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Individual variation in tolerance of human activity by urban Dark-eyed Juncos (*Junco hyemalis*)

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ABSTRACT—An important goal of urban ecology is determining what differentiates urban-tolerant populations of birds from their non-urban ancestors and urban-intolerant species. One key to urban success may be reacting appropriately to human activity, and the degree to which birds view humans as threats can be quantified by their escape behavior. Understanding individual-level plasticity, however, requires the tracking of known individuals. We compared flight-initiation distances (FID) and distances fled (DF) from approaches by a human between an urban and a non-urban population of individually marked Dark-eyed Juncos (*Junco hyemalis*) in Southern California. The urban population is more tolerant to people as evidenced by attenuated FIDs and DFs relative to non-urban birds. Although individual urban birds either habituated or sensitized to repeated approaches, there was no significant pattern at the population level. Overall, the behavioral patterns exhibited by this urban population of juncos is more supportive of in situ evolution of tolerance than either being a biased sample from an ancestral non-urban population or intrinsic behavioral plasticity that produces a uniform adjustment to urban life. *Received 10 December 2020. Accepted 7 December 2021.*

Key words: anti-predator behavior, avian, fleeing, flight-initiation distance, urban ecology.

Variación individual en la tolerancia a la actividad humana por juncos (*Junco hyemalis*) urbanos

RESUMEN (Spanish)—Un objetivo principal en el estudio de ecología urbana es identificar las diferencias entre poblaciones de aves urbanas con poblaciones ancestrales no-urbanas o poblaciones que no toleran el ambiente urbano. Una clave para su éxito urbano es la manera en que las aves reaccionan a la actividad humana y el grado en que las aves se sienten amenazadas por la presencia humana puede ser cuantificada por su comportamiento de escape. Para tener un conocimiento fundamental sobre la plasticidad a nivel individual, se requiere el seguimiento de individuos marcados. Nosotros comparamos la distancia de iniciación al vuelo (FID) y la distancia de huida (DF) de acercamientos por humanos entre poblaciones urbanas y no-urbanas de junco de ojos oscuros (*Junco hyemalis*) en el sur de California. Según las FIDs y DFs que medimos, encontramos que individuos de la población urbana pueden tolerar la presencia humana más que la población no-urbana. Aunque encontramos individuos que son tolerantes o vulnerables a los múltiples acercamientos humanos, no encontramos un patrón significativo a nivel de población. En conjunto, los patrones de comportamiento mostrado por los juncos urbanos apoyan la evolución *en situ,* en vez de apoyar una muestra sesgada de una población ancestral no urbana ni la plasticidad conductual intrínseca que produce un ajuste uniforme a la vida urbana.

Palabras clave: aviar, comportamiento anti-depredador, distancia de inicio de vuelo, ecología urbana, escape.

Urbanization creates both costs and benefits across bird species. Some species thrive in urbanized settings due to factors such as feeders providing abundant and stable food supplies (Reynolds et al. 2017), structures for nests (Cooper et al. 2020), and potential reduced risk from predators (Samia et al. 2017). Nevertheless, urbanized areas have significantly fewer species than nearby non-urban areas (Chace and Walsh 2006, Sandstrom et al. 2006, Bonier et al. 2007, Schlesinger et al. 2008), suggesting that for a number of birds urban settings are too stressful. Understanding how some species adapt and change to survive in cities can inform conservation and urban planning decisions to support the maintenance of native biodiversity in proximity to human activity (Fernández-Juricic et al. 2001, Chace and Walsh 2006, Aronson et al. 2014).

