AVIAN CONSERVATION
& ECOLOGY

VOLUME 17, ISSUE 1, ARTICLE 7

Gray, M., K. E. Sieving, and J. A. Cox. 2022. The nuthatch and the hare: Slow explorers dominate in a re-established population of the Brown-headed Nuthatch (*Sitta pusilla*) two decades later. Avian Conservation and Ecology 17(1):7. https://doi.org/10.5751/ACE-02111-170107

Research Paper

The nuthatch and the hare: Slow explorers dominate in a re-established population of the Brown-headed Nuthatch (*Sitta pusilla*) two decades later

Mary Mack Gray [1], *Kathryn E. Sieving* [2] *and James A. Cox* [1]
[1]Tall Timbers Research Station and Land Conservancy, Tallahassee, Florida, USA, [2]University of Florida, Department of Wildlife Ecology and Conservation

ABSTRACT. Animal behavior regularly has substantial effects on the outcomes of reintroduction efforts. Reintroduction involves capturing a subset of individuals from a source population and releasing them into novel environments where variation in retention rates, predation, and territory acquisition could affect the age-class structure, sex ratio, and genetic and phenotypic characteristics of restored populations. Exploratory behavior, quantified as the rate that individuals explore novel settings, is one such heritable trait that might be affected by translocation, especially given recent studies suggesting that exploratory behavior can predict the survival and retention of individuals in unfamiliar environments. To assess the potential effects that translocation may have on exploratory behavior, we compared exploratory behavior for three Brown-headed Nuthatch (*Sitta pusilla*) populations: (1) a population reintroduced to Everglades National Park in 1998; (2) a population close to the original source population, and (3) a distant control population in north Florida. Exploratory behavior was quantified by placing individuals (n=17 per population) in an exploratory chamber and comparing flights/hops, scanning events, thoroughness of exploration, and other movement behaviors. We found that individuals in the reintroduced population scanned less, conducted fewer flights/hops, and were more sedentary than individuals in the other populations. Our findings suggest a shift in the prevalence of personality types toward slow explorers has taken place in the 20 years since reintroduction, adding to other studies suggesting that slow explorers fare better in novel environments. Although the reintroduced population contained fewer fast-exploring individuals relative to the other populations studied, fast-explorer phenotypes may increase over time if they convey the fitness benefits described in other studies.

Le lièvre et la sitelle : les explorateurs lents dominent dans une population réintroduite de sitelles à tête brune (*Sitta pusilla*) deux décennies plus tard

RÉSUMÉ. Le comportement animal influe souvent considérablement sur le résultat des efforts de réintroduction. La réintroduction implique la capture d'un sous-ensemble d'individus parmi une population source et leur libération dans de nouveaux environnements où la variation des taux de rétention, la prédation et l'acquisition de territoires pourraient affecter la structure des catégories d'âge, le ratio entre les sexes et les caractéristiques génétiques et phénotypiques des populations restaurées. Le comportement exploratoire, quantifié comme le rythme auquel les individus explorent les nouveaux environnements, est l'un de ces traits héréditaires qui peuvent être affectés par le déplacement, en particulier si l'on tient compte des études récentes suggérant que le comportement exploratoire peut prédire la survie et l'implantation des individus dans des environnements non familiers. Pour évaluer les effets potentiels du déplacement sur le comportement exploratoire, nous avons comparé cette dernière caractéristique chez trois populations de sitelles à tête brune (*Sitta pusilla*) : (1) une population réintroduite dans le parc national des Everglades en 1998 ; (2) une population proche de la population source originale ; et (3) une population témoin distante au nord de la Floride. Le comportement exploratoire a été quantifié en plaçant des individus (n=17 par population) dans une chambre exploratoire et en comparant les vols/sauts, les événements d'observation, la rigueur de l'exploration et les autres déplacements. Nous avons constaté que les individus des populations réintroduites observaient moins, réalisaient moins de vols/sauts et étaient plus sédentaires que les individus des autres populations. Nos résultats suggèrent un changement dans la prévalence des types de personnalité en faveur des explorateurs lents au cours des 20 années qui se sont écoulées depuis la réintroduction, ce qui vient s'ajouter aux autres études suggérant que les explorateurs lents obtiennent de meilleurs résultats dans les environnements nouveaux. Même si la population réintroduite comprenait moins d'individus explorateurs rapides que les autres populations étudiées, les phénotypes d'explorateurs rapides peuvent augmenter au fil du temps s'ils manifestent les avantages en termes de condition physique décrits dans d'autres études.

Key Words: *animal personality; exploratory behavior; Florida; reintroduction; Sitta pusilla; translocation*

Correspondent author: Mary Mack Gray, 13093 Henry beadel dr, Tallahassee, FL 32312, graymarymack@gmail

INTRODUCTION

Efforts to restore wild bird populations to formerly occupied areas have increased steadily in recent years to counter the negative effects of habitat loss and fragmentation (Armstrong and Seddon 2008). Such reintroductions typically occur in areas that have undergone extensive restoration and satisfy pre-extirpation conditions (Armstrong et al. 2015). Translocation is an important conservation tool, but the process of capturing birds and then releasing them in foreign settings likely has many potentially unintended and as yet undocumented effects (Smith and Blumstein 2013). For example, the procedures used to capture individuals for translocation can lead to biases in the age, sex, or behavioral phenotype of individuals moved (Garamszegi et al. 2009, Merrick and Koprowski 2017). Variation in the responses to the stress associated with translocation may introduce additional biases among individuals comprising the founding population (Mihoub et al. 2011). Furthermore, the unusual conditions present during the early phases of reintroduction when conspecifics occur at low densities could affect dispersal and breeding behavior for years (Komdeur 1992, Moseby et al. 2020).

Behavioral phenotypes are increasingly recognized as influential factors in reintroduction efforts. Individuals in a population exhibit temporally consistent behavioral differences that are often heritable and predictable across contexts. Such "personality" or behavioral types are increasingly linked to differential performance of individuals in reintroductions to novel environments (Reale et al. 2007, May et al. 2016, Cornelius et al. 2017). For example, brushtail possums (*Trichosurus vulpecula*) that exhibited risk-taking behaviors prior to translocation had lower survival than individuals exhibiting less risky behavior (May et al. 2016). If individual variation in risk-taking behavior relates to adaptive polymorphisms in a source population (Wolf and Weissing 2012), translocation may artificially alter the prevalence of the behavior and lead to a reduction in the behavioral diversity of reintroduced populations (McDougall et al. 2006, Geffroy et al. 2020).

Exploratory behavior, expressed as the rate at which individuals investigate novel environments, is often consistent within individuals but varies among individuals in a population and is also heritable in many avian taxa (Sih et al. 2004, Dochtermann et al. 2019). Exploratory behavior co-varies with other behaviors, and quantifying exploratory behavior can be used to position individuals along a proactive-reactive continuum where proactive individuals are aggressive, bold, and actively explore novel environments and reactive individuals are shy, less active, and respond carefully to changes in their environment (Koolhaas et al. 1999, Sih et al. 2004, Reale et al. 2007). Russell (1983), and Dingemanse et al. (2004) established a framework that linked movements within novel environments to the exploratory tendencies of individuals outside novel environments. Proactive or fast explorers flew, hopped, and scanned more frequently within the test environment while reactive or slow explorers visited fewer positions, hopped less, and scanned less frequently (Huang et al. 2016, Cornelius et al. 2017). Slow explorers appear to be more sensitive to environmental changes, more behaviorally flexible in response, and better at responding to vocal cues received as social information while exploring novel environments (Dingemanse et al. 2002, Guillette et al. 2011, Smit and van Oers 2019). Importantly, measurements of exploratory behavior in birds have also been linked to survival (May et al. 2016, Cornelius et al. 2017), response to stress (Carere et al. 2003), productivity (Both et al. 2005), behavioral flexibility (Wright et al. 2010), and propensity to disperse when placed in unfamiliar environments (Dingemanse et al. 2003, Reale and Montiglio 2020), all factors that could influence translocation success. Further, among-individual behavioral variation in small populations is a key determinant of population viability (Sæther & Engen 2019). Slow exploration has been shown to enhance short-term survival of individuals in novel settings (Bremner-Harrison et al. 2004, May et al. 2016, Cornelius et al. 2017, Geffroy et al. 2020), but few (if any) studies have examined the long-term effect of such behaviors generations after reintroduction. Therefore, monitoring behavioral phenotypes of surviving individuals years, even decades, following reintroductions can be an important assessment tool.

Research Design

We assessed exploratory behavior in a Brown-headed Nuthatch population that was reintroduced to Everglades National Park in south Florida ~20 years earlier (Lloyd et al. 2009). Prior to the establishment of Everglades National Park (hereafter "EVER") in 1947, over 85% of the forest was logged and fire was suppressed resulting in the extirpation of four cavity-nesting bird species by the mid-1960s. In the mid-1990s significant restoration efforts were underway and the focus turned to the restoration of native cavity-nesting birds (Slater 2001). We conducted similar assessments in (1) a south Florida population near the original source population (Picayune Strand State Forest; hereafter "PSSF") used to repopulate the Everglades and (2) a geographically and genetically distinct population in north Florida (hereafter "NFLA"; Han et al. 2019).

We sampled NFLA sites in order to compare exploratory behavior in an un-manipulated population (i.e., never reintroduced or extirpated) from continuous habitats. PSSF and EVER are embedded in a fragmented landscape which likely affects movement behavior and influences the variation in exploratory phenotypes found there (Clobert et al. 2009, Sih et al. 2011, Berger-Tal and Saltz 2019). For example, Cornelius et al. (2017) found that fragmentation explained intra-population variation in exploratory behavior and dispersal success in two populations of White-shouldered Fire-eyes (*Pyriglena leucoptera*). Individuals from fragmented forests were slower explorers than those from continuous habitats, who quickly dispersed away from a novel patch. Further, slow explorers dispersed successfully through a high-risk matrix and arrived at a new patch, while fast explorers from continuous habitats experienced high mortality in the matrix and low dispersal success. Fragmentation in south Florida has resulted in increasing genetic differentiation between northern and southern nuthatch populations (Han et al. 2019); because exploratory behavior is often heritable, it follows that this behavioral type could be under selection in southern populations, which could skew our observations (Sih et al. 2012, Geffroy et al. 2020). Therefore, we also sampled in continuous NFLA in order to exclude the possibility that fragmentation might explain similarities between PSSF and EVER.

Given the growing evidence that slow explorers fare better when introduced to novel environments (Geffroy et al. 2020, Maspons

Table 1. Predicted effects on behavior by reintroduction and fragmentation.

Location	EVER	PSSF	NFLA
Fragmentation	Fragmented	Fragmented	Continuous
Degree Fragmentation	Isolated	Corridors to other populations embedded in dangerous matrix	No significant barriers to dispersal
Population History	Reintroduced	Never reintroduced “Source”	Never reintroduced
Predicted Exploratory Behavior			
Effect Fragmentation	Slower	Slower	Fastest
Effect Reintroduction	Slowest	Faster than EVER	Fastest

et al. 2020) and assuming exploratory behavior is moderately heritable in this species (Dochtermann et al. 2019), we predicted that birds in the reintroduced EVER population would be the slowest explorers. We predicted that PSSF birds would explore faster than EVER birds, but made no predictions about differences in behavior between PSSF and NFLA. We further predicted that NFLA birds from continuous habitats that presumably have no experience with the risks of habitat boundaries would be the fastest explorers (Cornelius et al. 2017). Finally, if fragmentation rather than reintroduction could explain similarities in exploratory behavior, we would expect PSSF and EVER birds to explore at similar rates. Rather, we predicted that PSSF birds would be faster explorers than EVER (Table 1).

Most studies assessing the effects translocation may have on behavioral traits have focused on the time periods just before or just after translocations were performed (Bremner-Harrison et al. 2004, May et al. 2016). Translocation has effectively restored scores of avian populations (Seddon et al. 2007), but the long-term effects have not been monitored regularly despite repeated calls for long-term studies of reintroduced populations (Smith and Blumstein 2013, Richardson et al. 2017). To our knowledge, this is the first assessment of exploratory behavior in a wild bird population approximately five generations after restoration of the population to a portion of its former range.

METHODS

Study species

The Brown-headed Nuthatch (*Sitta pusilla*) is a cavity-nesting, sedentary bird that maintains year-round territories and lives in social groups of 1-5 birds. Nuthatches exhibit a range of complex behaviors that include cooperative breeding (Cox and Slater 2007), seed caching (Yaukey 1995), social grooming (Cox 2012), male-female duets (J. Cox, unpublished manuscript), and tool usage (Gray et al. 2016). Nuthatches are declining in many parts of their range (Sauer et al. 2019). Habitat loss and fragmentation have led to the extirpation of several populations (Withgott and Smith 1998, Lloyd and Slater 2007) and also affected genetic structure within extant populations (Haas et al. 2010, Han et al. 2019). Efforts to offset the effects of habitat loss and fragmentation include two reintroduction attempts in south Florida (Lloyd et al. 2009; Cox et al. in press) and another reintroduction attempt now underway in the northwestern portion of the formerly-occupied range (S. Kendrick, Missouri Department of Conservation, pers. communication). Furthermore, unmitigated climate change is predicted to displace nuthatches from 95% of the current range by 2080, suggesting additional reintroduction projects could be necessary in the future (Matthews et al. 2011).

