg and Dill 1986, Cooper and Pérez-Mellado 2004, Cooper 2009, Cooper and Blumstein 2015), so a reduction in DF alongside FID among urban birds is expected. However, Tätte et al. (2018), was the first study to compare the relationship between FID and DF, found that the relationship between FID and DF for birds was mass-dependent, with small-bodied birds lacking the relationship. This echoes the general relationship between body mass and FID reported across a variety of species (Stankowich and Blumstein 2005, Blumstein 2006, Samia et al. 2015, 2016). For small species such as juncos, short flight distances should be expected due to energy efficiency, more uniform food availability, and relatively abundant cover (reviewed in Tätte et al. 2018). Indeed, urban juncos seem to find many foraging opportunities on lawns (Nolan et al. 2002; Chace and Walsh 2006), and were found significantly closer to cover in this study, which may be an artifact of urban landscape design providing more abundant cover overall. Furthermore, urban juncos may elect to simply move out of the trajectory of the observer and increase distance between themselves and the approaching threat. Our results taken together with results from previous literature indicate that FID may not always predict DF, and that DF may be influenced by a variety of factors (Tätte et al. 2018); however, more study of DF is needed (Cooper and Blumstein 2015).

Variables sampled to describe the setting of each flush (e.g., distance to cover, number of conspecifics) generally failed to predict escape decisions in either population. Only distance to cover was significantly associated with DF among repeated measures of urban birds across days,

and not within days. A bird may consider seeking refuge when initially flushed each day, but base their DF on some other criteria as they are flushed again and again. Furthermore, it is important to consider how refuges are used to avoid predation for a given species (Cooper 1997). Pedestrian activity did not seem to predict FID or DF, in contrast to literature which suggests that birds may adapt their FID in a highly-plastic manner in response to changes in pedestrian density over short time scales (Rodriguez-Prieto et al. 2009, Mikula 2014). It is possible that because there were so many people on the UCLA campus, variation in pedestrian activity on average provided limited information about risk to the juncos. This question requires further study.

The results from our analyses of repeated flushes suggest that individual differences among urban juncos may significantly explain variation in FID, yet individual identity does not seem to explain variation in DF. Exclusion of individual effect in models for DF does not necessarily mean that there is no individual variation in distance fled, only that individual variation lacks predictive power in our model. Overall, repeated samples show that birds which habituate within one day also habituate across days, while others sensitize across both time scales. These data suggest within-individual consistency of response to human disturbance. However, At the population level, urban juncos do not appear to consistently react one way or another. In terms of their mean response, they neither habituate as a whole nor sensitize in FID or DF. These results are consistent with those of Carrete and Tella (2010), who found high within-individual repeatability ($R \approx 0.9$) among burrowing owls (*Athene cunicularia*), as well as considerable variation between individuals resulting in little net habituation or sensitization across the sample population. Echoing our results, they found that individual owls were consistent in how and whether they adjusted their behavioral response to repeated disturbance, and that these individual tendencies vary from bird to bird. Sprau and Dingemanse (2017) tested

the relative effects of plasticity and non-random sorting of behavioral types among great tits (*Parus major*), and found that individual birds did not adjust their behavior across repeated samples, but rather were distributed along an urban gradient such that bolder individuals were in more disturbed areas than shy individuals. Ultimately, these studies and our results suggest that individual plasticity may not directly explain population-level changes in escape behavior associated with urbanization. In fact, they suggest that the observed variation in escape behavior does not reflect plasticity at all, but rather the degree of between individual variation present within each population. The reduced mean and variance in FID and DF among urban juncos, in conjunction with observed within-individual consistency, together suggest that it is not the variation within individuals, but between them that drives these population-level differences in behavior. This supports the notion that urbanized populations of birds originate from ancestor populations with high inter-individual variation in escape behavior (Møller 2010), and constitute a subset of disturbance-tolerant individuals (Carrete and Tella 2011).

Relating reaction norm data to fitness consequences for individuals along an urbanization gradient may tell us about selection pressure acting on personality (Smith and Blumstein 2008, Dingemanse et al. 2010). Arroyo et al. (2017) present support for this idea in their work on harriers (*Circus pygargus*). They found that over a 20 year period of repeated nest checks by observers, the population sampled became significantly more bold in defending their nests as the composition of personality present in the population shifted. Shy individuals had reduced fitness and became less abundant over time, such that the majority of individuals at the end of the study were bold. Future research should further examine how personality among populations along the urban-rural gradient is driven by components of plasticity and genetics (Réale et al. 2007, Miranda et al. 2013). Common garden experiments have demonstrated that morphological and

behavioral differences between urban and non-urban populations likely indicate microevolutionary change (Rasner et al. 2004, Miranda et al. 2013). Successfully collecting repeated data within a species along an urban-non-urban gradient, in conjunction with genetic and fitness data, could parse how each of these sources of individual variation ultimately produces the consistent changes in escape behavior observed (Réale et al. 2007).