Direct disturbance by human activity may be one of the primary stressors faced by urban birds (Partecke et al. 2006, Strasser and Heath 2013). One way to understand the cost of human disturbance on wildlife is based on the premise that escape behavior shows how wildlife perceive humans as a risk to avoid (Frid and Dill 2002, Blumstein 2014). Escape decisions can vary depending on the economics of fleeing, lost opportunity cost, and perceived risk of predation (Ydenberg and Dill 1986, Cooper and Blumstein 2015). All of these factors could differ for urban and non-urban birds, leading to consistent differences observed in escape behavior as can be measured by the flight initiation distance (FID) to an approaching human (Møller 2008; Evans et al. 2010; Mikula 2014; Samia et al. 2015, 2017; Sprau and Dingemanse 2017; Sol et al. 2018).

Dark-eyed Juncos (*Junco hyemalis*) are particularly interesting in that until relatively recently they

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were uncommon or absent in urban areas of Southern California. Sometime likely in the early 1980s juncos colonized San Diego and in the space of 20+ years, the expanding population differed significantly in physiology, morphology, and behavior from nearby populations of non-urban birds (Yeh 2004; Yeh and Price 2004; Newman et al. 2006; Atwell et al. 2012, 2014). One behavioral difference that may have allowed this population of juncos to thrive in the city is increased tolerance to human activity. Such tolerant urban populations may arise in several ways (Sol et al. 2013). Urban populations may result from differential habitat selection by intrinsically more human-tolerant subsets of individuals from non-urban ancestor populations (Carrete and Tella 2011). Thus, within a non-urban population one would find that some birds fear humans less and are less affected by human activity. When approached their FIDs would be similar to those observed in urban birds. Alternatively, individuals could vary in their behavioral plasticity such that some are capable of appropriately adjusting to high levels of human activity in urban areas (Fernández-Juricic et al. 2001, Rodriguez-Prieto et al. 2009, Møller 2010, Rodríguez-Prieto et al. 2011, Blumstein 2016, Vincze et al. 2016). Thus, one might expect an "urban personality" whereby urban birds respond in a consistent pattern to a series of identical challenges. Finally, urban birds may have genetically evolved to be more tolerant of disturbance (Møller 2008, Carrete et al. 2016). In this case, urban birds would consistently exhibit lower FIDs than non-urban birds, but there may not be a consistent response pattern across urban birds.

Our goal was to measure both the inter-individual variation and within-individual plasticity to human presence in a population of urban juncos. We gathered repeated samples of their FID and distance fled (DF) in response to an approaching person over both short time intervals (within-day) and longer intervals (across consecutive days). For comparison to the urban population, we also measured FID and DF values from a nearby non-urban population.

Methods

Study species

The Dark-eyed Junco is a small passerine species native to montane habitats throughout much of the United States, including in Southern California. It is typically a ground-nesting, socially monogamous species. Within the last few decades, juncos have begun breeding in coastal, urban Southern California areas, including San Diego—likely starting in the early 1980s, and Los Angeles—likely starting in the 2000s.

Study sites and banding birds

The urban site was the 170 ha campus of the University of California Los Angeles (UCLA), located in the northwest portion of the Los Angeles Basin (34.0695°N, 118.4452°W) at ~100–150 m in elevation. Summers are hot and dry, with rainfall occurring mostly during a cool winter (mean temperature: 14–22 °C over the year; 44.5 cm mean annual precipitation). Vegetation is a mix of grass lawns and largely nonnative plant species popular to Southern California such as eucalyptus (*Eucalyptus* spp.) and Moreton Bay fig (*Ficus macrophylla*). There is abundant human activity across the campus throughout most of the year. Pedestrian density can fluctuate daily in accordance with class schedules: from a low rate of a few dozen or less per hour passing a site on weekends or while classes are meeting, to a high rate of hundreds during the brief changeover periods between classes. A UCLA map is available at http://map.ucla.edu/downloads/pdf/UCLA_Campus_Colored_Map.pdf.

