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Publication Date

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UNIVERSITY OF CALIFORNIA

Los Angeles

Nests in the Cities: Adaptive and Non-adaptive Plasticity
and Behavioral Convergence in an Urban Bird

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

by

Samuel Ari Bressler

2020

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ABSTRACT OF THE THESIS

Nests in the Cities: Adaptive and Non-adaptive Plasticity and Behavioral Convergence in an
Urban Bird

by

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Master of Science in Biology

University of California, Los Angeles, 2020

Professor Pamela J. Yeh, Chair

Behavioral plasticity is an important mechanism for rapid adaptation to novel environments, including urban ecosystems. However, whether such plasticity is adaptive, and if plasticity is convergent among urban populations, is poorly understood. We studied an “urban-adapting” species, the dark-eyed junco (*Junco hyemalis*), to understand the role of nesting plasticity in adapting to city life. We examined 1) whether novel nesting behaviors are adaptive, 2) whether pairs practice informed re-nesting, and 3) whether two urban populations exhibit similar nesting behavior. We monitored 170 junco nests in Los Angeles and compared our results to prior data on 579 nests from San Diego. We found that nests placed in ecologically novel locations increased fitness, and that pairs practiced informed re-nesting. The Los Angeles population more frequently nested off-ground than the San Diego population and exhibited a higher success rate. Our findings suggest that plasticity facilitates adaptation to urban environments.

The thesis of Samuel Ari Bressler is approved

Daniel T. Blumstein

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University of California, Los Angeles

2020

This thesis is dedicated to:

My parents, for supporting me in my academic pursuits, and always lending an ear.

Pam, for your guidance and patience, and ultimately, believing in me.

Ellie, I couldn't have done this with you. Thanks for being an awesome bander, a mentor, editor, interpreter, and friend.

The Junco Field Crew, thank you for your passion, drive, knowledge, and spirit. You will all go onto great things.

And finally, the very first junco, identity lost to time, to build a nest on a Los Angeles building:

“That’s one small hop for a bird, one giant flight for birdkind.”

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Acknowledgements

We thank Christina Cen, Taylor Kang, Julia Lung, Michelle Olavarrieta, Carissa Reulbach, Gloria Verdugo, and Lauren Williams for assistance in the field, and Madeline Cowen and Gaurav Kandlikar for assistance with statistical analysis. For funding, we thank UCLA Ecology and Evolutionary Biology, the UCLA/La Kretz Center for California Conservation Science, Pasadena Audubon Society, Santa Monica Bay Audubon Society, the American Ornithological Society, and the Hellman Foundation.

This thesis is a version of: Bressler SA, Diamant ED, Tingley MT, Yeh PJ (In Prep) Nests in the Cities: Adaptive and Non-adaptive Plasticity and Behavioral Convergence in an Urban Bird.

Statement of Authorship: P.J.Y. designed the study. S.A.B. and E.S.D. conducted field work.

S.A.B. and M.W.T. conducted statistical analyses. S.A.B., E.S.D., M.W.T., and P.J.Y. wrote and revised the manuscript.

Chapter 1

Introduction

Phenotypic plasticity can manifest in an individual's development and behavior, and may help facilitate adaptation to new environments (1,2). Behavioral plasticity has been extensively documented in a wide variety of animals, and in behaviors ranging from communication (3–6) to nest-site selection (7,8) to breeding phenology (9,10). In situations where organisms encounter unfamiliar conditions, whether due to environmental change or by colonizing a novel environment, plasticity may allow for more rapid adaptation to new conditions than slower mechanisms such as evolution by natural selection (11,12).

While plasticity can facilitate local adaptation, plasticity is not always adaptive. Recent work has shown that non-adaptive plasticity may be more common than typically assumed (13). Plasticity in novel environments can be maladaptive when individuals react to unfamiliar conditions in ways that lower fitness (11). These phenotypic mismatches can lead to evolutionary traps, where maladaptive behaviors can lead to local population decline or extirpation (14). Examples of this include preferentially establishing territories in suboptimal habitats or building nests in substrates with higher predation pressure (15). Thus, when documenting plasticity, it is important to evaluate the effect that it has on individual fitness to determine whether it is adaptive, nonadaptive, or maladaptive.

For either adaptive or nonadaptive plasticity to be expressed, individuals rely on environmental cues(2). These cues may be public information accessible to all individuals (16), or private information available only to a given individual (17). Private and public cues may influence the same behavior. For example, individuals might select nest sites based on public information on predator presence (8,18,19) along with private information in the form of

previous nesting experience (7,20). One of the simplest forms of plasticity based on private information is known as the “win-stay/lose-switch” strategy (WSLS). With this strategy, individuals repeat a behavior if it led to a successful outcome, but choose a different behavior otherwise (17,21,22). By allowing individuals to explore alternative behaviors and learn which behaviors maximize fitness, private information strategies such as WSLS can facilitate local adaptation to a novel environment.