Study sites

Everglades National Park (EVER)

Forty-two nuthatches were translocated to Long Pine Key in EVER (25.40°N, 80.66°W; Dade Co.) from a population in Big Cypress National Preserve (25.98N°, 80.98W°; Collier Co.) beginning in 1998 (Lloyd and Slater 2007). Long Pine Key contains ~4600 ha of second-growth South Florida slash pine (*Pinus ellioti* var. *densa*) habitat surrounded by freshwater marsh, tropical hardwood forests, and agricultural areas that are not used regularly by the nuthatch (Lloyd et al. 2009, Cox et al. 2012). Patches of pine forest north of EVER that historically connected this site to other nuthatch populations have disappeared as a result of human development. EVER is functionally isolated at the southern-most periphery of Brown-headed Nuthatches’ range as a result of fragmentation (Slater 2001, Han et al. 2019). Demography in this reintroduced population was monitored for several years (Lloyd et al. 2009) but was suspended in 2004 when short-term goals were met (offspring produced successfully bred, population size increased annually, and demographic metrics were similar to the donor population; Lloyd et al. 2009).

Picayune Strand State Forest (PSSF)

PSSF (26.00°N, 81.44°W; Collier Co.) in southwest Florida is ≤ 60 km west of the original donor population and also dominated by second-growth South Florida slash pine interspersed with subtropical cypress strands and hardwood swamps that are not used by nuthatches (Walls et al. 2014). We used PSSF as a surrogate for the original source population used in the EVER reintroduction because the special equipment (swamp buggies) and staff support needed to sample at Big Cypress were not available. An analysis of genetic structure found that nuthatch populations in southwest Florida (PSSF, BCNP, and others) were genetically homogenous (Han et al. 2019). We conducted sampling on the Belle Meade tract (> 5800 ha) which is bordered by major highways to the north and the south, ranches, and the fast-growing city of Naples to the west (Fl. Forest Service 2008). PSSF adjoins a number of large conservation holdings that support other nuthatch populations; however, corridors and suitable habitats in the region are heavily bisected by residential/agricultural developments, forested wetlands, and open marshes that nuthatches do not use.

North Florida properties (NFLA)

We conducted sampling on private properties in the Red Hills region of NFLA (30.66°N, 84.21°W; Leon and Jefferson Cos.).

NFLA properties are located closer to the core of this species' range within a vast, continuous expanse (~176,000 ha) of forest dominated by mature longleaf (*P. palustris*), loblolly (*P. taeda*), and shortleaf pines (*P. echinata*) within intervening fields (< 30%), hardwood forests, and residential areas. NFLA is well-connected to numerous large, suitable habitat patches, and historical logging and human development have been slower and less extensive than in south Florida (Snyder et al. 1990, Moore 2013).

Capture methods

Nuthatches were lured into mist nets using recorded conspecific male and female vocalizations mixed with Eastern Screech-Owl (*Megascops asio*) vocalizations. The same vocalization mix was used across all sites and broadcast through an MP3 player (Cox and Slater 2007). Netting procedures were also the same (6 m mist nets hung 0.5-2.0 m above ground by aluminum poles) with sampling locations selected opportunistically based on habitat conditions and the detection of nuthatches during a 3-min playback period conducted prior to each capture attempt. We targeted individuals that responded within 6-min (one repeat of 3-min playback) and revisited areas where birds were not detected or did not respond aggressively on different days. Capture locations were also separated ≥ 800 m to minimize pseudo-replication (the width of approx. 4 territories; Cox and Slater 2007). Sampling was conducted in the post-breeding season from May to July 2018.

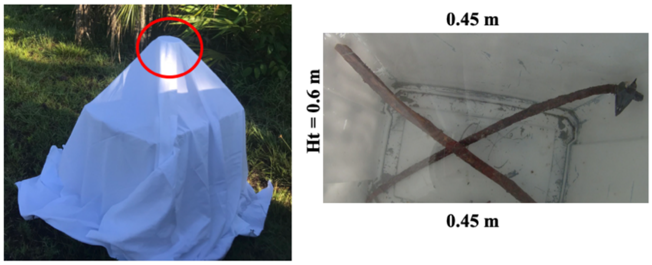
All individuals were captured between 0700 and 1140 and marked with a unique federal band (US Geological Survey Permit 22446; National Park Permit EVER-2018-SCI-0042). A small blood sample (20-40 µl; avg. mass of adult nuthatch = 10 g) was taken from the brachial vein (Han et al. 2019), and a combination of genetic, morphometric, and plumage characteristics was used to estimate age (adult or hatch year) and sex (Matthysen 2010, Tietze and Martens 2009, Li et al. 2010). Blood samples for a subset of individuals (n = 22) were analyzed to determine sex (R. Kimball and M. Zhang, University of Florida). The subset of individuals sexed molecularly (n = 22) included 8 females (n = 2 and 6 for EVER and PSSF, respectively) and 14 males (n = 5 and 9 from EVER and PSSF, respectively). The adults and juveniles sampled across sites were also evenly distributed with 21 adults (n = 7, 8, and 6 from EVER, PSSF, and NFLA, respectively) and 30 juveniles (n = 10, 9, and 11).

Behavioral trials were then performed using either solo birds or individuals tested sequentially in cases where multiple captures occurred (n = 3, 4, and 6 for EVER, PSSF, and NFLA, respectively). Most instances of multiple captures were 2 individuals, but there was also one site at each location where 3 birds were captured and tested. At sites with multiple captures, the amount of time between the first capture and subsequent captures varied from 0-min (two birds caught and extracted at the same time, n = 3) to 16-min. We only held 2 birds at any given time; at sites with 3 captures, the third individual was never captured before we released the first. In some instances (n = 6; 1, 3, 5 for EVER, PSSF, NFLA), a bird vocalized in the chamber while another was being held nearby which may have affected the behavior of the second individual. Holding time might also have influenced behavior. The potential effects that multiple captures may have had on results were assessed by comparing these captures with randomly selected captures of single birds.

Novel-environment evaluations

We assessed exploratory behavior using the "novel-environment" evaluation in which individuals were released in a closed, unfamiliar environment (Verbeek et al. 1994, Dingemanse et al. 2002). To collect samples efficiently among distant field sites, we used a portable observation chamber based on designs used by Kluen et al. (2012) and Polekoff (2018). The body of the chamber was an opaque plastic bin (45 x 45 x 60 cm) with ventilation holes drilled in a 10 cm x 10 cm grid (Fig. 1). A flat sheet of clear, acrylic Plexiglass (75 x 45 cm) with four 2.5 cm holes drilled in each corner covered the chamber. Four PVC tubes were inserted into the corner holes and used to hold a camera (Vivitar DVR786HD HD) approximately 75 cm directly above the chamber. Two pine dowels (approx. 90 cm long) were placed in the chamber in an X formation and 50 cm apart (low and high perches). Tape was affixed to each stem every 20 cm to define 8 possible positions where individuals might perch. The bottom of the chamber and the point where the two stems crossed were scored as additional perch positions (n = 10 positions). Once individuals were placed in the chamber, we covered the PVC tubes, camera, and chamber with a white sheet to mask all external features during the trial (Huang et al. 2012). Each bird was video recorded continuously for 10 minutes and immediately released; total handling time did not exceed 22 minutes. Ten minutes is commonly used in similar assays to define the novel environment exploration period (Drent et al. 2003, Kozlovsky et al. 2014, Devost et al. 2016).

Fig. 1. Exploratory chamber. External (left) and internal (right). Red circle indicates camera.



Quantifying behavioral activities

Behavioral activities were scored after a settlement period that ended when an individual perched in one place for ≥ 20 sec and ceased rapid flights and alarm calling (Kluen et al. 2012). Latency to settle was quantified as the time that elapsed before individuals perched ≥ 20 sec. Behavioral assessments were subdivided into two consecutive 3-min observation periods to evaluate variation over time (Kluen et al. 2012, Thompson et al. 2018). Five individuals (n = 2 from EVER; 1 from PSSF; 2 from NFLA) did not settle in ≤ 4-min and were not included in our analyses due to the 10-min time limit. The 3-min bins used here allowed us to assess within-trial changes in exploratory behavior as well as potential habituation that might occur as a result of increased holding time (Kluen et al. 2012, Thompson et al. 2018).

The novel-environment test yields multiple measures of exploratory behavior under the assumption that animals with different behavioral types will move differently in novel cage environments (Russell 1983, Dingemanse et al. 2004). Following Cornelius et al. (2017) and Dingemanse et al. (2002), we recorded three distinct activities commonly linked to exploratory behavior: the number of flights/hops, the number of scanning events (head movement ≥ 90 degrees), and total positions taken. Additionally, we recorded the number of times each individual pecked an object, swiped its bill on an object, or preened. We also counted whether or not a bird vocalized in addition to time spent gaping during trials as potential measures of stress (Sieving et al. 2010). Vocal output has also been linked to exploratory behavior in other species (Guillette and Sturdy 2011, Ramos et al. 2021a). We noted some birds dropped to the bottom of the cage while others did not, so we recorded the time (sec) individuals spent on or below the lower perches (hereafter “time low”) to identify these different movement patterns within the chamber (Kluen et al. 2012). Scanning and vocalizing are thought to be important behaviors birds use to acquire information about their surroundings (Lima and Zollner 1996, Huang et al. 2016); maintenance behaviors (preening, pecking, and bill swipes) are thought to indicate comfort in a novel environment (Clark 1970, Nephew and Romero 2003, Walther and Clayton, 2005); gaping is indicative of stress (Groombridge et al. 2004).

Statistical analyses

Exploratory activities

We analyzed exploratory behavior in two steps with a focus on three commonly used metrics for exploratory behavior: counts of flights/hops, head turns (scans), and the number of positions taken in the pen. In the first step, we combine the three key measures into an exploratory score that could identify faster or slower exploring birds using a factor analysis. Factor analysis combines related metrics to represent a latent variable that underlies those metrics (in this case exploratory rate; faster to slower). One significant and normally distributed factor score was obtained (eigenvalue = 1.83) where all three measures were positively loaded on the factor score (0.62 for scans, 0.80 for flights and hops, and 0.85 for positions; Tables 2, 3). Individuals that had higher scores were more active during exploration of the chamber. See Table A1 for boxplots of raw factors summarized by location and time period. In step two, we used a generalized linear model (GLM; Gaussian distribution; Zuur et al. 2009) to analyze location and temporal effects on the exploratory factor score (see below for model parameters).

Table 2. Summary statistics for factor analysis (flights & hops, scans, and positions). LR test: independence vs. saturated, Χ2 (3) = 133.3. Prob > Χ2 = 0.00.

Factor	Eigenvalue	Difference	Proportion	Cumulative
Factor 1	1.83	1.90	1.15	1.15
Factor 2	-0.07	0.09	-0.05	1.10
Factor 3	-0.16	.	-0.10	1.00

Maintenance activities

Preening, pecking, and bill-wiping were each somewhat rare, therefore we added up counts of all three behaviors for each individual in each time period and used the total count as an indicator of maintenance activities. As the counts were zero inflated (a number of birds did none of the three), we applied a GLM with a negative binomial link function to test for location and time effects (see below for model parameters).

Table 3. Factor loadings and unique variances on the retained factor (bottom panel).

Variable	Loadings	Uniqueness
Flights/hops	0.80	0.35
Scan	0.68	0.54
Positions	0.85	0.29

Stress indicators: calling, gaping, and seconds perched low in the chamber

Calling behavior was represented by a binary variable (called or not), so we applied a GLM with logit link function. Seconds spent gaping, and seconds spent low in the cage were zero-inflated count metrics, so we applied a GLM with a negative binomial link function for these two measures (Maxwell et al. 2018).

GLM specifications

All GLMs included location (EVER, PSSF, and NFLA) and time period (1st 3-min and 2nd 3-min of observations) and an interaction term (location x time period) as fixed effects. We used an individual bird ID as a random effect to account for the repeated measures across the two time periods. To conduct pairwise comparisons of factor levels (3 locations and 2 time periods) we ran marginal contrasts using $P < 0.05$ as an indication of significant differences among sites and time periods. However, given the high inter-individual variability (e. g., see SD measures in Tables A1.1, A1.2), we also deemed $0.05 < P < 0.10$ on any tests to be indicative of potentially significant trends. GLMs were performed using STATA version 16.1.