The non-urban site was the 20 ha James Reserve (33.8083°N, 116.7778°W), located in the San Jacinto Mountains around 300 km east of UCLA campus. The reserve elevation is ~1,650 m. Compared with UCLA, the James and adjacent areas have a cooler and wetter climate (4–19 °C mean annual temperature range, 66 cm mean annual precipitation). There is no public access to the study site, such that pedestrian activity is usually low and within a range of 0–10 per h. The habitat includes montane riparian forest and mixed conifer and hardwood forest with open understory consisting of gravel roads, parking areas, and grassy meadows. Further information about the James is available at https://james.ucnrs.org/.

Mist-netted birds were individually marked at each site with USGS aluminum bands and a unique set of color bands. After banding, birds were given at least a week to recover before any behavioral data were taken. Mated pairs were never simultaneously tested with at least a week between taking data on the first and second bird.

Sampling

All encounters were recorded by the same individual (HMS) following the protocol commonly used to study FID (Cooper and Blumstein 2015). An encounter began when a bird was observed foraging or stationary, and not alarm calling or otherwise visibly agitated. Because juncos are territorial, most encounters with a given bird occurred near where it was initially captured and banded. Birds were always approached in a straight line at a practiced pace (approximating 0.5 m/s) 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, Tätte et al. 2018). A colored marker was dropped at the location where the experimental approach began (the starting distance, SD), a second at the observer location when the focal subject fled (the FID), and a third at the location from where the focal subject fled, later converting paces to meters (0.825 m/step). The distance fled (DF) was recorded by visually estimating the horizontal and vertical distance traveled in meters, then converting to a Euclidian distance. In some cases, it was not possible to collect data on DF because the bird left the immediate area. Such occurrences were arbitrarily recorded as a distance fled of 50 m.

We also recorded the time of day, presence/absence of conspecifics within a 5 m radius of the focal bird, distance to nearest cover (either bushes and trees, or structures such as walls and outdoor furniture), and pedestrian density. Distance to cover was measured in paces from the targeted bird's location when the approach began. Pedestrian density (only at UCLA—there were almost never pedestrians at the James) was recorded categorically as low (defined as <5 people/min crossing a 10 m sample transect in the immediate vicinity of the approach) or moderate to high (≥ 5 people/min).

At UCLA, we collected repeated measures for 22 series on both a short time scale (4 attempted approaches to the same bird on the same day) and on a longer time scale (over a consecutive 4 d period). Not every series had the complete sequence of 16 approaches (6 had 1 missing value in terms of a missed approach on one day, 4 had 2 missing values, and 1 had 4 missing values because of a missed day). The median time between sequential approaches within a day across 198 approaches was 3 min, with 183 times being 30 min or less. Only 6 approaches were separated by more than an hour. Birds were approached during the 2017 breeding season while rearing chicks (Feb–Jul at UCLA; Jun–Jul at the James) in order to be consistent across sites relative to foraging needs (i.e., risk-taking can differ in individuals when breeding versus non-breeding: Mikula et al. 2018). In total, we collected 404 approaches across 31 individuals at UCLA and 104 approaches across 22 individuals at the James Reserve. At both sites, the majority of data were collected between 0800 and 1300 h.

Statistical tests on the multiple approaches toward marked birds in UCLA followed standardized analytical methodology (Pezner et al. 2017, Dehaudt et al. 2019, Andrade and Blumstein 2020). All analyses used R 3.4.2 (R Core Team 2017), on code modeled after Pezner et al. (2017), which had an identical experimental design: 4 trials per day, repeated across 4 consecutive days. We used linear (FID) and logistic (DF, with distances ≤ 2 m as near and >2 m as far) mixed-effects models for individual responses to repeated approaches on the UCLA campus. Effects within UCLA and across the James population values were compared by regression analysis, paired *t*-tests, and 2-sample unpaired *t*-tests, as appropriate.

We fitted models using the R package *lme4* v1.1-14 (Bates et al. 2015) (supporting package *car* v2.1-6; Fox and Weisberg 2011). A null model used individual bird as a random intercept, then iteratively incorporated fixed effects (contextual variables), with stepwise selection to find the combination of fixed effects with the lowest AIC value. Each predictor variable was added to the model and then selectively removed depending on their effect on AIC relative to the null model. In cases where a fixed effect resulted in only a nonsignificant decrease in AIC, likelihood ratio tests used *lmerTest* v2.0-33 (Kuznetsova et al. 2016) to measure significance. Fixed effects without significant model improvement were discarded.