Because cities are evolutionarily novel environments with unfamiliar challenges for wildlife, urban landscapes provide ideal systems for understanding how plasticity might promote or hinder adaptation to new environments (23). Urban birds are particularly excellent systems for studying the effects of behavioral plasticity on urban adaptation as they are frequently found in close proximity to humans, are generally diurnal and easy to observe, and their various behaviors, such as foraging, nesting, and singing, are impacted by urbanization (24,25). Unsurprisingly, behavioral plasticity in urban birds has been extensively documented, and the extent of plasticity may play a role in allowing species to colonize or persist in cities. For example, plasticity has been implicated in changes in vocalization (6), fear response (26–28), breeding season length (29,30), and nest site selection (31,32) in response to urbanization. However, whether plasticity is adaptive for urban populations is less well understood (23). A still outstanding question is to what extent does plasticity in urban wildlife populations impact fitness outcomes, and whether urban ecosystems might selectively filter out species that either do not exhibit behavioral plasticity or show maladaptive plasticity in their new environment (33).

Behaviors associated with nesting and reproduction are critically important for population persistence. As a result, birds that thrive in urban areas frequently exhibit novel nesting behaviors. Many urban populations of raptors, swifts, and swallows have adapted to use buildings and other artificial sites for nests, in lieu of natural cliffs and riverbanks (34). Bird

species such as tawny frogmouths (*Podargus strigoides*) (28), dark-eyed juncos (*Junco hyemalis*) (29), and black-billed magpies (*Pica pica*) (34), exhibit a protracted breeding season in urban areas, possibly a result of mild climates and/or greater food abundance compared to surrounding wildlands. Some urban species, such as house finches (*Haemorhous mexicanus*), incorporate anthropogenic materials such as twine, plastic, or even cigarette butts into the construction of their nests (34), where such novel nest material may reduce parasite load of nestlings (36).

While much has been learned about urban nesting behavior in recent years, relatively little is known about the predictability of nesting behavioral shifts in urban areas. Cities do not share identical ecological characteristics; instead, they can differ in key traits such as canopy cover, dominant vegetation, and percent impervious surfaces (37). Consequently, do different urban populations of the same species adapt to these novel conditions in the same way, or will they demonstrate different adaptations depending on the unique conditions each population faces? One study has demonstrated that great tits (*Parus major*) modify their song characteristics in similar ways in at least ten different cities (6), but our understanding of how plasticity in nesting behavior is expressed in isolated urban populations remains poorly understood.

The dark-eyed junco (hereafter “junco”) is an ideal species to study plasticity in urban nesting behavior and convergence across multiple urban populations. Traditionally a breeding resident of mixed-pine forests in North America, this sparrow has successfully colonized many urban areas throughout Southern California since the late twentieth century (38). Urban junco populations have diverged rapidly from their wildland counterparts, such as in the loss of migratory behavior and a protracted breeding season (30). While this species typically builds cup-shaped nests on the ground and under vegetation, prior research on an urban population near San Diego, California demonstrated plasticity in nesting sites, including off-ground locations and placement of nests on artificial substrates (32). However, we do not know whether this

behavioral plasticity is replicated across urban-colonizing populations, or what consequences may arise from nesting off of the ground or on artificial substrates. Understanding the role of plasticity in nesting success and its predictability across cities is essential to understanding what makes this urban colonizer successful.

Here, we examine plasticity in nest-site selection in an established population of juncos in urban Los Angeles. We ask three questions. (1) Is plasticity in nest-site selection adaptive or nonadaptive? (2) Do juncos practice “informed re-nesting” by changing nest site characteristics based on prior nest outcomes? (3) Are nesting plasticity and nest outcomes convergent between two urban junco populations? We predicted that behavioral plasticity in nest-site selection would be adaptive, and that use of off-ground, artificial nest sites would increase nest success, similar to findings from the San Diego population (32). Furthermore, we predicted that breeding pairs would be more likely to change nest heights and substrate types after a failure than after a success. Finally, we predicted that the Los Angeles population would show a similar proportion of nests above the ground as the San Diego population, with a corresponding similarity of success.

Methods

Study Sites

Field work was conducted on the campus of the University of California, Los Angeles (UCLA). The campus is located in the foothills of the Santa Monica Mountains, and is primarily surrounded by an urban matrix including commercial development, residential communities, and urban green space. The nearest significant natural habitat lies approximately 2 km away in the Santa Monica Mountains. The campus is heavily urbanized and is characterized by impervious

surface cover (buildings and walkways) and extensive grassy lawns interspersed with ornamental trees (particularly *Pinus canariensis*, *Platanus* sp. and *Eucalyptus* sp.). Juncos did not breed in Los Angeles prior to 2000 (39), but commonly wintered throughout West Los Angeles (38). Juncos were first recorded summering in nearby Stone Canyon sometime between 2004 and 2008 (Jared Diamond pers. comm.). Fledglings were seen on the UCLA campus by summer 2008 (P. Yeh, pers. obs.). They have recently expanded their breeding range throughout much of West Los Angeles. The portion of the Los Angeles population located directly on the UCLA campus consists of approximately 100–120 breeding pairs.

Comparison data for our convergence analysis was obtained from previously published data from an urban junco population at the University of California, San Diego (UCSD) in San Diego County, California. Juncos colonized this suburban campus in the early 1980s, and rapidly established a resident population on and around the campus (30). Data on San Diego juncos was collected between 1998 and 2002, so data was collected between fifteen and twenty years after colonization at both sites. Colonists likely originated from the Laguna Mountains of San Diego. The San Diego population is sedentary and is isolated from the Los Angeles population by over 170 km; as a result, there is likely negligible intermixing between these two populations, although genetic connectivity has not been tested.

Field Methods

Adult juncos were captured and banded in Los Angeles from January–July in 2018 and 2019. Juncos were captured with mist nets using audio playback of regional junco songs. The vast majority of juncos captured in this way were territorial males, but some females were also captured. Once captured, juncos were immediately extracted from the net and fitted with one aluminum USGS leg band along with a unique combination of three colored plastic leg bands.