Assessing potential biases

To assess any effects associated with the capture of multiple birds at one location rather than captures of a single bird, we calculated differences in behavioral measures for each individual caught with a group and compared these to differences observed among 10 paired samples of 40 randomly selected individuals. The capture of males/females and different age classes also varied among sites but could not be evaluated in GLMs because of missing genetic sex at some sites. To assess the potential effects this might have had, we used nonparametric multivariate analysis of variance with 1000 permutations and the “npmv” package in R (Burchett et al. 2017). We tested for an overall effect of sex and age among populations as well as relative effects across groups (e.g., whether females' scores differed from scores selected randomly). We used a one-way Kruskal-Wallis test to assess variation in latency to settle among sex and age cohorts (the only metric with one sample per individual). We also quantified the absence of movement among populations based on the proportion of individuals that sat stationary in a single position during each 3-min observation period. These assessments were conducted in R version 3.4.2 (R Core Team 2017).

Based on known sex and age data, birds caught at the same time at the same location were likely family groups. The composition of groups caught together and of known sex and age is: male and female pair with 1 male offspring (1 EVER), adult female with male offspring (1 PSSF), and 5 groups of juvenile siblings: 2 males with 1 female (EVER), 2 females with 1 male (PSSF), 1 pair of brothers (PSSF), and male-female siblings (1 PSSF, 1 EVER). Based on age, NFLA birds were likely also family groups: 2 adults with 1 offspring, 1 adult with 1 offspring, and 4 pairs of juveniles, likely siblings. While we did not assess relatedness, juvenile nuthatches, particularly philopatric males, often remain on the natal territory for months after fledging (Cox and Slater 2007).

RESULTS

Descriptives and bias tests

We quantified exploratory behavior for 17 individuals from each population (*n* = 51). Individuals from all populations explored the chamber thoroughly, and ≥ 4 individuals from each population visited all 10 possible positions within one of the 3-min observation periods. Mean time to settle (41 s ± 36 s) did not differ among populations (Kruskal-Wallis X^2 = 1.4, *P* = 0.49). Sex did not have an effect on exploratory behavior ($F_{3.5,\ 61.4}$ = 0.77, *P* = 0.53) nor did age ($F_{4.0,\ 189.4}$ = 0.31, *P* = 0.87). We also found no evidence of capture bias. The *P*-values for all 10 Wilcoxon signed rank tests were ≥ 0.15, suggesting birds captured together (and tested sequentially) displayed behavioral variation similar to that of birds captured individually. No differences in gaping behavior between locations or time periods were detected. See Tables A1.1, A1.2 for descriptive statistics on raw behavioral measures.

Exploratory activities

A clear but non-significant trend toward faster exploration occurred from EVER to PSSF to NFLA populations (Fig. 2). The model interaction term and marginal contrasts show that NFLA birds explored significantly faster than EVER birds (β= 0.6, SE = 0.3, Z = 2.5, *P* = 0.01 and X^2 = 4.0, *P* = 0.04; Tables 4, 5). Activity differences between NFLA and EVER were most pronounced in period 2 (X^2 = 8.4, *P* = 0.004; Table 6), when NFLA birds significantly increased exploratory activity (X^2 = 5.8, *P* = 0.02; Table 7). There was no significant difference in exploratory activity between EVER and PSSF (β = 0.3, SE = 0.3, Z = 1.3, *P* = 0.2). EVER and PSSF maintained the same level of activity over both time periods (Table 7), though we observed a decreasing trend in EVER activity during period 2 (Fig. 2).

Other activities

PSSF birds conducted significantly fewer maintenance activities than birds at the other two sites (z = -2.27; *P* = 0.02; Fig. A2.1, Table A2.1(a)), but marginal contrasts were not significant (Tables A2.1(b-d)). PSSF birds spent more time at the bottom of the cage than other populations (z = 2.1; *P* = 0.03 and X^2 = 3.16; P = 0.07; see Fig. A2.2, and Tables A2.2(a, b)), particularly during period 2 (marginal contrast: X^2 = 3.0; *P* = 0.08; Table A2.2(c)), but within each location, periods did not differ (Table A2.2(d)). NFLA birds called more often than others (z = 1.68; *P* = 0.09; Fig. A2.3, Table A2.3(a)) and marginal contrasts revealed that this trend occurred primarily in period 1 when NFLA birds called more than EVER birds (X^2 = 3.32; *P* = 0.07; Table A2.3(c)). Marginal contrasts between locations and by period within each location were not significant (Tables A2.3(b, d)).

Fig. 2. Marginal predicted mean exploratory (factor) scores based on the mixed effects GLM (Table 3), with 95% confidence intervals, for nuthatches tested at the three locations and in each of the two time periods. Increasing scores indicate ‘faster’ exploration: more flights and hops, more positions visited, and more scans (head turns). See text for location abbreviations. NFLA birds explored faster than EVER birds (Table 4) but this is primarily due to period 2 differences (Table 5). NFLA birds significantly increased exploration in period 2 (Table 6) but exploration was similar in the two sample periods for EVER and PSSF birds.

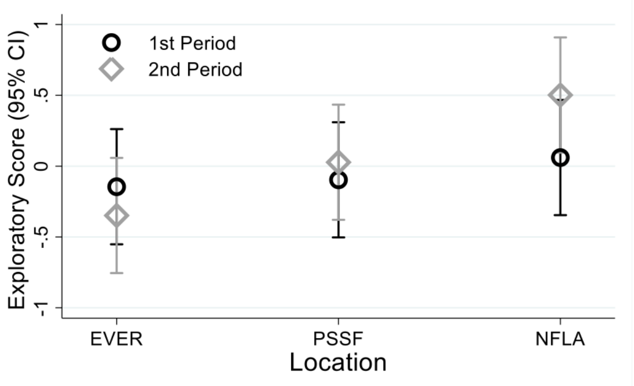


Table 4. Mixed-effects GLM results with main effects and interaction terms for Location (1= EVER, 2 = PSSF, 3 = NFLA) and Period (1st or 2nd sample period in the exploratory chamber) and bird ID as the random effect, and the exploratory (factor) score as the response variable. Z tests refer to comparisons of factor levels to reference levels (as indicated by the numbers in column 1).

Factor	Coef.	SE	Z	*P*>|z|	95% CI
Location					
2 vs 1	0.05	0.29	0.17	0.87	(-0.53, 0.62)
3 vs 1	0.21	0.29	0.70	0.48	(-0.37, 0.78)
Period	-0.20	0.18	-1.11	0.27	(-0.56, 0.16)
Location by Period					
22 vs 1 1	0.33	0.26	1.26	0.21	(-0.19, 0.84)
32 vs 1 1	0.64	0.26	2.49	0.01*	(0.14, 1.15)
_cons	-0.15	0.21	-0.70	0.48	(-0.55, 0.26)
Bird ID					
var(_cons)	0.45	0.12	-	-	(0.26, 0.76)
var(e.explore)	0.29	0.06	-	-	(0.19, 0.42)

DISCUSSION

Slow-exploring Everglades nuthatches

A Brown-headed Nuthatch population reintroduced to EVER 20 years ago contained the slowest exploring individuals evaluated here. EVER nuthatches were significantly slower than NFLA birds (*P* = 0.01; Fig. 2, Table 4), particularly in the second observation period (*P* = 0.004; Table 6). PSSF nuthatches sampled from a population near the original source population used for the EVER reintroduction explored at rates intermediate to EVER and NFLA, though these differences were not statistically significant. We observed a trend toward faster exploration from EVER to PSSF to NFLA (Fig. 2), among other behavioral differences.

Table 5. Marginal contrasts for location effects on exploratory (factor) score factor.

Contrast	df	Chi^2	$P > Chi^2$
Location			
(NFLA vs. EVER)	1	4.03	0.04*
(PSSF vs. EVER)	1	0.65	0.42
Joint	2	4.08	0.13

Table 6. Marginal contrasts for location effects within each period.

Contrast	df	Chi^2	$P > Chi^2$
Location@Period			
(NFLA vs EVER) 1	1	0.49	0.48
(NFLA vs EVER) 2	1	8.40	0.004*
(PSSF vs EVER) 1	1	0.03	0.87
(PSSF vs EVER) 2	1	1.64	0.20
Joint	4	10.26	0.04*

Table 7. Marginal contrasts for period differences within each location.

Contrast	df	Chi^2	$P > Chi^2$
Period@Location			
(2 vs 1) EVER	1	1.23	0.27
(2 vs 1) NFLA	1	5.80	0.02*
(2 vs 1) PSSF	1	0.46	0.50
Joint	3	7.49	0.06

As in this study, others find that fast-exploring individuals typically vocalize more than slow (Guillette and Sturdy 2011, Kerman et al. 2016, Ramos et al. 2021a; but see Cornelius et al. 2017). The best current interpretation of this pattern may be that slow explorers are likely to be more predation-risk averse; as such, less vocalizing may help avoid predator detection (Burnett and Sieving 2016). Maintenance behaviors are often associated with security and relaxation (Nephew and Romero 2003), especially following disruptive events (capture). Preening was positively correlated with proactive individuals in social psittacids (van Zeeland et al. 2013, Ramos et al. 2021b) and chickens (van Hierden et al. 2002). Perching above ground is also more typical of nuthatches than sitting on the ground, suggesting that EVER and NFLA birds were both less stressed than PSSF birds by the novel environment.

We found intra-population variation in exploratory behavior consistent with many of our predictions. Although our prediction that PSSF would be faster explorers than EVER was not supported statistically, we found clear indications of slower exploration in EVER, as well as an effect of fragmentation consistent with other theories (Fahrig 2007, Cornelius et al. 2017). Despite strong differences between NFLA and EVER, pairwise contrasts of PSSF to NFLA/EVER were not statistically significant, pointing to underlying variation between PSSF and EVER that may be the result of reintroduction. PSSF shared some traits with both populations. Similarities between PSSF and EVER are likely adaptive responses to fragmentation, and similarities between PSSF and NFLA are consistent with predictions about never-reintroduced populations. Additionally, exploratory behavior in EVER and NFLA was especially divergent, suggesting that the differences were naturally expressed and may have arisen as a result of reintroduction.

Potential biases

While reasonable, the potential for personality-related sampling bias at the initial capture of birds translocated to EVER seems unlikely given that Slater (2001) captured randomly selected pairs at nighttime roosts. These capture procedures should lessen any bias toward translocation of a specific personality type (e.g., aggressive/bold individuals responding to playback; Both et al. 2005, Gabriel and Black 2012). However, capture procedures used here (mist netting birds using conspecific vocalizations) may have biased samples toward bolder, more exploratory individuals (Biro and Dingemanse 2009). Apparently, slow-exploring birds can identify mist nets and may avoid capture (Stuber et al. 2013), though evidence of biased responses to playback is not uniform among birds (Amy et al. 2010, Jacobs et al. 2014). We targeted individuals that were most responsive to playback in each population, focusing on birds that responded within 6-min of beginning playback (one repeat of 3-min playback). However, if a bias toward boldness did occur, it would favor relatively more fast-exploring individuals across all populations given the positive correlation between boldness and fast exploration (Reale et al. 2010). This would make our assays conservative in the sense that the boldest individuals in EVER were still slower explorers than the boldest birds in the other two populations (minimizing type I error).

Underlying causes

Based on better survival and performance of slow-exploring individuals in translocations of birds to novel habitat patches we predicted that EVER nuthatches would be slower explorers than the other sites sampled. We also predicted that NFLA birds from continuous habitats that have not encountered barriers to movement or risky edges would be the fastest explorers (Fahrig 2007, Cornelius et al. 2017). Evidence that reactive, slow explorers fare better when moved to a strange place is accumulating (Geffroy et al. 2020, Maspons et al. 2020). Slow explorers are often better at gathering and utilizing novel sources of information (Guillette et al. 2011), they exhibit flexibility in response to sudden environmental changes (Coppens et al. 2010, Herborn et al. 2014), they disperse more slowly and over shorter distances (Cote et al. 2010), they act to minimize risk (Hall et al. 2015), and (because of lower activity and conspicuousness) they are better at avoiding predation (McDougall et al. 2006, Bremner-Harrison et al. 2004, Huang et al. 2015, Cornelius et al. 2017, Smit and van Oers 2019). These traits would benefit birds in a strange new place. However, in 20 years a number of other genetic and resource-related factors might also favor or promote slow exploration in the reintroduced Everglades population.