After selecting a model via this process, a likelihood ratio test evaluated whether either the

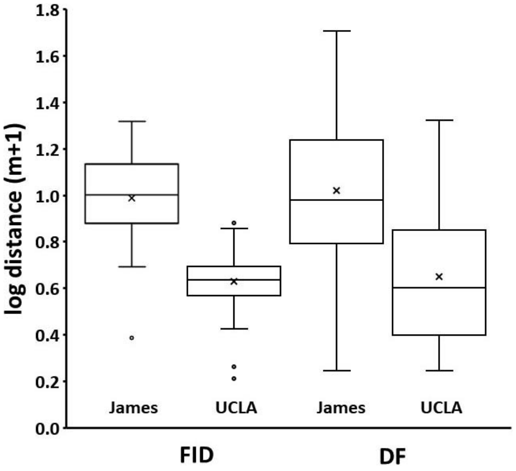

Figure 1. Differences in flight initiation distance and distance fled by urban Dark-eyed Juncos in response to human activity. Data are presented for the first approach a bird received at the non-urban (James, $n = 22$) and urban (UCLA, $n = 31$) sites.

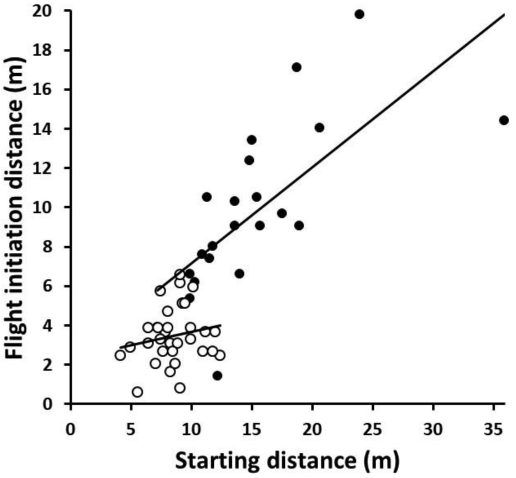

Figure 2. Effect of starting distance on flight initiation distance on a Dark-eyed Junco's first flush. Open points are for urban (UCLA, $n = 31$) birds and solid points are for non-urban (James, $n = 22$) birds. Lines show the respective regressions.

inclusion of trial iteration as a fixed effect or as a random slope significantly improved the explanatory power over the model containing contextual predictor variables and the random intercept. Best mixed-models were compared 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 and *arm* v1.9-3 (Gelman and Su 2016), to determine whether individual differences among birds explained a significant portion of behavioral variation. Where individual was a significant random effect in models, adjusted repeatability was calculated using code provided by Jean-Nicolas Audet, modified from *rptR* v0.9.21 (Stoffel et al. 2017). Analyses were based on 334 individual approaches.

Results

Comparison of urban and non-urban populations

In comparing their first flushes, urban juncos had both significantly shorter and less variable FIDs than non-urban birds (Fig. 1; in all cases, mean ± SD: urban = 3.49 ± 1.47 m, $n = 31$; non-urban = 9.67 ± 4.29 m, $n = 22$; $t = 7.46$, $P < 0.001$). Urban birds were encountered closer to cover than non-urban birds (1.36 ± 1.51 m versus 4.23 ± 2.12 m, $t = 5.64$, $P < 0.001$). This may help account for the shorter mean distances fled by urban juncos relative to non-urban (Fig. 1: 4.94 ± 4.63 m versus 14.31 ± 14.95 m, $t = 3.32$, $P = 0.002$).