The major limitation of this study was the inability to collect repeated measures of non-urban juncos. Often it was impossible to get close enough to resight color bands without disturbing the focal bird. Ultimately, the difficulty in collecting repeated samples among non-urban juncos may reflect the differences in perceived threats experienced by urban and non-urban juncos when approached by an observer. Differences between the urban and non-urban sites may also limit the interpretation of results. The UCLA campus is intricately planted with hedges, herbaceous plants, and trees scattered among a dense built environment, whereas the James Reserve is forest with a generally open understory. Differences in abundance and density of cover between urban and non-urban sites makes interpretation of FID and DF more difficult. Starting distance at UCLA was often restricted due to the more confined habitat structure and presence of other people and wildlife. It might be helpful to conduct further research in the manner of Tätte et al. (2018) and compare between cities and non-urban human settlements, which are likely to have more comparable conditions.

Conclusion

Overall, these results suggest that escape behavior in dark-eyed juncos is driven by the same forces in urban and non-urban settings, though to differing degree. Flight-initiation distance is primarily driven by starting distance, and distance fled driven by FID. As illustrated in

Stankowich and Blumstein's meta-analysis (2005), different taxa base their escape decisions on different factors; nonetheless, universally prey seem to take into account predator behavior (Stankowich and Blumstein 2005, Cooper and Blumstein 2015, Samia et al. 2016), which is reflected by the relationship between SD, FID, and DF. This seems that in the case for juncos, with escape decisions focused on increasing distance between themselves and the approaching threat. Urban juncos behave in a way that suggests they do not view humans as a threat, unlike non-urban juncos. Human activity has minimal effect on behavior at UCLA, and juncos continue to forage and persist across the campus, allowing an observer to get close and often moving only a short distance when flushed. These results raise the question of how much and what kind of anthropogenic disturbance is needed to produce such a change in perceived risk among species able to adapt to urban life. They also call for further research into individual variation in temperament and plasticity within and between species. Understanding how genetic, behavioral, and fitness variation within individuals give rise to urban-adapted populations may prove useful in estimating which species will persist close to human disturbance and inform management practices.

Figures

Figure 1: Box plots illustrating differences in antipredator behaviors between urban and rural juncos. Urban juncos have much shorter FID (plot a; Welch's t-test, $t(23.35) = 6.56$) and DF (plot b; Welch's t-test, $t(22.12) = 2.53$).

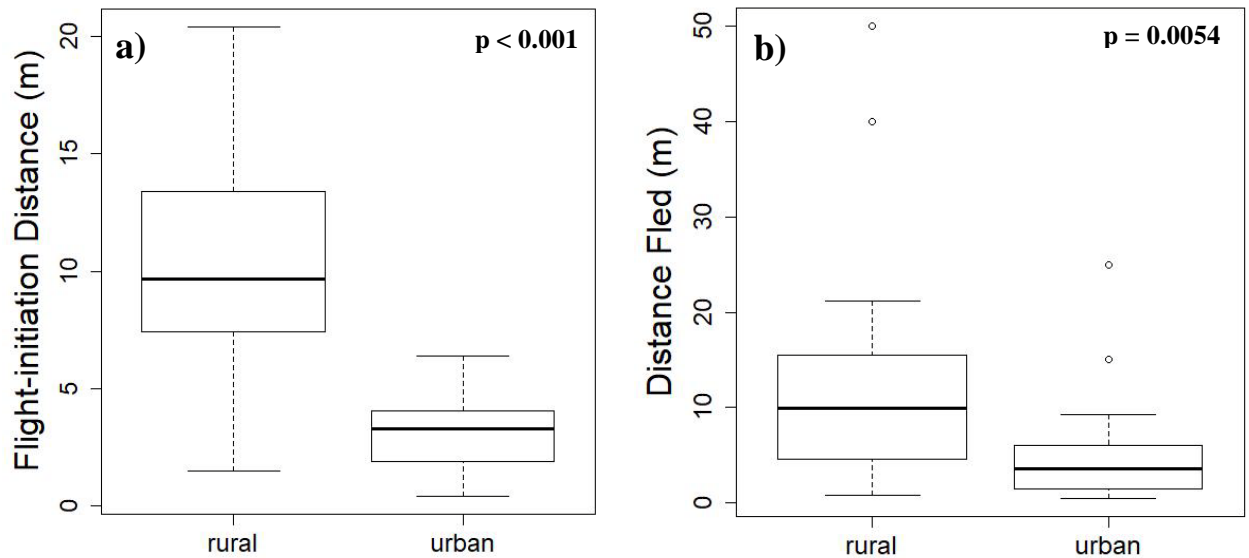


Figure 2: When examining first samples per individual, starting distance significantly predicts FID among rural juncos (plot a; $p < 0.001$, linear regression), but not among urban juncos (plot b; $p = 0.328$, linear regression). The Samia and Blumstein Phi Index (2014) supports the same conclusion (rural $\Phi = 0.64$, $p = 0.012$, $N = 20$; urban $\Phi = 0.41$, $p = 0.94$, $N = 22$).