Genetic causes

Populations established via translocation are vulnerable to stochastic and deterministic forces that can yield outsized effects in small, newly established populations (Gregory et al. 2012). Potential stochastic factors include changes brought about by inbreeding, genetic drift, and other factors that can lower genetic and behavioral diversity within small populations, as well as potential biases associated with the individuals initially captured and translocated. The EVER population was reintroduced in part because recolonization was unlikely given the distance to other populations (~40km, Slater 2001); this isolation has likely also precluded gene flow and exacerbated a loss of genetic diversity (Frankham 2015) in this dispersal-restricted species (Cox and Slater 2007). Indeed, a nuthatch population similarly isolated by freshwater marsh and grasslands of the St. John's River were the most genetically distinct among the 13 populations sampled by Han et al. (2019). Only 26 nuthatches (54% of translocated cohort) established territories after their release at EVER. No breeding occurred in the first year post-release, only 16 individuals were observed ≥ 2 years, and adult survival within the population fell sharply following a major storm (Lloyd et al. 2009). While the population has since rebounded (approx. 100 individuals in 2018), the effective population size of the reintroduced population likely fell within the range of 10-20 individuals, which may have resulted in pronounced stochastic effects, including emergence of slower explorers by chance (Griffith et al. 1989, van Oers et al. 2004b).

Alternatively, it is possible that the founding population was composed of slower explorers. If exploratory behavior is heritable in this species (and assuming behavioral variation in PSSF is similar to the original source), we would expect descendants to also retain some characteristics of slow exploration (van Oers et al. 2004a), which is likely reinforced by the lack of gene flow to EVER. The similarities observed among PSSF and EVER may therefore reflect a genetic component of exploratory behavior in Brown-headed Nuthatches rather than the process of reintroduction. However, the observed trend toward slower exploration in EVER suggests both factors (among others) are likely at play; larger sample sizes and repeated testing (including at the time of reintroduction) would aid in explaining the limited differences among these populations; further genetic assessments are underway.

Variation in spatiotemporal resources

Habitat conditions, predators, food, and nesting resources also likely varied among the sites and can influence exploratory behavior in birds (Biz et al. 2017). We did not quantify variation in these spatiotemporal resources, but we completed sampling within a narrow timeframe during the post-breeding period in an effort to minimize potential seasonal effects. Food resources are thought to be less plentiful for nuthatches during winter months (Morse 1967), a season in which food resources have been shown to influence personality types in other birds. Dingemanse et al. (2004) found that fast-exploring male and slow-exploring female Great Tits (*Parus major*) experience greater reproductive success following winters with rich food resources while slow males and fast females do better following food-sparse winters. Winter food resources were likely most similar for the two south Florida populations, and both of these populations were affected by a hurricane 7 months before we collected our samples. Additionally, high-intensity wildfires in PSSF approximately 5 months before sampling further reduced the pine canopy at that site which may explain the disproportionate amount of time PSSF nuthatches spent perched low; while nuthatches preferentially move and forage high in the canopy, the altered landscape may have led PSSF nuthatches to perceive low areas within the chamber as "safe" (Brown and Sherry 2008). White-breasted Nuthatches (*Sitta carolinensis*) exposed to higher winds at newly-created habitat edges began to forage lower on trees than inland birds (Dolby and Grubb 1999). The hurricane may have also reduced food availability (e.g., stripped pine cones, reduced insect abundance) which was the cause of significant population declines in EVER in the years following multiple hurricanes in 2005 (Lloyd et al. 2007). Food scarcity and a reduction in canopy cover and other habitat structures may have affected exploratory behavior in PSSF and EVER, though, such disturbances are regular occurrences for nuthatches in Florida. Regular, low-intensity fires and occasional hurricanes also create nesting snags and help maintain an open mid- and understory. The interaction between spatiotemporal conditions and exploratory behavior can influence fitness outcomes (Haage et al. 2017, Maspons et al. 2020), suggesting a pathway for the maintenance of exploratory types in reintroduced populations over evolutionary time.

Social environments

Social behavior can be fundamental to reintroduction success and many translocations fail when individuals leave the release site and perish or become isolated from conspecifics (Rowe and Bell 2007, Mihoub et al. 2011, Debeffe et al. 2013, Richardson et al. 2015). Individuals that disperse away quickly risk increased exposure to novel predators (Le Gouar et al. 2012, Berger-Tal and Satlz 2019) and unsuitable landscapes (Sih et al. 2011), and lose access to crucial social information at a time when rapid learning is essential to survival (Sih and Del Giudice 2012). In the early years of a restoration effort when conspecific densities are low, dispersal-averse, slow-exploring individuals that remain near the release site benefit from group vigilance and defense, transmission of social information such as resource location, and are able to form social bonds necessary for reproduction and survival (Cote et al. 2010, Reale and Dingemanse 2010). For example, juvenile Hihis (*Notiomystis cincta*; another cooperative breeder) that broadened their social affiliations following translocation were more likely to survive their first year than individuals that did not make this adjustment (Franks et al. 2019). The loss of fast-exploring individuals also results in decreased behavioral (and likely genetic) diversity of the founding population (Reale and Montiglio 2020), which could explain the predominance of slow explorers in EVER today.

Translocated social species may need to reconfigure group structures after their release (Maldonado-Chapparo et al. 2018). Though exploratory behavior and sociability are less explicitly linked than exploratory behavior and boldness/aggression (i.e., sociality is not on the "proactive-reactive" continuum), they are often closely correlated (albeit context-dependent; Reale et al. 2007, Cote et al. 2010). For example, proactive, fast-exploring Great Tits (*Parus major*) also tend to be less "socially bound" and more likely to disperse than slow explorers (Carere et al. 2013). Variation in the manner in which fast/slow explorers socialize might therefore also affect individuals' ability to form groups, and was likely an important component of nuthatch establishment in EVER (Reale et al. 2010). While there are important differences between exploratory-related dispersal and sociability-related dispersal (Cote et al. 2010), in general, slow explorers (which tend to be less aggressive), form long-lasting, stable social bonds and maintain group cohesion while fast explorers tend to have shallow interactions with many individuals and engage in more agnostic displays (Verbeek et al. 1996, Cote et al. 2010, Aplin et al. 2013). Socialization and exploratory behavior can also co-vary with population densities. In Western Bluebirds (*Siala mexicana*), highly social individuals secure more extra-pair fertilizations and fledge more offspring than dispersive, aggressive birds when population densities are high (Duckworth 2006).

Brown-headed Nuthatches appear to make settlement decisions in part based on the presence of conspecifics, a characteristic found in other birds (Fletcher 2007, Aplin et al. 2012). Some dispersing males preferentially settle in male-saturated habitats even though suitable habitats and breeding opportunities are available nearby (Cox et al. 2019), suggesting the presence of conspecifics may serve as an indicator of habitat or mate quality (Reed and Dobson 1993, Clobert et al. 2009). This signals the advantages of sociality in nuthatches likely outweigh the costs of competition or dispersing to find novel resources. Reintroduction to EVER and the subsequent bottlenecks likely enforced a social selective pressure (Snijders et al. 2014) that may have favored a less-exploratory but more social phenotype (Goldenberg et al. 2019), thus resulting in slow-exploring nuthatches to this day. Alternatively, slow exploration may be the result of socially-transmitted, learned risk-avoidance due to experience with habitat edges (Reader 2015, Cornelius et al. 2017), though such learned behaviors can become canalized when reinforced by selection (Shefferson et al. 2018).

Cooperative breeding

Unique characteristics of nuthatch breeding biology may also favor retention of different exploratory phenotypes. Cooperative breeding appeared early in the EVER reintroduction effort (Cox et al. in press) and likely was associated with the retention of juveniles with lower exploratory behavior (Cornelius et al. 2017, Cusick et al. 2018). Personality-dependent dispersal has been documented in a variety of other cooperatively breeding birds (Cote et al. 2010, Duckworth et al. 2015, Botero-Delgadillo et al. 2020) and delayed dispersal is one of the precursors to cooperative breeding (Ekman et al. 2004). Slow-exploring individuals that forgo dispersal and instead provision young produced by others, defend nests, and enhance group productivity collectively raise a cohort of future potential mates and helpers (Kokko et al. 2001, Teunissen et al. 2019). Expósito-Granados et al. (2016) found that exploratory phenotype mediates helping behavior in Iberian Magpies (*Cyanopica cooki*); fast-exploring males that dispersed to join an unfamiliar group were more likely to be helpers, while fast-exploring males that remained in the natal territory were more likely to be breeders. Division of helping labor (i.e., provisioning chicks vs. nest defense) can also be influenced by behavioral phenotypes (Bergmuller and Taborsky 2010, Le Vin et al. 2011, Loftus et al. 2021); fast-exploring Superb Fairy-Wrens (*Malurus cyaneus*) and Great Tits (*Parus major*) acting as helpers exhibited more nest defense behaviors, while slow-exploring Great Tits provisioned young (Hollander et al. 2008, van Asten et al. 2016). Further, Hammers et al. (2019) found that female Seychelles Warblers (*Acrocephalus sechellensis*) that had helpers senesced later than unhelped females, and Dingemanse et al. (2020) similarly found slow-exploring Great Tits senesced later than fast explorers, potentially resulting in higher lifetime productivity. We do not have data documenting whether slow-exploring nuthatches are more likely to participate in cooperative groups, but these studies suggest a self-reinforcing pathway to the maintenance of slow exploratory phenotypes in EVER may be tied to cooperative behavior.

CONCLUSION

Our study suggests that changes in behavior of reintroduced populations are likely to occur and may be predictable. For example, if fast explorers disperse further (Dingemanse et al. 2003, Reale and Montiglio 2020) than slow explorers, we would expect higher retention of slow explorers near the release site in other reintroduced populations. If the prevalence of slow explorers we observed in the reintroduced population relates to factors associated with cooperative breeding, we might expect to see a preponderance of slow explorers when other cooperative breeders are reintroduced but not when non-cooperative breeders are reintroduced. Another factor that should yield a predictable outcome is the tendency for slow explorers to fare better when subjected to environmental and situational stress (Nicolaus et al. 2015, Martins et al. 2007, Cornelius et al. 2017). Conversely, if random forces such as genetic drift, demographic stochasticity, or weather events led to changes in the prevalence of exploratory phenotypes, we should expect to see fast explorers become more prevalent in some reintroduced populations. Comparison of the behavioral phenotypes present in reintroduced and source populations might help to target the personality types best suited for early restoration phases when translocated individuals must explore and settle down in novel areas. More broadly, reintroductions feature low-density social environments that provide opportunities for assessing density-dependent behavioral variation.

Only 55.7% of the 524 attempts to reintroduce wild-caught birds have led to successful reproduction after the initial translocations (Lincoln Park Zoo Avian Reintroduction and Translocation Database 2020 http://www.lpzoosites.org/artd/). Among birds, the average length of post-release monitoring is 8.5 years (Bubac et al. 2019). This timeframe allows benchmarks on survival and reproduction to be cataloged, but it may not be sufficient to assess potential behavioral changes that might arise as a byproduct of translocation. Assessing behavioral variation generations after establishment could provide key insights into the resilience of reintroduced populations (Watters and Meehan 2007), the evolutionary consequences of behavioral differences (Reale et al. 2007, Smith and Blumstein 2013), and the emergence of evolutionary trajectories as populations adapt to novel surroundings (Stockwell et al. 2003, Merrick and Koprowski 2017). Moreover, behavior can be a cost-effective way to monitor warning signs of population decline (Wildermuth et al. 2012, Berger-Tal and Saltz 2019). Our results also point to the potential importance of anticipating the effects that stochastic and deterministic factors might have on the behavioral diversity of translocated populations.

Responses to this article can be read online at:
https://www.ace-eco.org/issues/responses.php/2111

Acknowledgments:

We thank M. Chappelle for field assistance, R. Kimball and M. Zhang for molecular analysis, R. Meyer for constructive feedback, and P. Monte for assisting with exploratory chamber design. Thanks also to T. Dean (Everglades National Park) and M. Knight (Picayune Strand State Forest) for facilitating access to sites. Financial support for this research was provided by the Florida Ornithological Society (Cruickshank Research Award) and the Wildlife Research Endowment at Tall Timbers Research Station.