Starting distances strongly influenced the first-flush FID (Fig. 2) for non-urban juncos ($F_{1,20} = 18.84$, $R^2 = 0.459$, $P < 0.001$), but not significantly for urban juncos ($F_{1,29} = 1.04$, $R^2 = 0.001$, $P = 0.317$). Starting distance had no significant effect on DF for either non-urban or urban birds on their first flush (non-urban: $F_{1,18} = 0.600$, $R^2 < 0.001$, $P = 0.449$; urban: $F_{1,29} = 0.063$, $R^2 < 0.001$, $P = 0.804$).

Individual variation in the urban population

For within-day mixed effects models of FID, starting distance was also the only fixed effect retained in mixed models across days (Supplementary Table S1). Increasing starting distance was associated with an increased FID. Increasing FID was associated with an increased DF on both time scales. Distance to cover, retained as a fixed effect, was not significant with a change in DF over short time scales (Supplementary Table S2).

Trial number does not explain significant variation in FID within or across days (Supplementary Tables S3 and S4), nor in DF (Supple-

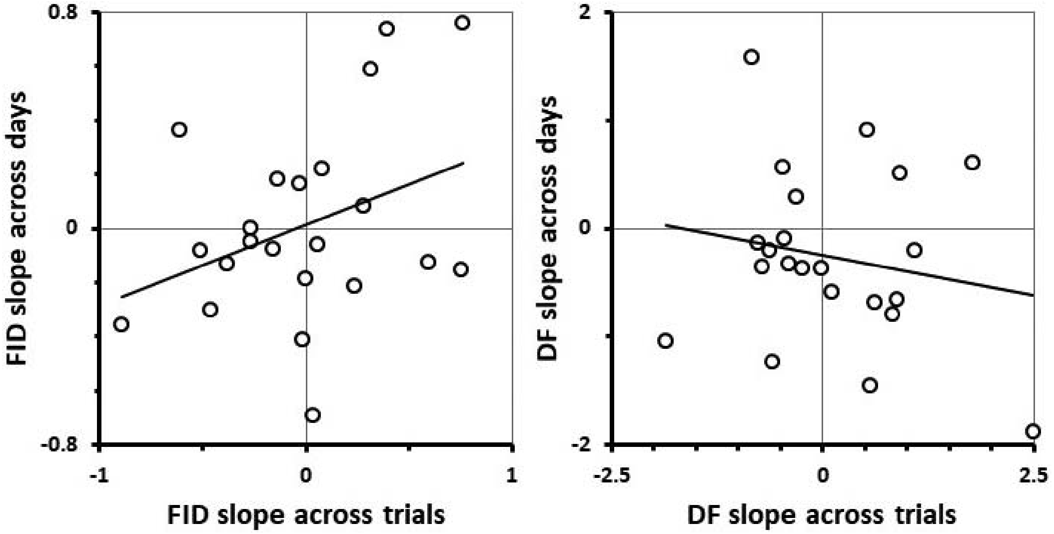

Figure 3. Response of urban Dark-eyed Juncos to human activity. Regressions of FID and DF slopes. Each data point ($n =$ 22) represents one series of approaches. Slopes for Trials are the mean of the 4 individual slopes for each consecutive approach (i.e., the 4 slopes of the changes in FID or DF from day 1 to day 4 for approaches #1, 2, 3, or 4). Slopes for Days are the mean of the 4 individual slopes for each consecutive day (calculated as the change in FID or DF from the first to fourth approach of that day).

mentary Tables S5 and S6). Trial number as either a fixed effect or a random slope failed to significantly improve model fit compared to a random-intercept-only model. Therefore, repetition in flushes does not significantly affect FID or DF as would be predicted by either all birds habituating or sensitizing.

Likelihood ratio tests comparing mixed models against linear models indicated a significant individual bird effect ($P < 0.01$ for both time scales) on FID. Therefore, there is significant and consistent differences across birds in their FIDs. Similarly, adjusted repeatability tests suggest a large proportion of the variation in FID, but not in DF, is explained by individual bird after controlling for fixed effects ($R^2 = 0.46$ within-day, $R^2 =$ 0.43 across-days; Supplementary Tables S1, S5, and S6).