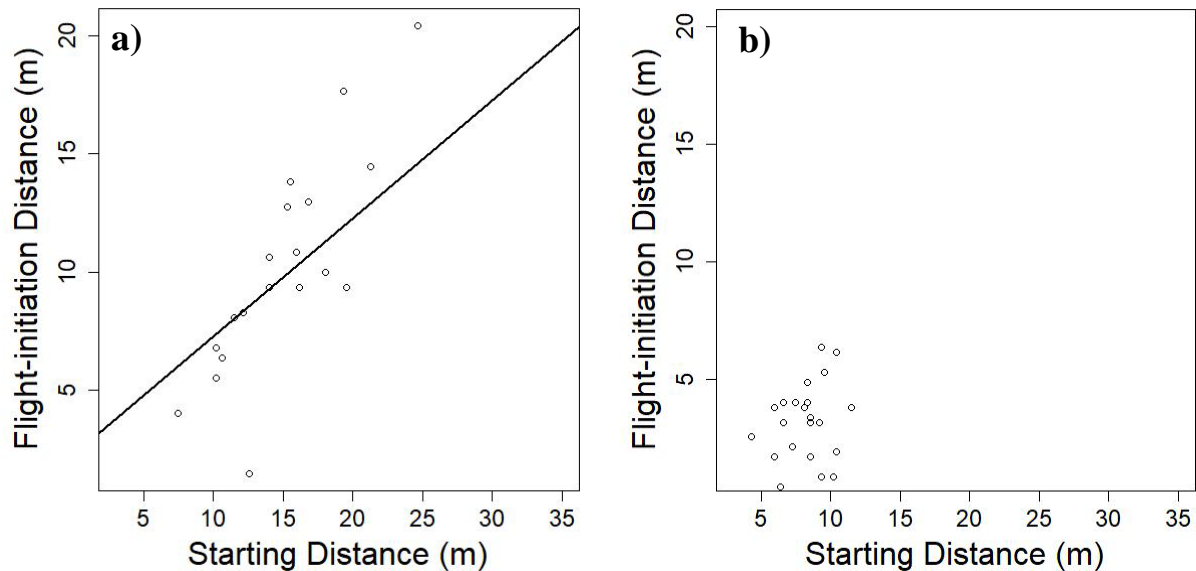


Table 1: Information for fixed and random effects in chosen linear mixed-effects models for flight-initiation distance. Fixed-effects are mean-estimates, while random effects are variance estimates. P-values for fixed effects calculated using "lmerTest" (R package: "lmerTest"). LRT and p-values for the inclusion of random effects calculated using exactLRT (R package: "RLRsim"). Confidence intervals for fixed effects and estimates for random effects calculated using the "stats" base R package.

Sample interval	Fixed effect	Estimate (SE)	Confidence interval (95%)	t	df	P
Within-day (short)	Starting distance	0.30 (0.10)	0.10, 0.50	3.07	1,72	P = 0.00303
	Random effect	$N_{\text{groups}}, N_{\text{obs}}$	Adjusted Repeatability (SE)		LRT	P-value
	1 Bird	22,72	0.43 (0.12)		12.13	P < 0.001
Across-days (long)	Starting distance	0.27 (0.08)	0.10, 0.44	3.20	1,49	P = 0.0018
	Random effect	$N_{\text{groups}}, N_{\text{obs}}$	Adjusted Repeatability (SE)		LRT	P-value
	1 Bird	23,72	0.43 (0.12)		12.76	P < 0.001

Table 2: Information for chosen models for distance fled. For both sample durations, random effects of individual bird were found to be non-significant (via likelihood ratio test), so a model containing only fixed effects was selected. Models are generalized logistic models (GLM), with distance fled coded into near (0) and far (1), where "far" is a distance fled greater than 2 m. Confidence intervals were calculated using R. P-values are produced via Wald tests.

Sample interval	Fixed effect	Estimate (logit, SE)	Estimate(Odds)	Confidence interval (95%, Odds)	z	P
Within-day (short)	FID	0.44 (0.19)	1.55	1.09, 2.33	2.30	P = 0.022
Across-days (long)	FID	-0.86 (0.26)	0.42	0.23, 0.67	-3.25	P = 0.00115
	Distance to cover	-0.30 (0.17)	0.74	0.52, 0.999	-1.77	P = 0.07730.08

Figure 3: In general, behavioral reaction norms, measured as change in FID and DF over a given time scale, were consistent across short- and long- sample intervals. Linear regressions show a strong correlation between reaction norms within day and across days for both FID and DF ($p = 0.03$ for FID, $p < 0.01$ for DF, linear regression). However, a change in FID was not consistently associated with a concurrent change in DF ($p = 0.31$ within-day, $p = 0.64$ across days, linear regression). Each data point represents one individual, with the individual's reaction norm slope within the first day as the x-value, and slope across-days as the y-value.