LITERATURE CITED

Amy, M., P. Sprau, P. de Goede, and M. Naguib. 2010. Effects of personality on territory defence in communication networks: a playback experiment with radio-tagged great tits. Proceedings of the Royal Society B: Biological Sciences 277:3685-3692. https://doi.org/10.1098/rspb.2010.0598

Aplin, L. M., D. R. Farine, J. Morand-Ferron, and B. C. Sheldon. 2012. Social networks predict patch discovery in a wild population of songbirds. Proceedings of the Royal Society B: Biological Sciences 279:4199-4205. https://doi.org/10.1098/rspb.2012.1591

Aplin, L. M., D. R. Farine, J. Morand-Ferron, E. F. Cole, A. Cockburn, and B. C. Sheldon. 2013. Individual personalities predict social behaviour in wild networks of great tits (Parus major). Ecology Letters 16:1365-1372. https://doi.org/10.1111/ele.12181

Armstrong, D. P., and P. J. Seddon. 2008. Directions in reintroduction biology. Trends in Ecology & Evolution 23:20-25. https://doi.org/10.1016/j.tree.2007.10.003

Armstrong, D., M. Hayward, D. Moro, and P. Seddon. 2015. Advances in Reintroduction Biology of Australian and New Zealand Fauna. Csiro Publishing, Clayton, Victoria, Australia. https://doi.org/10.1071/9781486303021

Berger-Tal, O., and D. Saltz. 2019. Invisible barriers: anthropogenic impacts on inter- and intra-specific interactions as drivers of landscape-independent fragmentation. Philosophical Transactions of the Royal Society B: Biological Sciences 374:20180049. https://doi.org/10.1098/rstb.2018.0049

Bergmüller, R., and M. Taborsky. 2010. Animal personality due to social niche specialisation. Trends in Ecology & Evolution 25:504-511. https://doi.org/10.1016/j.tree.2010.06.012

Biro, P. A., and N. J. Dingemanse. 2009. Sampling bias resulting from animal personality. Trends in Ecology & Evolution 24:66-67. https://doi.org/10.1016/j.tree.2008.11.001

Biz, M., C. Cornelius, and J. P. W. Metzger. 2017. Matrix type affects movement behavior of a Neotropical understory forest bird. Perspectives in Ecology and Conservation 15:10-17. https://doi.org/10.1016/j.pecon.2017.03.001

Botero-Delgadillo, E., V. Quirici, Y. Poblete, E. Poulin, B. Kempenaers, and R. A. Vásquez. 2020. Exploratory behavior, but not aggressiveness, is correlated with breeding dispersal propensity in the highly philopatric thorn-tailed rayadito. Journal of Avian Biology 51. https://doi.org/https://doi.org/10.1111/jav.02262

Both, C., N. J. Dingemanse, P. J. Drent, and J. M. Tinbergen. 2005. Pairs of extreme avian personalities have highest reproductive success. Journal of Animal Ecology 74:667-674. https://doi.org/10.1111/j.1365-2656.2005.00962.x

Bremner-Harrison, S., P. A. Prodohl, and R. W. Elwood. 2004. Behavioural trait assessment as a release criterion: boldness predicts early death in a reintroduction programme of captive-bred swift fox (Vulpes velox). Animal Conservation forum 7:313-320. https://doi.org/10.1017/S1367943004001490

Brown, D., and T. Sherry. 2008. Alternative strategies of space use and response to resource change in a wintering migrant songbird. Behavioral Ecology 19:1314-1325. https://doi.org/10.1093/beheco/arn073

Bubac, C. M., A. C. Johnson, J. A. Fox, and C. I. Cullingham. 2019. Conservation translocations and post-release monitoring: Identifying trends in failures, biases, and challenges from around the world. Biological Conservation 238:108239. https://doi.org/10.1016/j.biocon.2019.108239

Burchett, W. W., A. R. Ellis, S. W. Harrar, and A. C. Bathke. 2017. Nonparametric Inference for Multivariate Data: The R Package npmv. Journal of Statistical Software 76. https://doi.org/10.18637/jss.v076.i04

Burnett, J. L., and K. E. Sieving. 2016. Songbird distress calls as an improved method for detecting red-shouldered hawks (Buteo lineatus). Florida Field Naturalist 44(4):157-168.

Clark, G. A. 1970. Avian bill-wiping. The Wilson Bulletin 82 (3):279-288. https://www.jstor.org/stable/4159979

Clobert, J., J.-F. Le Galliard, J. Cote, S. Meylan, and M. Massot. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. Ecology Letters 12:197-209. https://doi.org/10.1111/j.1461-0248.2008.01267.x

Coppens, C. M., S. F. de Boer, and J. M. Koolhaas. 2010. Coping styles and behavioural flexibility: towards underlying mechanisms. Philosophical Transactions of the Royal Society B: Biological Sciences 365:4021-4028. https://doi.org/10.1098/rstb.2010.0217

Cornelius, C., M. Awade, C. Cândia-Gallardo, K. E. Sieving, and J. P. Metzger. 2017. Habitat fragmentation drives inter-population variation in dispersal behavior in a Neotropical rainforest bird. Perspectives in Ecology and Conservation 15:3-9. https://doi.org/10.1016/j.pecon.2017.02.002

Cote, J., J. Clobert, T. Brodin, S. Fogarty, and A. Sih. 2010. Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. Philosophical Transactions of the Royal Society B: Biological Sciences 365:4065-4076. https://doi.org/10.1098/rstb.2010.0176

Cox, J. A., and G. L. Slater. 2007. Cooperative breeding in the Brown-headed Nuthatch. The Wilson Journal of Ornithology 119:1-8. https://doi.org/10.1676/06-006.1

Cox, J. A. 2012. Social grooming in the Brown-headed Nuthatch may have expanded functions. Southeastern Naturalist 11:771-774. https://doi.org/10.1656/058.011.0415

Cox, J. A., L. C. Scopel, and M. R. Klostermann. 2012. Brown-headed Nuthatch occupancy in central Florida and its relationship to forest type, forest structure, and the presence of Red-cockaded Woodpeckers. The Condor 114:622-628. https://doi.org/10.1525/cond.2012.110167

Cox, J. A., J. A. Cusick, and E. H. DuVal. 2019. Manipulated sex ratios alter group structure and cooperation in the Brown-headed Nuthatch. Behavioral Ecology 30:883-893. https://doi.org/10.1093/beheco/arz030

Cox, J. A., M. M. Gray, H. E. Levy, G. L. Slater. In press. Cooperative breeding behavior emerges early in restored populations of the Brown-headed Nuthatch (Sitta pusilla). Wilson Journal of Ornithology.

Cusick, J. A., M. de Villa, E. H. DuVal, and J. A. Cox. 2018. How do helpers help? Helper contributions throughout the nesting cycle in the cooperatively breeding brown-headed nuthatch. Behavioral Ecology and Sociobiology 72:43. https://doi.org/10.1007/s00265-018-2470-1

Debeffe, L., N. Morellet, B. Cargnelutti, B. Lourtet, A. Coulon, J. M. Gaillard, R. Bon, and A. J. M. Hewison. 2013. Exploration as a key component of natal dispersal: Dispersers explore more than philopatric individuals in roe deer. Animal Behaviour 86:143-151. https://doi.org/10.1016/j.anbehav.2013.05.005

Devost, I., T. B. Jones, M. Cauchoix, C. Montreuil-Spencer, and J. Morand-Ferron. 2016. Personality does not predict social dominance in wild groups of black-capped chickadees. Animal Behaviour 122:67-76. https://doi.org/10.1016/j.anbehav.2016.10.001

Dingemanse, N. J., C. Both, P. J. Drent, K. van Oers, and A. J. van Noordwijk. 2002. Repeatability and heritability of exploratory behaviour in great tits from the wild. Animal Behaviour 64:929-938. https://doi.org/10.1006/anbe.2002.2006

Dingemanse, N. J., C. Both, A. J. van Noordwijk, A. L. Rutten, and P. J. Drent. 2003. Natal dispersal and personalities in great tits (Parus major). Proceedings of the Royal Society of London. Series B: Biological Sciences 270. https://doi.org/10.1098/rspb.2002.2300

Dingemanse, N. J., C. Both, P. J. Drent, and J. M. Tinbergen. 2004. Fitness consequences of avian personalities in a fluctuating environment. Proceedings of the Royal Society of London. Series B: Biological Sciences 271:847-852. https://doi.org/10.1098/rspb.2004.2680

Dingemanse, N. J., M. Moiron, Y. G. Araya-Ajoy, A. Mouchet, and R. N. Abbey-Lee. 2020. Individual variation in age-dependent reproduction: Fast explorers live fast but senesce young? Journal of Animal Ecology 89:601-613. https://doi.org/10.1111/1365-2656.13122

Dochtermann, N. A., T. Schwab, M. Anderson Berdal, J. Dalos, and R. Royauté. 2019. The heritability of behavior: A meta-analysis. Journal of Heredity 110:403-410. https://doi.org/10.1093/jhered/esz023

Dolby, A. S., and T. C. Grubb Jr. 1999. Effects of winter weather on horizontal and vertical use of isolated forest fragments by bark-foraging birds. The Condor 101:408-412. https://doi.org/10.2307/1370006

Drent, P. J., K. van Oers, and A. J. van Noordwijk. 2003. Realized heritability of personalities in the great tit (Parus major). Proceedings of the Royal Society of London. Series B: Biological Sciences 270:45-51. https://doi.org/10.1098/rspb.2002.2168

Duckworth, R. A. 2006. Behavioral correlations across breeding contexts provide a mechanism for a cost of aggression. Behavioral Ecology 17:1011-1019. https://doi.org/10.1093/beheco/arl035

Duckworth, R. A., V. Belloni, and S. R. Anderson. 2015. Cycles of species replacement emerge from locally induced maternal effects on offspring behavior in a passerine bird. Science 347:875-877. https://doi.org/10.1126/science.1260154

Ekman J., J. L Dickinson, B.J. Hatchwell, and M. Griesser. 2004. Delayed dispersal. Pages 35-47 in W.D Koenig and J.L. Dickinson, editors. Ecology and evolution of cooperative breeding in birds. Cambridge University Press, Cambridge, UK. https://doi.org/10.1017/CBO9780511606816.003

Expósito-Granados, M., C. De La Cruz, D. Parejo, J. Valencia, S. Alarcos, and J. M. Avilés. 2016. Exploratory behaviour modulates the relationship between colony familiarity and helping in a cooperative bird. Behavioural Processes 131:9-14. https://doi.org/10.1016/j.beproc.2016.07.013

Fahrig, L. 2007. Non-optimal animal movement in human-altered landscapes. Functional Ecology 21:1003-1015. https://doi.org/10.1111/j.1365-2435.2007.01326.x

Fletcher, R. J. 2007. Species interactions and population density mediate the use of social cues for habitat selection. Journal of Animal Ecology 76:598-606. https://doi.org/10.1111/j.1365-2656.2007.01230.x

Florida Forest Service. 2008. Picayune Strand State Forest Ten-year Resource Management Plan. Florida Department of Agriculture and Consumer Services, Tallahassee, Florida, USA. [online] URL: https://www.fdacs.gov/ezs3download/download/25619/516499/PSSF%2520FINAL%25202008%2520PLAN.pdf

Frankham, R. 2015. Genetic rescue of small inbred populations: meta-analysis reveals large and consistent benefits of gene flow. Molecular Ecology 24:2610-2618. https://doi.org/10.1111/mec.13139

Franks, V. R., C. E. Andrews, J. G. Ewen, M. McCready, K. A. Parker, and R. Thorogood. 2019. Changes in social groups across reintroductions and effects on post-release survival. Animal Conservation 23:443-454. https://doi.org/10.1111/acv.12557

Gabriel, P. O., and J. M. Black. 2012. Behavioural syndromes, partner compatibility and reproductive performance in Steller's Jays. Ethology 118:76-86. https://doi.org/10.1111/j.1439-0310.2011.01990.x

Garamszegi, L. Z., M. Eens, and J. Török. 2009. Behavioural syndromes and trappability in free-living collared flycatchers, Ficedula albicollis. Animal Behaviour 77:803-812. https://doi.org/10.1016/j.anbehav.2008.12.012

Geffroy, B., S. Alfonso, B. Sadoul, and D. T. Blumstein. 2020. A world for reactive phenotypes. Frontiers in Conservation Science 1:5. https://doi.org/10.3389/fcosc.2020.611919

Goldenberg, S. Z., M. A. Owen, J. L. Brown, G. Wittemyer, Z. M. Oo, and P. Leimgruber. 2019. Increasing conservation translocation success by building social functionality in released populations. Global Ecology and Conservation 18:e00604. https://doi.org/10.1016/j.gecco.2019.e00604

Gray, M. M., E. W. Schunke, and J. A. Cox. 2016. Tool usage by juvenile Sitta pusilla (Brown-headed Nuthatch). Southeastern Naturalist 15. https://doi.org/10.1656/058.015.0209

Gregory, A. J., R. S. A. Kaler, T. J. Prebyl, B. K. Sandercock, and S. M. Wisely. 2012. Influence of translocation strategy and mating system on the genetic structure of a newly established population of island ptarmigan. Conservation Genetics 13:465-474. http://doi.org/10.1007/s10592-011-0300-3

Griffith, B., J. M. Scott, J. W. Carpenter, and C. Reed. 1989. Translocation as a species conservation tool: Status and strategy. Science 245:477-480. https://doi.org/10.1126/science.245.4917.477

Groombridge, J. J., J. G. Massey, J. C. Bruch, T. R. Malcolm, C. N. Brosius, M. M. Okada, and B. Sparklin. 2004. Evaluating stress in a Hawaiian honeycreeper, Paroreomyza montana, following translocation. Journal of Field Ornithology 75:183-187. https://doi.org/10.1648/0273-8570-75.2.183

Guillette, L. M., A. R. Reddon, M. Hoeschele, and C. B. Sturdy. 2011. Sometimes slower is better: slow-exploring birds are more sensitive to changes in a vocal discrimination task. Proceedings of the Royal Society B: Biological Sciences 278:767-773. https://doi.org/10.1098/rspb.2010.1669