FID slopes within and across days (Fig. 3) are significantly positively correlated across series, but DF slopes are not (FID: $F_{1,20} = 4.886$, $R^2 = 0.156$, $P = 0.039$; DF: $F_{1,20} = 0.690$, $R^2 < 0.001$, $P =$ 0.416). Thus, birds that increased FID with each approach within a day also tended to increase FID with each subsequent day they were approached. Individual FID slopes did not significantly predict DF slopes (slopes within-day: $F_{1,20} = 0.404$, $R^2 <$ 0.001, $P = 0.532$; slopes across-days: $F_{1,20} =$ 1.252, $R^2 = 0.012$, $P = 0.276$). Some birds significantly decreased FID over repeated flushes (consistent with habituation), while others increased FID (consistent with sensitization; Fig. 4).

A variety of factors when directly examined do not significantly explain variation in FID. These include distance from cover (linear regression: $F_{1,369} = 2.573$, $R^2 = 0.004$, $P = 0.110$), sex (male mean FID = 3.23 m ± 1.06, $n = 17$; female mean FID = 3.72 ± 1.81, $n = 6$; $t = 0.809$, $P = 0.428$), and presence/absence of conspecifics within 5 m (within bird matched-pair $t = 0.349$, $P = 0.731$, $n =$ 19). Interestingly, birds fled at a greater distance when pedestrian density was low than when it was moderate or high, but the effect did not quite reach statistical significance (low: mean FID = 3.52 ± 1.38; moderate/high mean FID = 3.13 ± 1.48; within bird matched-pair $t = 2.013$, $P = 0.058$, $n =$ 21).

Discussion

The urban juncos on the UCLA campus differed significantly from a nearby non-urban population in tolerating closer approaches by humans before moving and then moving shorter distances away.

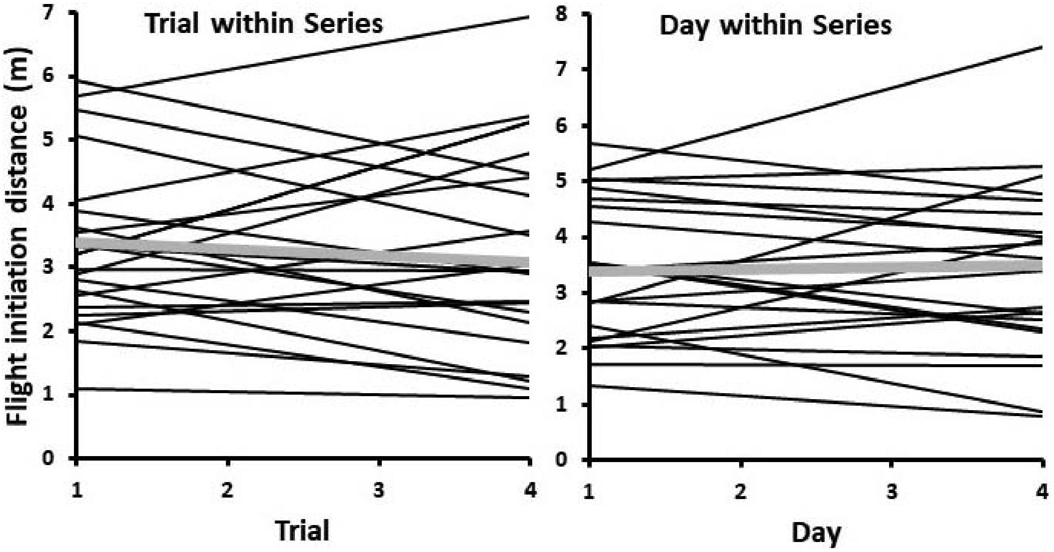

Figure 4. Individual urban Dark-eyed Junco FIDs by sequential approaches within a day and by their daily means across sequential days. Positive slopes indicate sensitization, negative ones indicate habituation. Thin black lines indicate individual series ($n = 22$), while the thick gray lines show the mean across all the series. While individual birds may sensitize or habituate to repeated approaches, at the population level neither behavioral response predominates.