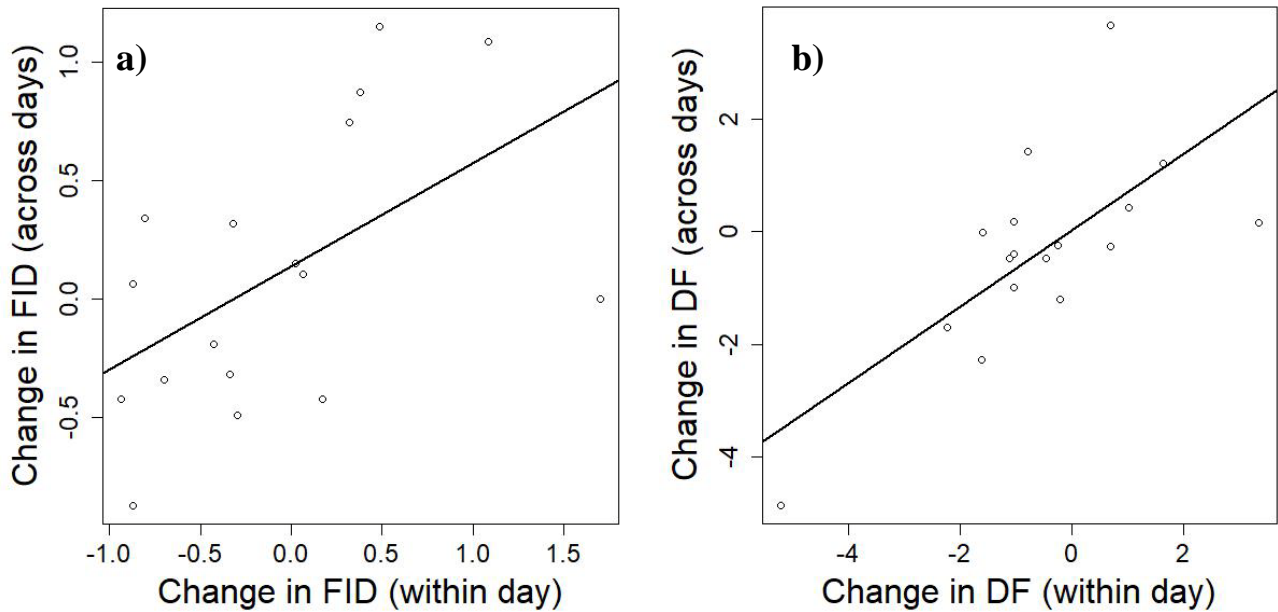
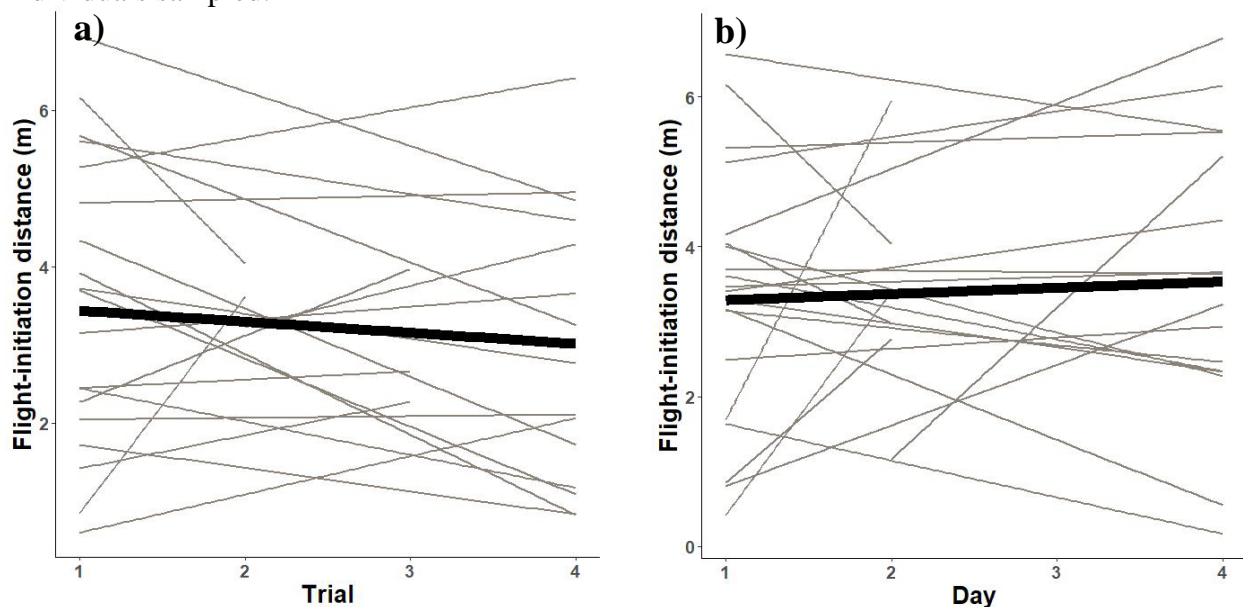