Guillette, L. M., and C. B. Sturdy. 2011. Individual differences and repeatability in vocal production: Stress-induced calling exposes a songbird's personality. Naturwissenschaften 98:977-981. https://doi.org/10.1007/s00114-011-0842-8

Haage, M., T. Maran, U. A. Bergvall, B. Elmhagen, and A. Angerbjörn. 2017. The influence of spatiotemporal conditions and personality on survival in reintroductions-evolutionary implications. Oecologia 183:45-56. https://doi.org/10.1007/s00442-016-3740-0

Haas, Sarah. E., J. A. Cox, J. V. Smith, and R. T. Kimball. 2010. Fine-scale spatial genetic structure in the cooperatively breeding Brown-headed Nuthatch (Sitta pusilla). Southeastern Naturalist 9:743-756. https://doi.org/10.1656/058.009.0409

Hall, M. L., T. van Asten, A. C. Katsis, N. J. Dingemanse, M. J. L. Magrath, and R. A. Mulder. 2015. Animal personality and pace-of-life syndromes: do fast-exploring fairy-wrens die young? Frontiers in Ecology and Evolution 3:28. https://doi.org/10.3389/fevo.2015.00028

Hammers, M., S. A. Kingma, L. G. Spurgin, K. Bebbington, H. L. Dugdale, T. Burke, J. Komdeur, and D. S. Richardson. 2019. Breeders that receive help age more slowly in a cooperatively breeding bird. Nature Communications 10:1301. https://doi.org/10.1038/s41467-019-09229-3

Han, K.-L., R. T. Kimball, and J. A. Cox. 2019. Testing hypotheses driving genetic structure in the cooperatively breeding Brown-headed Nuthatch Sitta pusilla. Ibis 161:387-400. https://doi.org/10.1111/ibi.12642

Herborn, K. A., B. J. Heidinger, L. Alexander, and K. E. Arnold. 2014. Personality predicts behavioral flexibility in a fluctuating, natural environment. Behavioral Ecology 25:1374-1379. https://doi.org/10.1093/beheco/aru131

Hollander, F. A., T. Van Overveld, I. Tokka, and E. Matthysen. 2008. Personality and nest defence in the Great Tit (Parus major). Ethology 114:405-412. https://doi.org/10.1111/j.1439-0310.2008.01488.x

Huang, P., K. E. Sieving, and C. M. S. Mary. 2012. Heterospecific information about predation risk influences exploratory behavior. Behavioral Ecology 23:463-472. https://doi.org/10.1093/beheco/arr212

Huang, P., K. Kerman, K. E. Sieving, and C. M. St. Mary. 2016. Evaluating the novel-environment test for measurement of exploration by bird species. Journal of Ethology 34:45-51. https://doi.org/10.1007/s10164-015-0444-6

Jacobs, C. G. C., T. van Overveld, V. Careau, E. Matthysen, F. Adriaensen, and H. Slabbekoorn. 2014. Personality-dependent response to field playback in great tits: Slow explorers can be strong responders. Animal Behaviour 90:65-71. https://doi.org/10.1016/j.anbehav.2014.01.016

Kerman, K., K. E. Sieving, C. S. Mary, and M. L. Avery. 2016. Evaluation of boldness assays and associated behavioral measures in a social parrot, monk parakeet (Myiopsitta monachus). Behaviour 153:1817-1838. https://doi.org/10.1163/1568539X-00003356

Kluen, E., S. Kuhn, B. Kempenaers, and J. E. Brommer. 2012. A simple cage test captures intrinsic differences in aspects of personality across individuals in a passerine bird. Animal Behaviour 84:279-287. https://doi.org/10.1016/j.anbehav.2012.04.022

Kokko, H., R. A. Johnstone, and C.-B. T. H. 2001. The evolution of cooperative breeding through group augmentation. Proceedings of the Royal Society of London. Series B: Biological Sciences 268:187-196. https://doi.org/10.1098/rspb.2000.1349

Koolhaas, J. M., S. M. Korte, S. F. De Boer, B. J. Van Der Vegt, C. G. Van Reenen, H. Hopster, I. C. De Jong, M. A. W. Ruis, and H. J. Blokhuis. 1999. Coping styles in animals: current status in behavior and stress-physiology. Neuroscience & Biobehavioral Reviews 23:925-935. https://doi.org/10.1016/S0149-7634(99)00026-3

Komdeur, J. 1992. Importance of habitat saturation and territory quality for evolution of cooperative breeding in the Seychelles warbler. Nature 358:493-495. https://doi.org/10.1038/358493a0

Kozlovsky, D., C. Branch, C. A. Freas, and V. V. Pravosudov. 2014. Elevation-related differences in novel environment exploration and social dominance in food-caching mountain chickadees. Behavioral Ecology and Sociobiology 68:1871-1881. https://doi.org/10.1007/s00265-014-1796-6

Le Gouar, P., J. B. Mihoub, and F. Sarrazin. 2012. Dispersal and Habitat Selection: Behavioural and Spatial Constraints for

Animal Translocations. Pages 138-164 in J. G. Ewen, D. P. Armstrong, K. A. Parker, P. J. Seddon, editors. Reintroduction Biology: Integrating Science and Management. John Wiley & Sons, Ltd., Hoboken, New Jersey, USA. https://doi.org/10.1002/9781444355833.ch5

Le Vin, A. L., B. K. Mable, M. Taborsky, D. Heg, and K. E. Arnold. 2011. Individual variation in helping in a cooperative breeder: relatedness versus behavioural type. Animal Behaviour 82:467-477. https://doi.org/10.1016/j.anbehav.2011.05.021

Li, J., N. Wang, Y. Wang, S. Lin, Q. Li, Y.-Y. Liu, X. Ruan, J. Zhu, B. Xi, and Z.-W. Zhang. 2010. Sexual size dimorphism and sex identification using morphological traits of two Aegithalidae species. Zoological Science 27:946-951. https://doi.org/10.2108/zsj.27.946

Lima, S. L., and P. A. Zollner. 1996. Towards a behavioral ecology of ecological landscapes. Trends in Ecology & Evolution 11:131-135. https://doi.org/10.1016/0169-5347(96)81094-9

Lincoln Park Zoo. Avian Reintroduction and Translocation Database. Available at: http://www.lpzoosites.org/artd/. Accessed March 13, 2020.

Lloyd, J. D., and G. L. Slater. 2007. Environmental factors affecting productivity of Brown-Headed Nuthatches. The Journal of Wildlife Management 71:1968-1975. https://doi.org/10.2193/2006-384

Lloyd, J. D., G. L. Slater, and S. Snow. 2009. Demography of reintroduced Eastern Bluebirds and Brown-Headed Nuthatches. The Journal of Wildlife Management 73:955-964. https://doi.org/10.2193/2008-009

Loftus, J. C., A. A. Perez, A. Sih, and L. Simmons. 2021. Task syndromes: Linking personality and task allocation in social animal groups. Behavioral Ecology 32:1-17. https://doi.org/10.1093/beheco/araa083

Maldonado-Chaparro, A. A., G. Alarcón-Nieto, J. A. Klarevas-Irby, and D. R. Farine. 2018. Experimental disturbances reveal group-level costs of social instability. Proceedings of the Royal Society B: Biological Sciences 285:20181577. https://doi.org/10.1098/rspb.2018.1577

Maspons, J., R. Molowny-Horas, and D. Sol. 2019. Behaviour, life history and persistence in novel environments. Philosophical Transactions of the Royal Society B: Biological Sciences 374:20180056. https://doi.org/10.1098/rstb.2018.0056

Matthews, S. N., L. R. Iverson, A. M. Prasad, and M. P. Peters. 2011. Changes in potential habitat of 147 North American breeding bird species in response to redistribution of trees and climate following predicted climate change. Ecography 34:933-945. https://doi.org/10.1111/j.1600-0587.2011.06803.x

Matthysen, E. 2010. The Nuthatches. T. & A. D. Poyser Ltd., London, UK.

Maxwell, O., B. A. Mayowa, I. U. Chinedu, and A. E. Peace. 2018. Modelling count data; a generalized linear model framework. American Journal of Mathematics and Statistics 8(6):179-183. http://article.sapub.org/10.5923.j.ajms.20180806.03.html

May, T. M., M. J. Page, and P. A. Fleming. 2016. Predicting survivors: animal temperament and translocation. Behavioral Ecology 27:969-977. https://doi.org/10.1093/beheco/arv242

McDougall, P. T., D. Réale, D. Sol, and S. M. Reader. 2006. Wildlife conservation and animal temperament: causes and consequences of evolutionary change for captive, reintroduced, and wild populations. Animal Conservation 9:39-48. https://doi.org/10.1111/j.1469-1795.2005.00004.x

Merrick, M. J., and J. L. Koprowski. 2017. Should we consider individual behavior differences in applied wildlife conservation studies? Biological Conservation 209:34-44. https://doi.org/10.1016/j.biocon.2017.01.021

Mihoub, J.-B., A. Robert, P. L. Gouar, and F. Sarrazin. 2011. Post-release dispersal in animal translocations: Social attraction and the "Vacuum Effect." PLOS ONE 6:e27453. https://doi.org/10.1371/journal.pone.0027453

Moore, R. 2013. Prioritizing ecosystem service protection and conservation efforts in the forest plantations of the Red Hills. Agricultural and Resource Economics Review 42:225-250. https://doi.org/10.1017/S106828050000770X

Moseby, K. E., D. T. Blumstein, M. Letnic, and R. West. 2020. Choice or opportunity: are post-release social groupings influenced by familiarity or reintroduction protocols? Oryx 54:215-221. https://doi.org/10.1017/S0030605318000054

Morse, D. H. 1967. Foraging Relationships of Brown-Headed Nuthatches and Pine Warblers. Ecology 48:94-103. https://doi.org/10.2307/1933421

Nephew, B. C., and L. M. Romero. 2003. Behavioral, physiological, and endocrine responses of starlings to acute increases in density. Hormones and Behavior 44:222-232. https://doi.org/10.1016/j.yhbeh.2003.06.002

Nicolaus, M., K. J. Mathot, Y. G. Araya-Ajoy, A. Mutzel, J. J. Wijmenga, B. Kempenaers, and N. J. Dingemanse. 2015. Does coping style predict optimization? An experimental test in a wild passerine bird. Proceedings of the Royal Society B: Biological Sciences 282:20142405. https://doi.org/10.1098/rspb.2014.2405

Norris, R. A. 1954. Comparative biosystematics and life history of the nuthatches Sitta pygmaea and Sitta pusilla, 56th edition. University of California Publications in Zoology, Berkeley, California, USA.

Polekoff, S. E. 2018, June. Exploratory behavior in Black-capped Chickadees, Carolina Chickadees, and their hybrids. Master's Thesis, Villanova University, Philadelphia, Pennsylvania, USA.

Ramos, G. de A. P., C. S. de Azevedo, T. H. A. Jardim, and A. C. Sant'Anna. 2021a. Temperament in captivity, environmental enrichment, flight ability, and response to humans in an endangered parrot species. Journal of Applied Animal Welfare Science 24:379-391. https://doi.org/https://doi.org/10.1080/10888705.2020.1765367

Ramos, G. de A. P., C. S. de Azevedo, D. D. C. Lovestain, T. H. A. Jardim, and A. C. Sant'Anna. 2021b. Is individual temperament related to behaviors in a social context for a Neotropical parakeet species? Applied Animal Behaviour Science 243:105455. https://doi.org/https://doi.org/10.1016/j.applanim.2021.105455

Reader, S. M. 2015. Causes of individual differences in animal exploration and search. Topics in Cognitive Science 7:451-468. https://doi.org/10.1111/j.1469-185X.2007.00010.x

Réale, D., D. Garant, M. M. Humphries, P. Bergeron, V. Careau, and P.-O. Montiglio. 2010. Personality and the emergence of the pace-of-life syndrome concept at the population level. Philosophical Transactions of the Royal Society B: Biological Sciences 365:4051-4063. https://doi.org/10.1098/rstb.2010.0208

Réale, D., and P.-O. Montiglio. 2020. Evolution of adaptive individual differences in non-human animals. Pages 279-299 in L. A. Schmidt and K. L. Poole, editors. Adaptive Shyness: Multiple Perspectives on Behavior and Development. Springer International Publishing. https://doi.org/10.1007/978-3-030-38877-5_15

Reed, J. M., and A. P. Dobson. 1993. Behavioural constraints and conservation biology: Conspecific attraction and recruitment. Trends in Ecology & Evolution 8:253-256. https://doi.org/10.1016/0169-5347(93)90201-Y

Richardson, K. M., J. G. Ewen, P. Brekke, L. R. Doerr, K. A. Parker, and D. P. Armstrong. 2017. Behaviour during handling predicts male natal dispersal distances in an establishing reintroduced hihi (Notiomystis cincta) population. Animal Conservation 20:135-143. https://doi.org/10.1111/acv.12296

Russell, P. A. 1983. Psychological studies of exploration in animals: a reappraisal. Pages 22-54 in J. Archer and L. I. A. Birke, editors. Exploration in Animals and Humans. Nostrand Reinhold, New York.