This enabled individuals to be reidentified in the field after release. Individuals were sexed using primary sexual traits and plumage characteristics and aged using molt limits. Blood, cloacal swabs, and morphometrics were taken, after which the birds were released.

Beginning in early March of 2019, pairs of juncos were monitored for nesting activity. Nest building began in early to mid-March, and was carried out by both sexes by bringing nesting material (primarily pine needles, dead grass, and hair) to a concealed spot on the ground, in a shrub or tree, or on an artificial surface. When a nest was found in the nest-building phase, it was monitored once every second day until the first egg was laid, and the first egg date determined. Subsequently, nests were checked after two weeks, close to the age of hatching. Other nests were found during the incubation phase and were located by following females exhibiting bouts of rapid feeding followed by disappearance. Nests found at this stage were monitored once per week until hatching. Nests were also found at the nestling stage by monitoring parents bringing food back to the nesting site. Nestlings were aged *in situ*, and were banded, measured, and sampled for blood seven days after hatching. In order to avoid disturbance, nestling measurements were taken when parents were away from the nest, and the process was carried out in five minutes or less. After banding, nests were monitored every two to three days until fledging occurred or the nest failed. Some nests were located in inaccessible areas (e.g. high in trees or buildings). These were monitored every five to seven days until fledging. Approximately 10 nests were found when the nestlings were older than eight days; to minimize the probability of pre-fledging, we did not band these chicks, but simply monitored their nests every two to three days until fledging occurred. When we did not observe the first egg date, we were able to estimate the first egg date for most nests by back-calculating from the observed age of nestlings, with the exception of inaccessible nests and nests that were predated prior to hatching. Pairs produced between two and four nests per year. Females initiated new

nesting attempts soon after a prior nest was fledged or predated (within a few days to two weeks). The latest nests were banded at the end of July, and the nesting season was complete by the second week of August, at which point captured adults had begun molting wing and/or tail feathers.

Multiple characteristics of nests were measured. Nest height from ground was estimated visually by a single trained observer. After nesting concluded, we revisited sites to identify the vegetation of nesting substrate. Juncos nested in a wide variety of vegetation species. To facilitate analysis, these substrates were lumped into eight different functional types: debris, bunchgrass, herbaceous/non-woody perennial, prostrate shrub, erect shrub, vine, tree, and artificial substrate. Artificial substrates encompassed all unnatural surfaces on which nests were directly placed, primarily on buildings but also on concrete surfaces.

Nesting attempts were considered successful if they produced at least one fledgling. Fledglings were located by careful monitoring of the territory surrounding the nest to watch for parents delivering food to concealed young. Nests with chicks that disappeared well before fledging (< 10 days since hatching) and those abandoned or predated during incubation were considered failed nests. Due to >900 hours of cumulative monitoring, we have very high confidence of the recorded nest outcomes. Only individuals for whom all nests were found and their outcome determined were used in our analysis. All parental pairs included at least one banded individual. While in most cases this was the male, in some cases only the female was banded, or both were banded. While it is possible that individuals might have swapped mates over the course of the breeding season, we consider this unlikely due to observed pair fidelity by pairs where both males and females were banded.

Statistical Analysis

Multiple analyses were conducted to test for behavioral plasticity and its impacts on breeding populations of juncos in Los Angeles and San Diego. In each analysis we included 130 nests produced by 48 breeding pairs during the 2019 breeding season in Los Angeles, and 579 nests monitored between 1998 and 2002 in San Diego. Models were built using a combination of Generalized Linear Models (GLMs) and Generalized Linear Mixed Models (GLMMs) and run in R version 3.6.1 (40) with the *lme4* package (41).

Adaptive or Non-adaptive Plasticity

We examined the binary response of nest success as a function of two plastic traits—nest height and nest substrate—using a Generalized Linear Model (GLM) with a logit link. To increase the power of our statistical analysis, we consolidated nest substrate data into two categories of a binary variable: nests placed directly on an artificial surface or on vegetation, such as vines, growing on an artificial surface, were coded as “artificial”. All other nests were categorized as “non-artificial”. We tested three different models: one that included nest height, but not artificial substrate, one that included artificial substrate but not nest height, and one that included both variables, to evaluate the explanatory power of each variable separately as well as together, and to account for covariance. Because many off-ground nests were difficult to monitor, it is possible that nests above the ground might have been more difficult to observe, and thus found at a later stage; consequently, each model also included age of nest at discovery as a fixed effect, as well as first egg date. As we monitored between two to four nests (median = 3) for each pair of birds, we evaluated using a random intercept for pair; however, the contribution of this random effect to explaining total variance was negligible, so we dropped it from the model. We were unable to determine the first egg date and discovery age for some nests; to avoid discarding samples, we imputed values for these nests using the multiple imputation package *mice* (42). Similar results

were obtained when data was not imputed. We generated values using a stochastic regression method, with vegetation type, discovery age, first egg date, and nest order as predictors. Five imputations were generated five times, and the model p-values were subsequently pooled. All continuous covariates – nest height, first egg date, and discovery age – were scaled to a mean of 0 and standard deviation of 1 prior to modeling. Variables were considered to have predictive power if their p-value in the best candidate model was less than 0.05. We expected that nests located on artificial substrates to be highly correlated to off-ground nests, owing to the location of most off-ground nests. To determine if one of these two correlated variables was a primary predictor of success, a Variance Inflation Factor (VIF) was determined using the package *car* (43), with a VIF over 5 indicating that one of the variables was a dominant predictor of nest success.