Figure 4: As a whole, urban juncos at UCLA did not appear to habituate or sensitize in their FID across repeated samples. This was found across both short (plot a) and long (plot b) sampling intervals. Thin lines indicate individuals, while the gray line indicates the mean for all individuals sampled.



Appendix

Table A1: Comparison of models incorporating samples collected within the first sample day for each urban individual. Fixed effects were chosen based on AIC. Sample iteration (Trial within day) does not appear to significantly improve model fit. Model m0.1 was selected as the best model for this subset of the data.

Model Name	AIC	Model Formula	Comparison	Result	P
m0	281.4	fid ~ (1 bird)	NA	NA	NA
m0.1	274.9	fid ~ starting distance + (1 bird)	m0.1,m0	significant	0.00344
m1	275.1	fid ~ starting distance + trial + (1 bird)	m1,m0.1	not significant	0.190
m2	277.6	fid ~ starting distance + trial + (1 + trial bird)	m2, m0.1	not significant	0.351
m2	see above	see above	m2,m1	not significant	0.459

Table A2: Comparison of models constructed from samples over long time scales, incorporating first flushes across sample days. Fixed effects were chosen based on AIC. Sample iteration (Day) was not found to have a significant influence on the quality of the model fit. Ultimately, model m0.1 was chosen based on AIC and comparison with other models using likelihood ratio tests.

Model Name	AIC	Model Formula	Comparison	Result	P
m0	274.8	fid ~ (1 bird)	NA	NA	NA
m0.1	267	fid ~ starting distance + (1 bird)	m0.1, m0	significant	0.00181
m1	269	fid ~ starting distance + day + (1 bird)	m1, m0.1	not significant	0.808
m2	272.9	fid ~ starting distance + day + (1 + day bird)	m2, m1	not significant	0.946

Table A3: Comparison of models constructed to examine distance fled over short time scales. We selected a model lacking random effects of individual birds based on likelihood ratio tests and AIC. Distance fled was binned into two levels, near (0) and far (1), where "far" is a distance fled greater than 2m. Fixed effects were chosen adding and removing predictor variables until the lowest AIC was reached.

Model Name	AIC	Model Formula	Comparison	Result	P
m0	77.45	nearfar ~ (1 bird)	N/A	N/A	N/A
m0.1	73.34	nearfar ~ fid + (1 bird)	m0.1,m0	significant	p = 0.0134
m1	73.28	nearfar ~ fid + trial + (1 bird)	m1,m0.1	not significant	0.151
m2	77.28	nearfar ~ fid + trial + (1 + trial bird)	m2, m0.1	not significant	0.560
m2	see above	see above	m2,m1	not significant	1
m0.1glm	71.34	nearfar ~ fid	m0.1,m0.1glm	not significant	1

Table A4: Model comparison for DF from samples collected across days. As with within-day data, we selected a model with no individual effect based on a combination of likelihood ratio tests and AIC. Fixed effects were selected by adding and removing predictor variables and comparing AIC. While distance to cover is not clearly significant (see Wald test result in Table 2), likelihood ratio tests suggest that its inclusion in both mixed-logistic and logistic models improve the fit of the models (likelihood ratio test, $p = 0.02$; logistic Δ residual deviance = -3.87 , $p = 0.05$).

Model Name	AIC	Model Formula	Comparison	Result	P
m0	83.85	nearfar ~ (1 bird)	NA	NA	NA
m0.1	68.05	nearfar ~ distance to cover + fid + (1 bird)	m0.1,m0	significant	p < 0.001 ***
m1	69.83	nearfar ~ distance to cover + fid + day + (1 bird)	m1,m0.1	not significant	0.638
m2	72.50	nearfar ~ distance to cover + fid + day + (1 + day bird)	m2,m0.1	not significant	0.668
m2	see above	see above	m2,m1	not significant	0.512
m0.1glm	67.92	nearfar ~ distance to cover + fid	m0.1, m0.1glm	not significant	0.172