Sæther, B.-E., and S. Engen. 2019. Towards a predictive conservation biology: the devil is in the behaviour. Philosophical Transactions of the Royal Society B: Biological Sciences 374:20190013. https://doi.org/10.1098/rstb.2019.0013

Sauer, J. R., W. A. Link, D. J. Ziolkowski, K. L. Pardieck, and D. J. Twedt. 2019. Consistency counts: Modeling the effects of a change in protocol on Breeding Bird Survey counts. The Condor 121: duz009. https://doi.org/10.1093/condor/duz009

Seddon, P. J., D. P. Armstrong, and R. F. Maloney. 2007. Developing the science of reintroduction biology. Conservation Biology 21:303-312. https://doi.org/10.1111/j.1523-1739.2006.00627.x

Shefferson, R. P., C. M. Mason, K. M. Kellett, E. W. Goolsby, E. Coughlin, and R. W. Flynn. 2018. The evolutionary impacts of conservation actions. Population Ecology 60:49-59. https://doi.org/10.1007/s10144-018-0614-9

Sieving, K. E., S. A. Hetrick, and M. L. Avery. 2010. The versatility of graded acoustic measures in classification of predation threats by the tufted titmouse Baeolophus bicolor: exploring a mixed framework for threat communication. Oikos 119:264-276. https://doi.org/10.1111/j.1600-0706.2009.17682.x

Sih, A., A. Bell, and J. C. Johnson. 2004. Behavioral syndromes: An ecological and evolutionary overview. Trends in Ecology & Evolution 19:372-378. https://doi.org/10.1016/j.tree.2004.04.009

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. https://doi.org/10.1111/j.1752-4571.2010.00166.x

Sih, A., and M. Del Giudice. 2012. Linking behavioural syndromes and cognition: A behavioural ecology perspective. Philosophical transactions of the Royal Society of London. Series B, Biological sciences 367:2762-72. https://doi.org/10.1098/rstb.2012.0216

Slater, G.L. 2001. Avian restoration in Everglades National Park (1997-2001): Translocation methodology, population demography, and evaluating success. Final Report to Everglades National Park. Ecostudies Institute, Mount Vernon, Washington, USA.

Smit, J. A. H., and K. van Oers. 2019. Personality types vary in their personal and social information use. Animal Behaviour 151:185-193. https://doi.org/10.1016/j.anbehav.2019.02.002

Smith, B. R., and D. T. Blumstein. 2013. Animal Personalities and Conservation Biology: The Importance of Behavioral Diversity. Pages 381-413 in C. Carere and D. Maestripieri, editors. Animal personalities: Behavior, physiology, and evolution. The University of Chicago Press, Chicago, Illinois, USA. https://doi.org/10.7208/chicago/9780226922065.003.0014

Snijders, L., E. P. van Rooij, J. M. Burt, C. A. Hinde, K. van Oers, and M. Naguib. 2014. Social networking in territorial great tits: slow explorers have the least central social network positions. Animal Behaviour 98:95-102. https://doi.org/10.1016/j.anbehav.2014.09.029

Snyder, J. R., A. Herndon, and W. B. Robertson Jr. 1990. South Florida rockland. R. Myers and J. Ewel, editors. Ecosystems of Florida. University of Central Florida Press, Orlando, FL.

Stockwell, C. A., A. P. Hendry, and M. T. Kinnison. 2003. Contemporary evolution meets conservation biology. Trends in Ecology & Evolution 18:94-101. https://doi.org/10.1016/S0169-5347(02)00044-7

Stuber, E. F., Y. G. Araya-Ajoy, K. J. Mathot, A. Mutzel, M. Nicolaus, J. J. Wijmenga, J. C. Mueller, and N. J. Dingemanse. 2013. Slow explorers take less risk: a problem of sampling bias in ecological studies. Behavioral Ecology 24:1092-1098. https://doi.org/10.1093/beheco/art035

Thompson, M. J., J. C. Evans, S. Parsons, and J. Morand-Ferron. 2018. Urbanization and individual differences in exploration and plasticity. Behavioral Ecology 29:1415-1425. 10.1093/beheco/ary103 https://doi.org/10.1093/beheco/ary044

Teunissen, N., S. A. Kingma, and A. Peters. 2020. Nest defence and offspring provisioning in a cooperative bird: individual subordinates vary in total contribution, but no division of tasks among breeders and subordinates. Behavioral Ecology and Sociobiology 74:94. https://doi.org/10.1007/s00265-020-02877-2

Tietze, D. T., and J. Martens. 2009. Morphometric characterisation of treecreepers (genus Certhia). Journal of Ornithology 150:431-457. https://doi.org/10.1007/s10336-008-0363-1

van Asten, T., M. L. Hall, and R. A. Mulder. 2016. Who cares? Effect of coping style and social context on brood care and defense in superb fairy-wrens. Behavioral Ecology 27:1745-1755. https://doi.org/10.1093/beheco/arw096

van Hierden, Y. M., S. M. Korte, E. W. Ruesink, C. G. van Reenen, B. Engel, J. M. Koolhaas, and H. J. Blokhuis. 2002. The development of feather pecking behaviour and targeting of pecking in chicks from a high and low feather pecking line of laying hens. Applied Animal Behaviour Science 77:183-196. https://doi.org/10.1016/S0168-1591(02)00046-1

van Oers, K., P. J. Drent, P. de Goede, and A. J. van Noordwijk. 2004a. Realized heritability and repeatability of risk-taking behaviour in relation to avian personalities. Proceedings of the Royal Society of London. Series B: Biological Sciences 271:65-73. https://doi.org/10.1098/rspb.2003.2518 https://doi.org/https://doi.org/10.1098/rspb.2003.2518

van Oers, K., G. de Jong, P. J. Drent, and A. J. van Noordwijk. 2004b. A genetic analysis of avian personality traits: Correlated, response to artificial selection. Behavior Genetics 34:611-619. https://doi.org/10.1007/s10519-004-5588-z

van Zeeland, Y. R. A., M. M. J. A. van der Aa, C. M. Vinke, J. T. Lumeij, and N. J. Schoemaker. 2013. Behavioural testing to determine differences between coping styles in Grey parrots (Psittacus erithacus erithacus) with and without feather damaging behaviour. Applied Animal Behaviour Science 148:218-231. https://doi.org/10.1016/j.applanim.2013.08.004

Verbeek, M. E. M., P. J. Drent, and P. R. Wiepkema. 1994. Consistent individual differences in early exploratory behaviour of male great tits. Animal Behaviour 48:1113-1121. https://doi.org/10.1006/anbe.1994.1344

Verbeek, M. E. M., A. Boon, and P. J. Drent. 1996. Exploration, aggressive behaviour and dominance in pair-wise confrontations of juvenile male Great Tits. Behaviour 133:945-963. https://doi.org/10.1163/156853996x00314

Walls, S. C., J. H. Waddle, W. J. Barichivich, I. A. Bartoszek, M. E. Brown, J. M. Hefner, and M. J. Schuman. 2014. Anuran site occupancy and species richness as tools for evaluating restoration of a hydrologically-modified landscape. Wetlands Ecology and Management 22:625-639. https://doi.org/10.1007/s11273-014-9356-4

Walther, B. A., and D. H. Clayton. 2005. Elaborate ornaments are costly to maintain: evidence for high maintenance handicaps. Behavioral Ecology 16:89-95. https://doi.org/10.1093/beheco/arh135

Watters, J. V., and C. L. Meehan. 2007. Different strokes: Can managing behavioral types increase post-release success? Applied Animal Behaviour Science 102:364-379. https://doi.org/10.1016/j.applanim.2006.05.036

Wildermuth, R. P., J. D. Anadón, and L. R. Gerber. 2013. Monitoring behavior: assessing population status with rapid behavioral assessment. Conservation Letters 6:86-97. https://doi.org/10.1111/j.1755-263X.2012.00298.x

Withgott, J. H., and K. G. Smith. 1998. Brown-headed nuthatch. Account 349 in: A. Poole and F. Gill, editors. The birds of North America. Cornell Lab of Ornithology, Ithaca, New York, USA. http://doi.org/10.2173/bna.349

Wolf, M., and F. J. Weissing. 2012. Animal personalities: Consequences for ecology and evolution. Trends in Ecology & Evolution 27:452-461. http://doi.org/10.1016/j.tree.2012.05.001

Wright, T. F., J. R. Eberhard, E. A. Hobson, M. L. Avery, and M. A. Russello. 2010. Behavioral flexibility and species invasions: the adaptive flexibility hypothesis. Ethology Ecology & Evolution 22:393-404. https://doi.org/10.1080/03949370.2010.505580

Yaukey, P. H. 1995. Effects of food supplementation and predator simulation on Nuthatches and Parids within mixed-species flocks. The Wilson Bulletin 107:542-547.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. in A. F. Zuur, E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith, editors. Mixed effects models and extensions in ecology with R. Springer, New York, NY. https://doi.org/10.1007/978-0-387-87458-6_13

SCO - SOC

Sponsored by the Society of Canadian Ornithologists and Birds Canada

Parrainée par la Société des ornithologistes du Canada et Oiseaux Canada

BIRDS CANADA
OISEAUX CANADA

Table A1.1. Descriptive statistics (μ ± 1 SD) for latency to settle (sec) and three key exploratory behaviors (flights/hops, scanning, and total positions) across three Brown-headed Nuthatch populations in Florida and Georgia, USA. EVER = reintroduced Everglades population; PSSF = Picayune State Forest population (nearby source population); NFLA = geographically distinct population in Red Hills region of north Florida. Periods refer to two consecutive 3-min observation periods. Time low (sec) represents time spent in the bottom 20 cm of the exploratory cage.

Sample	**Behavior**	**EVER**	**PSSF**	**NFLA**
Pre-scoring	Latency to settle	48.9 ± 54.1	33.2 ± 31.0	39.9 ± 23.7
First period	Flights/hops	18.4 ± 18.7	20.8 ± 19.4	25.8 ± 23.2
	Scanning	108.8 ± 43.4	127.1 ± 55.6	147.3 ± 55.5
	Positions	5.7 ± 3.3	5.4 ± 3.2	5.6 ± 2.5
	Time low	57.4 ± 67.8	103.9 ± 73.6	37.3 ± 49.8
Second period	Flights/hops	17.0 ± 23.1	28.4 ± 28.6	39.5 ± 42.4
	Scanning	87.5 ± 49.8	138.4 ± 66.5	156.2 ± 56.0
	Positions	4.9 ± 3.5	5.3 ± 3.7	7.2 ± 2.4
	Time low	48.2 ± 67.6	102.5 ± 66.4	48.0 ± 50.0
Total Observations	Flights/hops	17.7 ± 21.2	24.6 ± 24.9	32.6 ± 35.1
	Scanning	98.2 ± 47.3	132.7 ± 61.8	151.8 ± 56.2
	Positions	5.3 ± 3.4	5.4 ± 3.4	6.4 ± 2.6
	Time low	52.8 ± 66.8	103.2 ± 70.4	42.7 ± 50.3

Table A1.2 Descriptive statistics (μ ± 1 SD) for all other recorded behaviors (counts) by population and observation period.