Informed Re-nesting

We defined informed re-nesting as individuals selecting nest sites based on the “win-stay lose-switch” model (7), or WSLS. We used Pearson’s χ^2 test of independence to examine whether parent juncos changed their nest height (off-ground versus on-ground) and substrate preference (vegetation functional type) at a greater frequency after a nest failure than after a success, in accordance WSLS. Additionally, to determine if WSLS was adaptive, we examined nests that were built after the previous nest failed, and used Pearson’s χ^2 test of independence to evaluate whether nest success differed by either substrate reuse or nest height reuse.

Behavioral Convergence

Behavioral convergence between the Los Angeles and San Diego populations was tested by comparing all of our Los Angeles nest records with data collected from 579 nests by Yeh et al.

(32) from 1999–2002. We used Pearson's χ^2 test of homogeneity to evaluate whether there was a difference in the proportion of off-ground nests between the sites. To determine if success varied between the two sites and by nest height, we used a binomial GLMM with nest success as a response variable, population location and nest height (off-ground versus on-ground), as well as their interaction, as fixed effects, and year of data collection as a random effect.

Results

Nest characteristics of the Los Angeles population

In total, 170 nests were found in the Los Angeles population during the 2019 breeding season. Of these, 130 nests belonged to 48 pairs that were intensively monitored throughout the breeding season in Los Angeles and were used for statistical analysis. The 130 nests were found in 37 taxa of vegetation. *Hedera* sp. (Common Ivy) was the most frequently used nest substrate, with 28 nests (21.5% of the total), followed by *Lantana* sp. (Lantana) and *Parthenocissus tricuspidata* (Boston Ivy) with eight and six (6.2% and 4.6%) nests respectively. The 37 vegetation taxa were consolidated into functional categories. A plurality of nests was found in herbaceous cover (39; 30%); the next most abundant functional types used were: grass/bunchgrass (18; 14.3%), artificial (18; 13.8%), and prostrate shrub (16; 15.1%). Erect shrubs (12; 9.5%), vines (12; 9.5%), trees (8; 6.2%), and debris (7; 5.6%) were used less frequently as substrates (Table 1).

Eighteen nests (13.8%) were located directly on artificial structures, along with 12 (9.5%) that were placed on vines growing on the walls of buildings, for a total of 30 nests (23.1%). Generally, nests located directly on buildings were placed on horizontal ledges on the sides of buildings. For example, one pair nested four times in two abandoned black phoebe (*Sayornis nigricans*) nests seven meters above the ground in the inner eave of a building. Another pair nested

twice on top of an external window shutter. One pair nested twice in the stairwell of a building, connected via skylights to the outside. One pair nested twice on the window ledge of an office building, while another nested in the outside decorative brickwork of a parking structure. One pair nested four times in two unusual locations, alternating between nesting underneath a cardboard box in a trench and five meters below-ground in a storm gutter.

Forty-nine nests (38%) were located off the ground – on artificial structures, vines, trees, or shrubs. Nest heights ranged from less than 0.25 m off the ground (near the base of a small *Nandina* bush) to greater than seven meters off the ground (e.g., multiple nests located on artificial structures and trees up to 12 m tall).

Adaptive or Non-adaptive Plasticity

Overall, 95 of 130 nests (71.5%) fledged at least one offspring. We found that nests placed on artificial surfaces or on vines on artificial surfaces had a significantly higher success rate than nests on other substrates (slope \pm SE = 0.21 ± 0.09 ; $p = 0.03$). We found that height above ground by itself had a marginally positive impact on nest success, but that this effect was not significant (slope \pm SE = 0.07 ± 0.04 ; $p = 0.08$). Including both variables in the same model diluted the effect (artificial: slope \pm SE = 1.18 ± 0.75 , $p = 0.12$; height: 0.19 ± 0.24 , $p = 0.52$). Because nest height above ground and substrate were highly correlated ($r^2 = 0.57$), we ran a variable inflation factor analysis to determine if a driving variable could be identified. However, this test was inconclusive (VIF = 1.32). Neither first egg date (slope \pm SE = -0.23 ± 0.22 ; $p = 0.26$) nor discovery age (slope \pm SE = 0.33 ± 0.22 ; $p = 0.14$) showed a strong influence on nest success based on our full model.

Informed Re-nesting

WSLS was practiced by at least some members of this population. Juncos were more likely to change type of nesting vegetation after a failure than after a success ($\chi^2 = 4.93$, $df = 1$, $p = 0.03$; Figure 1). Pairs reused the same substrate 68% of the time if their previous nest was successful, compared to only 40% of the time if their previous nest had failed. Prior success also showed a marginal correlation with re-nesting at a different height, though this effect was not significant ($\chi^2 = 2.85$, $df = 1$, $p = 0.09$). Pairs re-nested at a similar position, either on-ground or off-ground, 79% of the time following a successful nesting attempt, compared to only 59% of the time following a nesting failure. Finally, pairs that changed either nest substrate or off-ground status after a prior failure were not more successful than those that used the same substrate and height, although the sample size was small ($n = 21$; substrate: $\chi^2 = 1.66$, $df = 1$, $p = 0.20$; height: $\chi^2 = 0.42$, $df = 1$, $p = 0.52$).