Pedestrian Analysis

Pedestrian density for this study was collected as a qualitative value ("low" or "high") at the time of each flush, indicating the relative density of people passing through the immediate vicinity during sampling. Following data collection, we chose to find a quantitative value to delimit the two categories of pedestrian density. Initially, we considered a strategy where the observer collects quantitative data across campus and associates it with the category they would have used during flushing data samples; however, we ultimately decided it would be best, instead, to allow the flushing data to tell us what delimiting value is associated with a change in behavior. To do so, we used data collected for an associated project seeking to test for non-random habitat sorting by personality. Using the same birds in this study, territories were sampled in two or three locations, with pedestrian data collected four times at each location. For each sample, an observer counted the number of pedestrians crossing a 10 meter line over the

course of 10 minutes, with double-counting of the same pedestrian allowed. We aimed to sample the range of pedestrian values which fluctuate throughout the day, so each site was sampled in the morning and afternoon, midway through classes and during class changes. We then used these data to best estimate what "low" and "high" pedestrian densities each bird experiences within their own territory. These estimated quantitative values were substituted into the original flushing data set, such that each flush was attributed to a best estimate of pedestrian density at the time of the FID. From there, we then did a series of t-tests which compared FID in low and high, delimited at different values (Table A5). The smallest p-values were found between 40 and 60 people over 10 minutes. Thus we elected to use 50 people over 10 minutes as our delimiter.

Table A5: Results of Welch's t-tests comparing FID in categories of "low" or "high" pedestrian activity, based on a range of delimiter values. These delimiters were used to split sample data based on best estimates of pedestrian density at the time of each flush.

Delimiter (persons per 10 minutes)	P
100	0.51
80	0.01**
70	0.18
60	p < 0.0001***
50	p < 0.0001***
40	p < 0.0001***
30	p < 0.01**

Literature Cited

- Aronson, M. F. J., F. A. La Sorte, C. H. Nilon, M. Katti, M. A. Goddard, C. A. Lepczyk, P. S. Warren, N. S. G. Williams, S. Cilliers, B. Clarkson, C. Dobbs, et al. (2014). A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proceedings of the Royal Society B: Biological Sciences* 281:20133330.
- Arroyo, B., F. Mougeot, and V. Bretagnolle (2017). Individual variation in behavioural responsiveness to humans leads to differences in breeding success and long-term population phenotypic changes. *Ecology Letters* 20:317–325.
- Atwell, J. W., G. C. Cardoso, D. J. Whittaker, S. Campbell-Nelson, K. W. Robertson, and E. D. Ketterson (2012). Boldness behavior and stress physiology in a novel urban environment suggest rapid correlated evolutionary adaptation. *Behavioral Ecology* 23:960–969.
- Atwell, J. W., G. C. Cardoso, D. J. Whittaker, T. D. Price, and E. D. Ketterson (2014). Hormonal, behavioral, and life-history traits exhibit correlated shifts in relation to population establishment in a novel environment. *The American Naturalist* 184:E147–E160.
- Bates, D., M. Mächler, B. Bolker, and S. Walker (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48.
- Blumstein, D. T. (2003). Flight-initiation distance in birds is dependent on intruder starting distance. *The Journal of Wildlife Management* 67:852–857.
- Blumstein, D. T. (2006). Developing an evolutionary ecology of fear: how life history and natural history traits affect disturbance tolerance in birds. *Animal Behaviour* 71:389–399.
- Blumstein, D. T. (2013). Attention, habituation, and antipredator behaviour: implications for urban birds. In *Avian Urban Ecology*. Oxford University Press, pp. 41–53.
- Blumstein, D. T. (2016). Habituation and sensitization: new thoughts about old ideas. *Animal Behaviour* 120:255–262.
- Carrete, M., J. Martínez-Padilla, S. Rodríguez-Martínez, N. Rebolo-Ifrán, A. Palma, and J. L. Tella (2016). Heritability of fear of humans in urban and rural populations of a bird species. *Scientific Reports* 6:31060. Carrete, M., and J. L. Tella (2010). Individual consistency in flight initiation distances in burrowing owls: a new hypothesis on disturbance-induced habitat selection. *Biology Letters* 6:167–170.
- Carrete, M., and J. L. Tella (2011). Inter-individual variability in fear of humans and relative brain size of the species are related to contemporary urban invasion in birds. *PLoS ONE* 6.
- Carrete, M., and J. L. Tella (2013). High individual consistency in fear of humans throughout the adult lifespan of rural and urban burrowing owls. *Scientific Reports* 3:3524.