The overall patterns in this study are consistent with urban birds behaviorally evolving, under directional selection, to become more tolerant than rural birds, rather than reflecting the movement from a subpopulation of rural birds that are already intrinsically tolerant of human presence (Yeh 2004; Atwell et al. 2012, 2014). The distributions of FID at the 2 sites barely overlapped: of the 31 birds with the smallest mean FIDs across all approaches, 30 were from UCLA, and of the 22 birds with the largest mean FIDs, only 1 was from UCLA. Non-urban bird FIDs were also attuned to the starting distance at which an approach began, which suggests they pay closer attention to someone coming directly toward them. In contrast, SD had no significant effect in the urban population. It is possible that because some pedestrian activity is omnipresent at UCLA, birds are more generally monitoring "people" and it is only when a person gets within a certain distance that it becomes apparent there is an intersecting path to the junco.

Also, multigenerational lags between when urban centers were first established and when juncos first colonized them argues against subpopulations within non-urban juncos intrinsically having either preexisting urban-friendly genotypes or sufficient behavioral plasticity to immediately accommodate to urban living (Yeh 2004, Yeh and Price 2004). The observed differences between UCLA and James birds are similar to what Yeh and Price found in their comparative work.

An alternative is that junco behavior is sufficiently plastic that birds can adjust to the different and varying demands of urban life. Indeed, individual birds at UCLA had behaviorally plastic responses to repeated human approaches. However, this plasticity yields diametrically opposite outcomes. Some birds consistently habituated in FID while others appear to become sensitized as they were approached within and across days. Because James birds could not be reliably approached multiple times within a day and then across consecutive days, it is unknown whether a similar diversity of response exists in the non-urban population.

The responses of urban juncos at UCLA adds to a growing body of studies of bird behavior relative to human activity. One commonly shared characteristic across multiple species is the greater tolerance of nearby human presence in urban populations than in non-urban ones (Møller 2008; Evans et al. 2010; Díaz et al. 2013, 2015; Samia et al. 2015, 2017; Battle et al. 2016; Cavalli et al.

2016; Vincze et al. 2016; Sprau and Dingemanse 2017). Beyond this broad pattern, however, species exhibit distinct differences in behavioral patterns. For example, as a population the UCLA juncos do not consistently habituate to being approached. This is similar to Great Tits (*Parus major*; Sprau and Dingemanse 2017), but unlike House Sparrows (*Passer domesticus*; Vincze et al. 2016). However, the within-population pattern seems more similar to that reported for Burrowing Owls (*Athene cunicularia*), where studies differ as to whether or not individual birds habituate (Carrete and Tella 2013, Cavalli et al. 2018). This existing across-individual variance in behavior suggests that the UCLA junco population did not arise due to differential colonization of genotypes from the ancestral non-urban population (Vincze et al. 2016), or that only certain behavioral types have segregated in the campus habitat (Sprau and Dingemnase 2017). Finally, unlike a survey across multiple bird species (Mikula 2014), we found a nonsignificant trend for urban juncos being more, not less, responsive at lower pedestrian density. This suggests these urban juncos do not quantitatively calibrate humans as a risk.

Another likely commonality shared with other urban populations of birds is that recent urban junco populations have likely experienced founder effects and reduced population-level genetic diversity (Møller 2010, Mueller et al. 2018). This may be creating opportunities for the suggested rapid genetic evolution (Atwell et al. 2012, 2014). The populations of Southern California juncos, therefore, appear to be an excellent system to investigate if behavioral tolerance for urban life provides evidence for an evolving genetic underpinning.

Acknowledgments

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