Behavioral Convergence

Both the Los Angeles and the San Diego populations had a sizable proportion of off-ground nests. However, off-ground nests were significantly more frequent in the Los Angeles population, 35%, than the San Diego population, 13% ($\chi^2 = 40.0$, $df = 1$, $p < 0.001$; Figure 2). Controlling for nest height, nest success was also significantly higher in the Los Angeles population (slope \pm SE = 0.88 ± 0.41 , $p = 0.03$), where 71% of nests in Los Angeles were successful compared to only 50% of San Diego nests (Table 2). In both locations, nest success was much higher in off-ground nests (slope \pm SE = 1.24 ± 0.27 ; $p < 0.001$). This difference is potentially due to the differential success of on-ground nests between the two areas: in Los Angeles, 67 % of on-ground nests were successful compared to only 45% in San Diego, whereas, 82% of off-ground nests in Los Angeles and 77% of off-ground nests in San Diego were successful (Figure 3). However, the model of nest success did not support this interaction between location and nest height (slope \pm SE = -0.47 ± 0.52 , $p = 0.39$).

Discussion

We found evidence that nest-site selection by juncos that have recently colonized urban Los Angeles was adaptively plastic and identified the WSLS strategy as a mechanism in some cases. Plasticity was demonstrated by the use of a wide variety of artificial nesting sites—such as on buildings and in artificial trenches—that are not available in wildland sites, along with a high proportion of off-ground nests. Nests built on artificial and off-ground sites were more successful than those built in vegetation or directly on the ground, as predicted by prior research on the San Diego population. As expected, juncos were more likely to use a different nesting substrate if their previous nest failed than if their previous nest was successful. However, contrary to our prediction, employing this strategy did not increase nest success, although our analysis of 21 re-nests may have lacked power. Our findings generally support the hypothesis that plasticity plays a role in adaptation to urban environments, although not always in the ways we predicted.

Pre-existing plasticity may predispose juncos to make use of novel nest sites in urban areas. When the expression of traits is constrained by environmental limitations, cryptic phenotypic variation may persist, only to be expressed when the environment changes (11). Peluc et al. (8) experimentally demonstrated this in orange-crowned warblers (*Leiothlypis celata*) on the California Channel Islands; individuals that did not co-inhabit islands with avian nest predators altered nest site and provisioning rate when exposed to those predators' calls (8). This suggests that plasticity in breeding behavior can be conserved even when the drivers responsible for those behaviors are no longer present.

Urban environments may favor species that harbor greater plasticity (44). Plasticity in junco nest site selection may be constrained in wildland populations due to a limitation of vertical surfaces, and subsequently released in urban areas, where surfaces such as walls and

building faces are abundant. Interestingly, juncos have been observed to use natural embankments in wildland areas as nesting sites (45). Artificial surfaces such as buildings and walls might mimic these similar natural surfaces.

In addition to facilitating local adaptation, plasticity may hasten evolution in a novel environment (46). Novel conditions in urban environments can be an evolutionary obstacle for many species, as populations may become extirpated before evolution resolves phenotypic mismatches. Plasticity may encourage local adaptation to their new environment, thus allowing populations to persist long enough for evolutionary adaptation to take place. In cases where plasticity is adaptive but does not produce the optimal phenotype in the new environment, evolution by natural selection can then close this gap (47,48). In certain situations, plasticity may reduce adaptive value, or even become maladaptive (49,50). For instance, as the frequency of a beneficial phenotype such as the use of artificial nest sites increases, switching to a different phenotype after a failure may become maladaptive. In such a situation, there could be selection against the recognition of other substrates as potential nesting sites. This reduction in plasticity after local adaptation may play a large role in evolution in novel environments (50).

Identifying mechanisms of plasticity is important for understanding how plasticity impacts adaptation (2). We found that informed re-nesting through WSLs explains some of the plasticity in junco nesting behavior. Informed re-nesting may facilitate local adaptation by allowing individuals to learn from prior experience (51). By switching nest substrates after failure, juncos may sample a wider variety of nest site characteristics, allowing them to discover and use safer sites. In comparing two species, an “urban adapter” versus an “urban avoider”, Kearns and Rodewald (44) found that the urban adapter altered nest characteristics after a prior failure, while the urban avoider did not. At the same time, juncos in our study were not more

likely to switch between artificial and non-artificial sites after failure than after success, suggesting that they may not evaluate nest-site success based on these specific criteria.

WSLS in nest-substrate choice did not increase nesting success. This runs counter to our expectations based on prior work by Chalfoun and Martin (7), which demonstrated that WSLS in nest location and characteristics increased nesting success in Brewer's sparrows (*Spizella breweri*) (7). One possible explanation for why informed re-nesting would be nonadaptive is that an individual that is switching to a different substrate after a nest failure has the choice to select between many different substrates, only some of which might increase nesting success. If a new substrate is chosen randomly, then most switches would not increase fitness, and thus would be nonadaptive. Additionally, plasticity in nest-substrate selection might be accompanied by associated costs (52). For example, while birds that remain in similar substrates may not happen upon the ideal nest substrate, by changing within-substrate nest characteristics, they may still be able to increase nest success. Finally, nesting success could be more heavily dependent on other factors besides nest placement, such as a parent's ability to obtain enough food for their offspring, or to be stealthy enough to keep predators from finding the nest.