- Chace, J. F., and J. J. Walsh (2006). Urban effects on native avifauna: a review. *Landscape and urban planning* 74:46–69.
- Cooper, W. E. (1997). Escape by a refuging prey, the broad-headed skink (*Eumeces laticeps*). *Canadian Journal of Zoology* 75:943–947.
- Cooper, W. E. (2006). Dynamic risk assessment: prey rapidly adjust flight initiation distance to changes in predator approach speed. *Ethology* 112:858–864.
- Cooper, W. E. (2009). Optimal escape theory predicts escape behaviors beyond flight initiation distance: risk assessment and escape by striped plateau lizards *Sceloporus virgatus*. *Current Zoology* 55:123–131.
- Cooper, W. E., and D. T. Blumstein (Editors) (2015). Escaping from predators: an integrative view of escape decisions. Cambridge University Press.
- Cooper, W. E., and V. Pérez-Mellado (2004). Tradeoffs Between Escape Behavior and Foraging Opportunity By the Balearic Lizard (*Podarcis lilfordi*). *Herpetologica* 60:321–324.
- Dingemanse, N. J., A. J. N. Kazem, D. Réale, and J. Wright (2010). Behavioural reaction norms: animal personality meets individual plasticity. *Trends in Ecology and Evolution* 25:81–89.
- Fernández-Juricic, E., M. D. Jimenez, and E. Lucas (2001a). Alert distance as an alternative measure of bird tolerance to human disturbance: implications for park design. *Environmental Conservation* 28:263–269.
- Fernández-Juricic, E., M. D. Jimenez, and E. Lucas (2001b). Bird tolerance to human disturbance in urban parks of Madrid (Spain): management implications. In *Avian Ecology and Conservation in an Urbanizing World*. Springer US, Boston, MA, pp. 259–273.
- Fernández-Juricic, E., R. Vaca, and N. Schroeder (2004). Spatial and temporal responses of forest birds to human approaches in a protected area and implications for two management strategies. *Biological Conservation* 117:407–416.
- Fox, J., and S. Weisberg (2011). An {R} Companion to Applied Regression. In. 2nd edition. Sage, Thousand Oaks, CA.
- Frid, A., and L. Dill (2002). Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology* 6:16.
- Garamszegi, L. Z., G. Markó, E. Szász, S. Zsebők, M. Azcárate, G. Herczeg, and J. Török (2015). Among-year variation in the repeatability, within- and between-individual, and phenotypic correlations of behaviors in a natural population. *Behavioral Ecology and Sociobiology* 69:2005–2017.

- Gelman, A., and Y.-S. Su (2016). arm: Data Analysis Using Regression and Multilevel/Hierarchical Models. [Online.] Available at <https://cran.r-project.org/package=arm>.
- Kuznetsova, A., P. Bruun Brockhoff, and R. Haubo Bojesen Christensen (2016). lmerTest: Tests in Linear Mixed Effects Models. [Online.] Available at <https://cran.r-project.org/package=lmerTest>.
- Martín, J., I. Rodríguez-Prieto, and E. Fernández-Juricic (2008). To run or to fly: low cost versus low risk escape strategies in blackbirds. *Behaviour* 145:1125–1138.
- McKinney, M. L. (2006). Urbanization as a major cause of biotic homogenization. *Biological Conservation* 127:247–260.
- Mikula, P. (2014). Pedestrian density influences flight distances of urban birds. *Ardea* 102:53–60.
- Miranda, A. C., H. Schielzeth, T. Sonntag, and J. Partecke (2013). Urbanization and its effects on personality traits: a result of microevolution or phenotypic plasticity? *Global change biology* 19:2634–2644.
- Møller, A. P. (2008). Flight distance of urban birds, predation, and selection for urban life. *Behavioral Ecology and Sociobiology* 63:63–75.
- Møller, A. P. (2010). Interspecific variation in fear responses predicts urbanization in birds. *Behavioral Ecology* 21:365–371.
- Møller, A. P., and J. D. Ibáñez-Álamo (2012). Escape behaviour of birds provides evidence of predation being involved in urbanization. *Animal Behaviour* 84:341–348.
- Newman, M. M., P. J. Yeh, and T. D. Price (2006). Reduced territorial responses in dark-eyed juncos following population establishment in a climatically mild environment. *Animal Behaviour* 71:893–899.
- Nolan Jr, V., E. D. Ketterson, D. A. Cristol, C. M. Rogers, E. D. Clotfelter, R. C. Titus, S. J. Schoech, and E. Snajdr (2002). Dark-eyed Junco (*Junco hyemalis*). In *The Birds of North America*. 2.0. Cornell Lab of Ornithology, Ithaca, NY, USA.
- Partecke, J., I. Schwabl, and E. Gwinner (2006). Stress and the city: urbanization and its effects on the stress physiology in European blackbirds. *Ecology* 87:1945–1952.
- Petelle, M. B., D. E. McCoy, V. Alejandro, J. G. A. Martin, and D. T. Blumstein (2013). Development of boldness and docility in yellow-bellied marmots. *Animal Behaviour* 86:1147–1154.
- R Core Team (2017). R: A Language and Environment for Statistical Computing. [Online.]