One important caveat is that due to a low nest failure rate, our sample size for this analysis was very small, and more data should be collected to better understand the impact of informed re-nesting on success. Further research should compare nest success for substrates between individuals that reuse the same nest substrate regardless of prior nesting outcome and those that do not. Juncos could be using private information gathered across multiple years to determine ideal nesting sites. Longer-term, longitudinal studies will allow for more sophisticated models to test the factors that play a role in nest site selection.

We found that this behavioral plasticity acted similarly across both the Los Angeles and San Diego populations, suggesting that there is behavioral convergence in these two urban areas.

Both populations showed far higher levels of off-ground nesting than has been observed for this subspecies in nonurban locations; prior research on nonurban juncos in Western North America found off-ground nesting rates from 0–6% (30,53). This suggests that plasticity can facilitate behavioral convergence, when isolated populations display similar behaviors in response to urbanization (6). Nevertheless, the two populations differed in the magnitude of this shift, with Los Angeles juncos nesting off-ground three times more often than San Diego juncos, suggesting behavioral divergence between the two populations. One possible explanation is that the use of off-ground nest sites is human-density-dependent and location of our Los Angeles study – the UCLA campus – is a more densely built and populated than its San Diego counterpart (54). Thus, if juncos harbor a preference for off-ground or artificial nesting sites, we could expect these sites to be more readily available for the Los Angeles population.

Additionally, increased urbanization may lead to more frequent off-ground nest sites as a result of increased human disturbance and traffic. Human disturbance can prevent organisms from utilizing urban spaces (55). However, we found very few cases of abandoned on-ground nests, even in highly trafficked parts of our study area, suggesting that juncos may be habituated to human disturbances. Overall, our findings suggest that while conditions in the two cities cause populations' nesting behavior to change in the same direction, the magnitude of the plastic response differs between populations.

Los Angeles juncos showed higher nest success rates than San Diego juncos. Increased nesting success may be a factor in the rapid colonization of West Los Angeles by juncos, compared to the more modest range expansion documented in San Diego, where juncos were largely restricted to the UCSD campus at the time of data collection (32,38). Interestingly, the disparity in nest success persisted even after accounting for a higher frequency of off-ground nests at the Los Angeles site. Possible explanations for this difference include a lower predator

density at the Los Angeles site, or the use of more secure nesting locations, That on-ground nests in Los Angeles seem to face lower predation pressure is unexpected, considering the high levels of off-ground nesting; this suggests that use of off-ground nesting sites may not necessarily be a response to predation. However, it is possible that by increasing the number of nest sites available and reducing the density of on-ground nests, off-ground nesting may reduce frequency-dependent predation (56). Use of novel nesting sites as a cause versus an outcome of predation rates should be further studied in the context of urban ecosystems.

Ultimately, we found that urban birds demonstrated plasticity, that this plasticity was adaptive, but the outcome of that plasticity varies across populations. For urban adapters, there may not be a “one size fits all” way to live in our cities. Understanding the importance of plasticity to urban adaptation will help us understand the patterns of both species and behavioral diversity in cities. Furthermore, understanding how and if convergence occurs within one species is necessary to understand the predictability of evolution in cities (57). Findings from one population might not be generalizable to other populations due to heterogeneity across populations and cities and variation in fitness trade-offs (58). Future research should take advantage of cities as independent ecological experiments to better understand how populations adapt to unique urban pressures.

Figures and Tables

Table 1. Outcomes of nesting attempts for each nest substrate type. (n = 130)

		# Successful nests	# Failed nests
Artificial	Artificial	17	1
	Vine	11	1
Non-artificial	Tree	5	8
	Shrub	9	3
	Prostrate	11	5
	Herb	22	17
	Debris	6	7
	Grass	15	3

Table 2. Outcomes of off-ground and on-ground nesting attempts at each site. (n =709)

		Off-Ground	On Ground
San Diego	Failure	23	276
	Success	57	223
Los Angeles	Failure	9	27
	Success	40	54

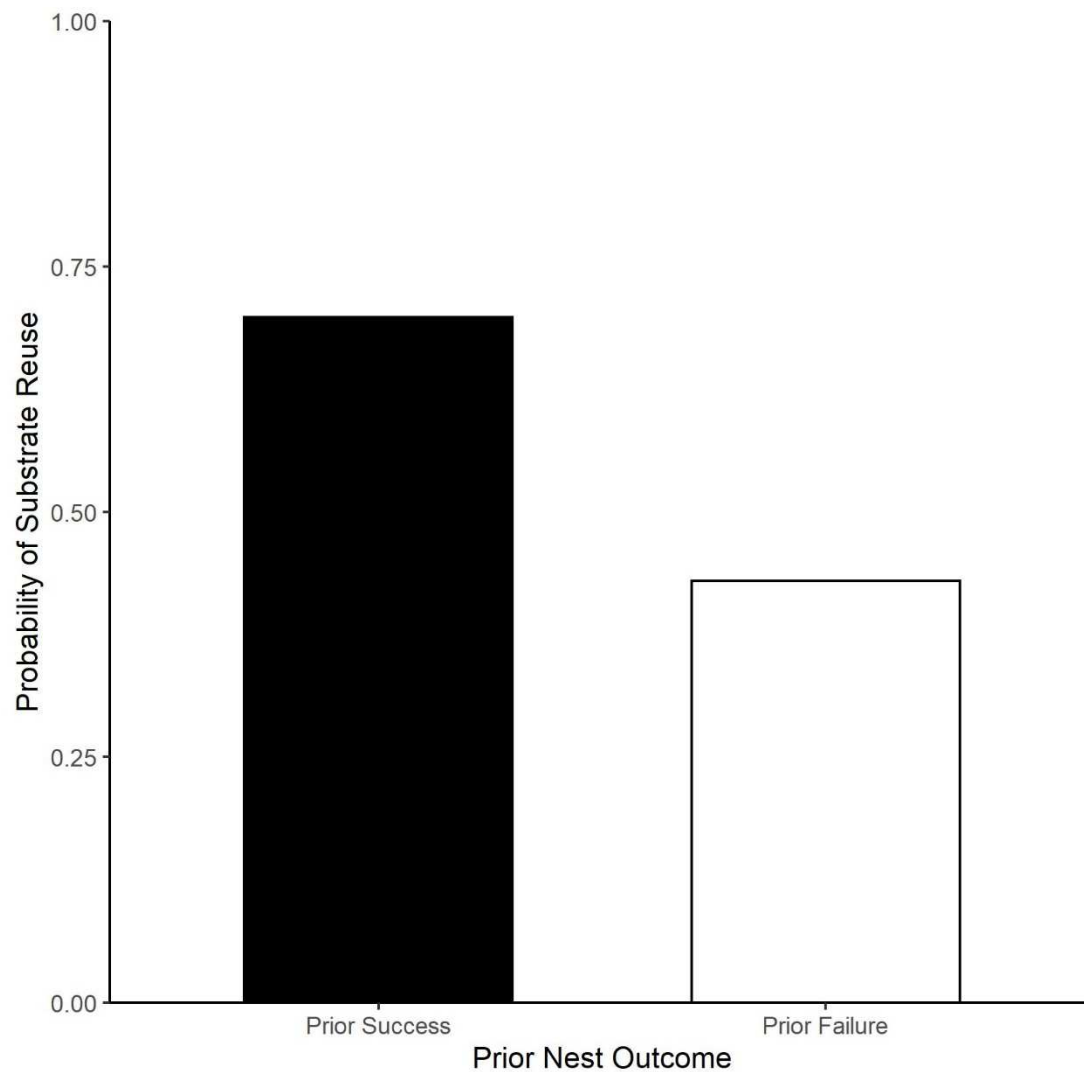


Figure 1. Relative frequency of vegetation substrate reuse for nests when the prior nest failed (n = 21) and was successful (n = 62) in Los Angeles. Substrate reuse occurred when a pair made their nest in the same substrate type as their immediate prior nest. Substrate types are described in the Field Methods section of the Materials and Methods. Initial nests produced by each pair were not considered for this analysis. Difference in substrate reuse rate was significant ($p = 0.03$).