Available at <https://www.r-project.org/>.

- Rasner, C. A., P. Yeh, L. S. Eggert, K. E. Hunt, D. S. Woodruff, and T. D. Price (2004). Genetic and morphological evolution following a founder event in the dark-eyed junco, *Junco hyemalis thurberi*. *Molecular Ecology* 13:671–681.
- Réale, D., S. M. Reader, D. Sol, P. T. McDougall, and N. J. Dingemanse (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews* 82:291–318.
- Rodriguez-Prieto, I., E. Fernandez-Juricic, J. Martin, and Y. Regis (2009). Antipredator behavior in blackbirds: habituation complements risk allocation. *Behavioral Ecology* 20:371–377.
- Runyan, A. M., and D. T. Blumstein (2004). Do individual differences influence flight initiation distance? *The Journal of wildlife management* 68:1124–1129.
- Samia, D. S. M., and D. T. Blumstein (2014). Phi Index: a new metric to test the flush early and avoid the rush hypothesis. *PLoS ONE* 9:e113134.
- Samia, D. S. M., and D. T. Blumstein (2015). Birds flush early and avoid the rush: an interspecific study. *PLoS ONE* 10:e0119906.
- Samia, D. S. M., D. T. Blumstein, M. Díaz, T. Grim, J. D. Ibáñez-Álamo, J. Jokimäki, K. Tätté, G. Markó, P. Tryjanowski, and A. P. Møller (2017). Rural-urban differences in escape behavior of European birds across a latitudinal gradient. *Frontiers in Ecology and Evolution*. [Online.] Available at <https://www.frontiersin.org/article/10.3389/fevo.2017.00066>.
- Samia, D. S. M., D. T. Blumstein, T. Stankowich, and W. E. Cooper Jr. (2016). Fifty years of chasing lizards: new insights advance optimal escape theory. *Biological Reviews* 91:349–366.
- Samia, D. S. M., A. Pape Møller, and D. T. Blumstein (2015). Brain size as a driver of avian escape strategy. *Scientific Reports* 5:11913.
- Sarkar, D. (2008). *Lattice: Multivariate Data Visualization with R*. In: Springer, New York.
- Scheipl, F., S. Greven, and H. Kuechenhoff (2008). Size and power of tests for a zero random effect variance or polynomial regression in additive and linear mixed models. *Computational Statistics & Data Analysis* 52:3283–3299.
- Schlesinger, M. D., P. N. Manley, and M. Holyoak (2008). Distinguishing stressors acting on land bird communities in an urbanizing environment. *Ecology* 89:2302–2314.
- Sih, A., M. C. O. Ferrari, and D. J. Harris (2011). Evolution and behavioural responses to human-induced rapid environmental change. *Evolutionary Applications* 4:367–387.

- Smith, B. R., and D. T. Blumstein (2008). Fitness consequences of personality: a meta-analysis. *Behavioral Ecology* 19:448–455. Sprau, P., and N. J. Dingemanse (2017). An approach to distinguish between plasticity and non-random distributions of behavioral types along urban gradients in a wild passerine bird. *Frontiers in Ecology and Evolution* 5:1–8.
- Stankowich, T., and D. T. Blumstein (2005). Fear in animals: a meta-analysis and review of risk assessment. *Proceedings of the Royal Society B: Biological Sciences* 272:2627 LP-2634.
- Stoffel, M., S. Nakagawa, and H. Schielzeth (2017). rptR: Repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods in Ecology and Evolution* 8:1639–1644.
- Strasser, E. H., and J. A. Heath (2013). Reproductive failure of a human-tolerant species, the American kestrel, is associated with stress and human disturbance. *Journal of Applied Ecology* 50:912–919.
- Tätte, K., A. P. Møller, and R. Mänd (2018). Towards an integrated view of escape decisions in birds: relation between flight initiation distance and distance fled. *Animal Behaviour* 136:75–86.
- UCLA Office of Academic Planning and Budget (2017). UCLA Common Data Set. [Online.] Available at <https://www.apb.ucla.edu/campus-statistics/common-data-set>.
- Venables, W., and B. Ripley (2002). *Modern Applied Statistics with S*. In. Fourth. Springer, New York.
- Wickham, H. (2009). *ggplot2: Elegant graphics for data analysis*. In. Springer-Verlag, New York.
- Ydenberg, R. C., and L. M. Dill (1986). The economics of fleeing from predators. In *Advances in the Study of Behavior*. Elsevier, pp. 229–249.
- Yeh, P. J. (2004). Rapid evolution of a sexually selected trait following population establishment in a novel habitat. *Evolution* 58:166–174.
- Yeh, P. J., and T. D. Price (2004). Adaptive phenotypic plasticity and the successful colonization of a novel environment. *American Naturalist* 164:531–42.