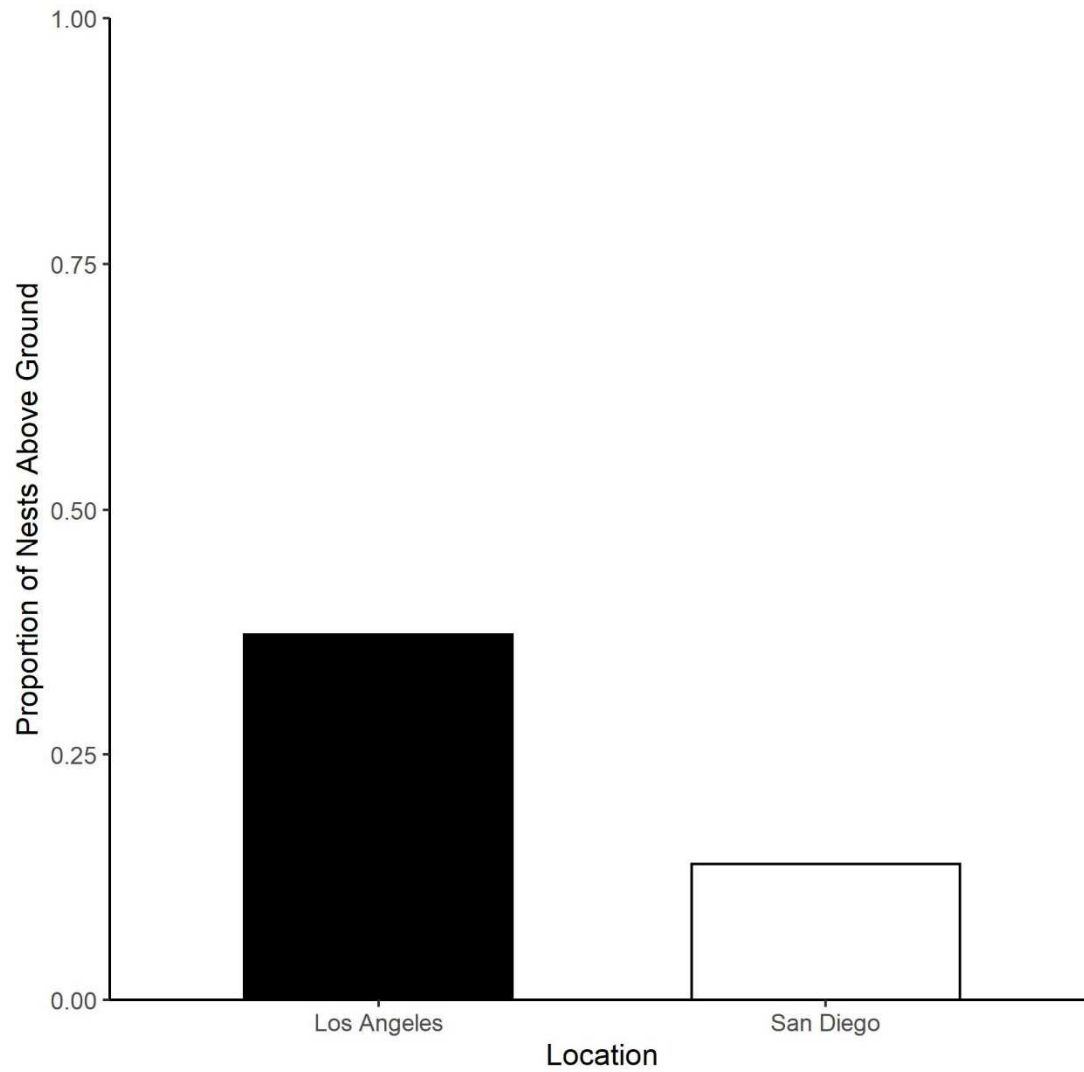


Figure 2. Proportion of off-ground nests in the Los Angeles (n = 130) and San Diego populations (n = 579). The difference in proportion of off-ground nests was significant ($p < 0.001$).

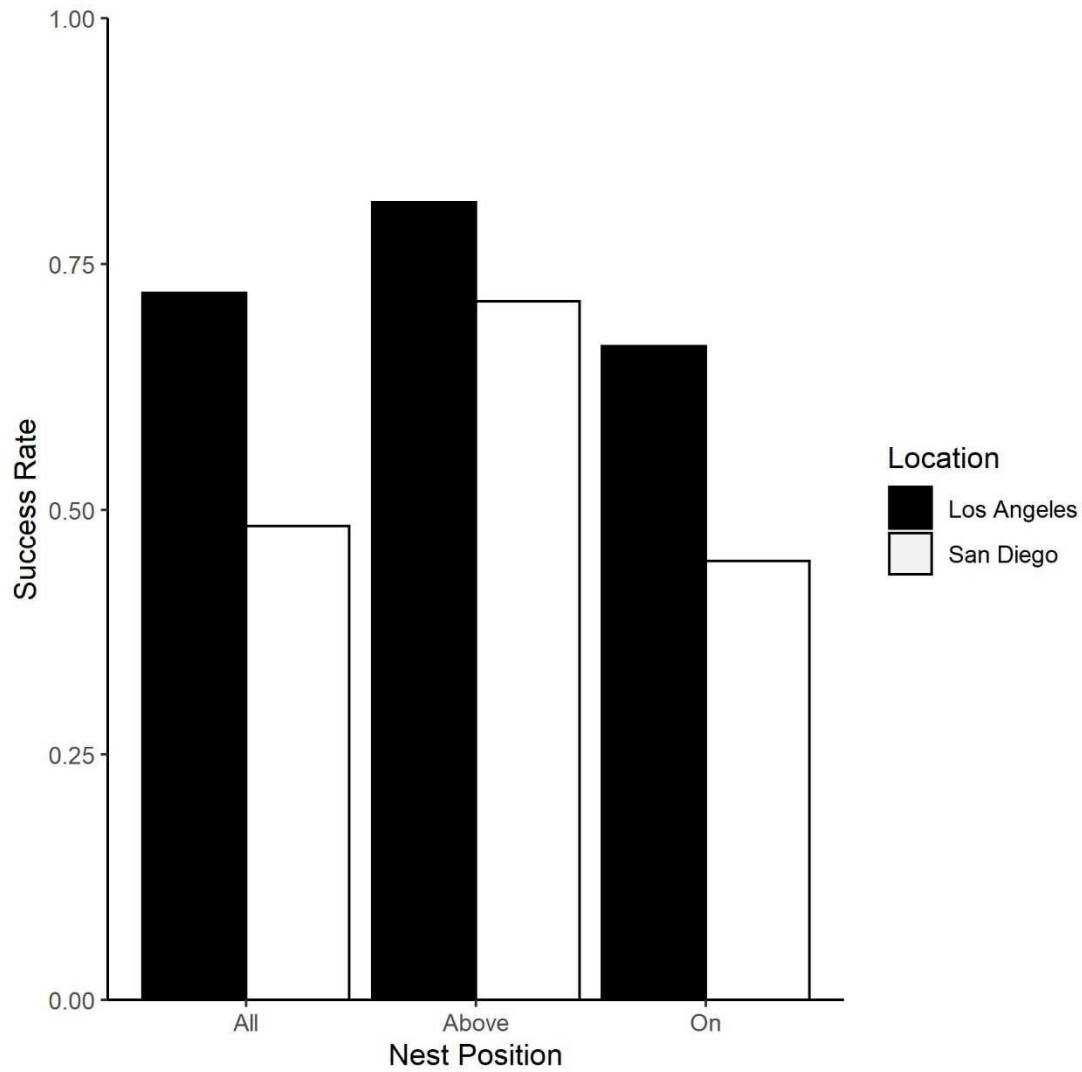


Figure 3. Comparison of success rates between the Los Angeles (n = 130) and San Diego (n = 579) populations for: all nests, off-ground nests (“above”) and on-ground nests (“on”). Difference in success rates between populations was significant (p = 0.042).

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