Sample	**Behavior**	**EVER**	**PSSF**	**NFLA**
First period	Preening	0.4 ± 1.2	0.5 ± 1.5	0.5 ± 1.1
	Bill swipe	2.4 ± 4.5	1.1 ± 3.2	1.4 ± 3.9
	Peck	0.7 ± 1.1	0.3 ± 0.8	0.1 ± 1.7
	Gaping (secs)	61.4 ± 69.7	31.8 ± 46.0	67.2 ± 77.9
	Vocalizations	1.8 ± 6.3	0.7 ± 1.6	0.9 ± 1.4
Second period	Preening	0.1 ± 0.2	0.4 ± 0.8	1.1 ± 1.4
	Bill swipe	1.5 ± 2.5	1.8 ± 5.9	0.4 ± 0.9
	Peck	1.9 ± 3.3	1.2 ± 2.8	2.5 ± 6.6
	Gaping (secs)	70.3 ± 72.7	71.5 ± 79.0	84.0 ± 74.1
	Vocalizations	2.1 ± 5.9	0.3 ± 0.8	1.6 ± 4.0
Total Observations	Preening	0.1 ± 0.2	0.4 ± 1.2	0.8 ± 1.3
	Bill swipe	1.9 ± 3.6	1.4 ± 4.8	0.9 ± 2.9
	Peck	1.3 ± 2.5	0.7 ± 2.1	1.4 ± 4.9
	Gaping (secs)	65.8 ± 71.7	51.7 ± 67.9	75.6 ± 76.9
	Vocalizations	1.9 ± 6.0	0.5 ± 1.3	1.3 ± 3.0

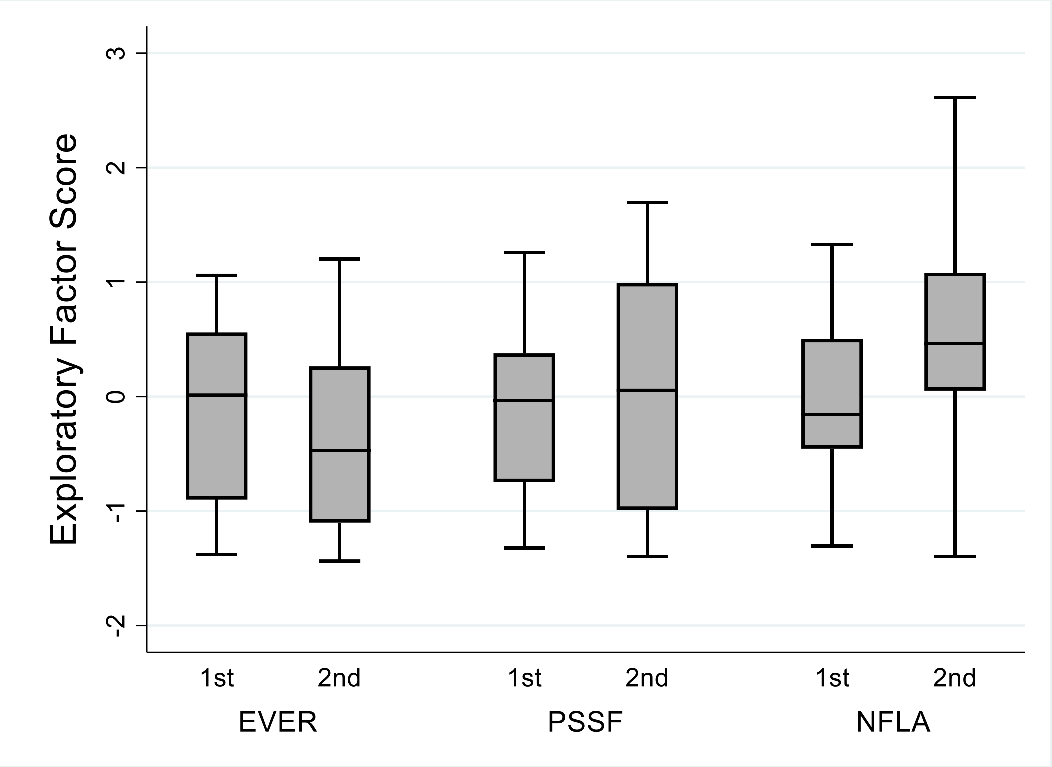


Figure A1. Boxplots of exploratory score derived from factor analysis (Factor 1) by location during each 3-min observation period (first and second). Increasing scores indicate 'faster' exploration: more flights and hops, more scans (head turns), and more positions visited. *N* = 17 birds/location for a total *n* = 51. See text for location abbreviations.

APPENDIX 2

Table A2.1(a). Mixed-effects GLM for summed counts of maintenance activities (negative binomial link function for zero-inflated counts) with main effects and interaction terms for Location (1= EVER, 2 = PSSF, 3 = NFLA) and Period (1st or 2nd sample period in the exploratory chamber) and bird ID as the random effect. Z tests refer to comparisons of factor levels to reference levels (as indicated by the numbers in column 1).

Factor	**Coef.**	**SE**	**Z**	***P*>|z|**	**95% CI**
Location					
2 vs 1	-1.98	0.88	-2.27	0.02*	(-3.71, -0.27)
3 vs 1	-0.82	0.80	-1.02	0.31	(-2.39, 0.75)
Period	0.18	0.38	0.47	0.64	(-0.56, 0.92)
Location by Period					
22 vs 11	0.54	0.63	0.85	0.40	(-0.71, 1.78)
32 vs 11	0.38	0.57	0.68	0.50	(-0.73, 1.49)
_cons	0.31	0.55	0.55	0.58	(-0.78, 1.39)
ID					
Var(_cons)	3.53	1.19	-	-	(1.83, 6.85)

Table A2.1 (b). Marginal contrasts of maintenance activities among locations.

Contrast	**df**	**Chi^2**	**P > Chi^2**
Location			
(NFLA vs. EVER)	1	0.48	0.49
(PSSF vs. EVER)	1	1.40	0.24
Joint	2	1.79	0.41

Table A2.1 (c). Marginal contrasts of maintenance activities for location effects within each period.

Contrast	**df**	**Chi^2**	**P > Chi^2**
Location@Period			
(NFLA vs EVER) 1	1	1.43	0.23
(NFLA vs EVER) 2	1	1.18	0.28
(PSSF vs EVER) 1	1	0.67	0.41
(PSSF vs EVER) 2	1	0.27	0.61
Joint	4	1.86	0.76

Table A2.1 (d). Marginal contrasts of maintenance activities for period differences within each location.

Contrast	**df**	**Chi^2**	**P > Chi^2**
Period@Location			
(2 vs 1) EVER	1	0.20	0.66
(2 vs 1) NFLA	1	0.96	0.33
(2 vs 1) PSSF	1	1.03	0.31
Joint	3	1.77	0.62

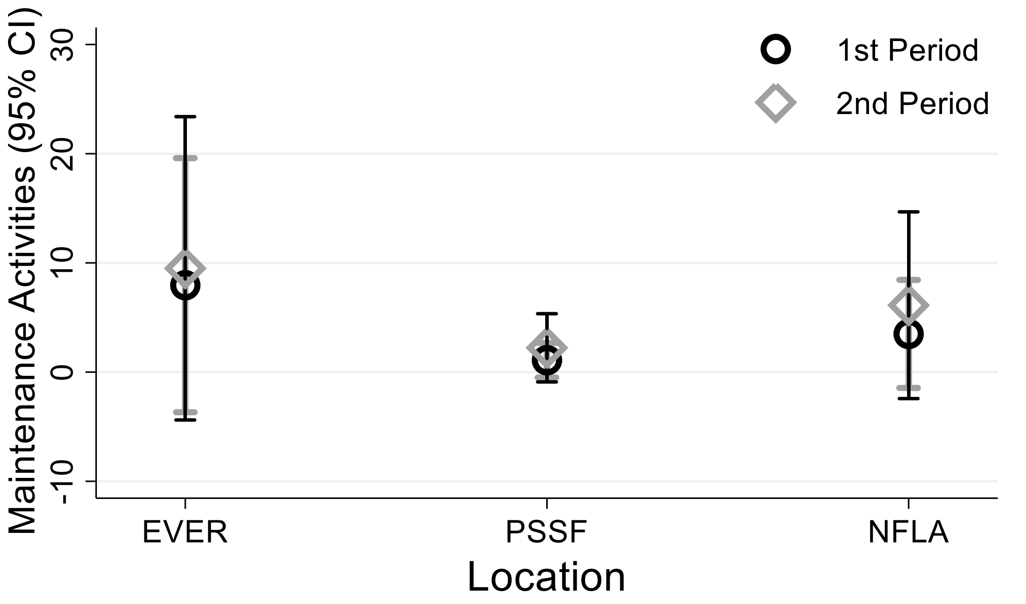


Figure A2.1. Marginal predicted mean maintenance activities (summed counts of bill-wipes, pecks, and preens), with 95% confidence intervals, for nuthatches tested at the three locations and in each of the two time periods. See text for location abbreviations.

Table A2.2 (a). Mixed-effects GLM for seconds spent low in the chamber (negative binomial link function for zero-inflated counts) with main effects and interaction term for Location (1= EVER, 2 = PSSF, 3 = NFLA) and Period (1st or 2nd sample period in the exploratory chamber) and bird ID as the random effect. Z tests refer to comparisons of factor levels to reference levels (as indicated by the numbers in column 1).

lowSecs	Coef.	Std. Err.	Z	*P*>|z|	95% CI
LocCD					
2	1.21	0.57	2.11	0.03*	(0.09, 2.33)
3	-0.26	0.58	-0.45	0.65	(-1.39, 0.87)
2. Period	-0.44	0.38	-1.16	0.25	(-1.19, 0.30)
LocCD#Period					
2 2	0.57	0.52	1.10	0.27	(-0.44, 1.58)
3 2	0.84	0.52	1.61	0.11	(-0.18, 1.86)
_cons	3.24	0.42	7.73	0.00	(2.42, 4.06)
/lnalpha	-0.15	0.24	-	-	(-0.62, 0.33)
ID			-	-	
Var(_cons)	1.72	0.57			(0.89, 3.30)

Table A2.2 (b). Marginal contrasts for time spent low by location.

Contrast	**df**	**Chi^2**	**P > Chi^2**
Location			
(NFLA vs. EVER)	1	0.09	0.77
(PSSF vs. EVER)	1	3.16	0.07*
Joint	2	3.16	0.21

Table A2.2 (c). Marginal contrasts of time spent low for location within period.

Contrast	**df**	**Chi^2**	**P > Chi^2**
Location@Period			
(NFLA vs EVER) 1	1	0.20	0.66
(NFLA vs EVER) 2	1	0.82	0.37
(PSSF vs EVER) 1	1	2.31	0.13
(PSSF vs EVER) 2	1	3.03	0.08*
Joint	4	4.45	0.35

Table A2.2 (d). Marginal contrasts of time spent low for period within each location.

Contrast	**df**	**Chi^2**	**P > Chi^2**
Period@Location			
(2 vs 1) EVER	1	1.04	0.31
(2 vs 1) NFLA	1	0.99	0.32
(2 vs 1) PSSF	1	0.13	0.72
Joint	3	1.96	0.58

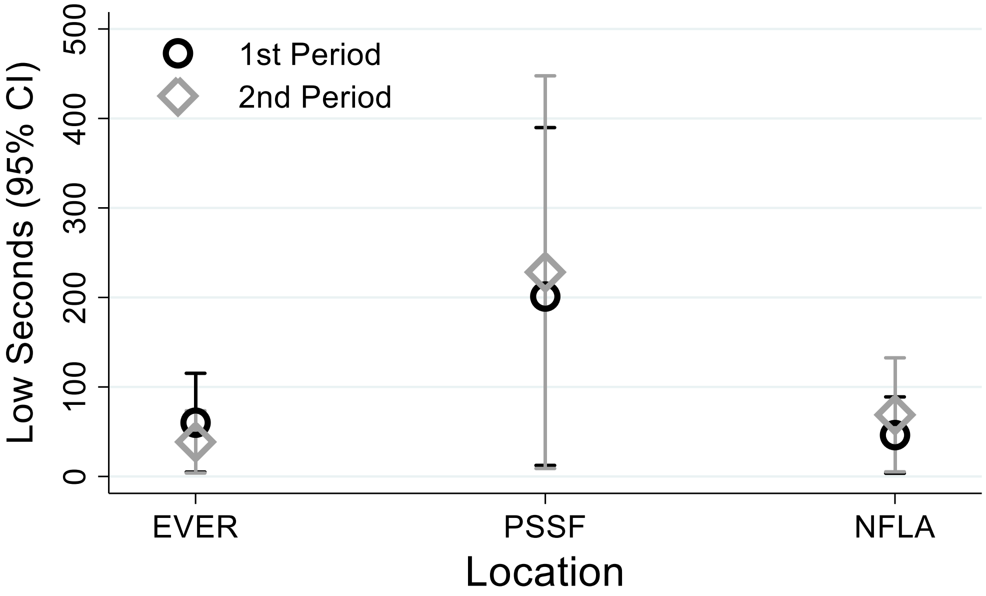


Figure A2.2. Marginal predicted mean number of seconds spent low in the exploratory cage, with 95% confidence intervals, for nuthatches tested at the three locations and in each of the two time periods. See text for location abbreviations.

Table A2.3 (a). Mixed-effects GLM for vocalizations (logit link function; bird called = 1; did not call = 0) with main effects and interaction term for Locations: 1= EVER, 2 = PSSF, 3 = NFLA and Period (1st or 2nd sample period in the exploratory chamber) and bird ID as the random effect. Z tests refer to comparisons of factor levels to reference levels (as indicated by the numbers in column 1).

Factor	**Coef.**	**SE**	**Z**	***P*>|z|**	**95% CI**
Location					
2 vs 1	0.70	1.49	0.47	0.64	(-2.21, 3.61)
3 vs 1	2.69	1.60	1.68	0.09*	(-0.45, 5.83)
Period	3.93e-17	1.22	0.00	1.00	(-2.38, 2.38)
Location by Period					
22 vs 11	-1.39	1.76	-0.79	0.43	(-4.83, 2.05)
32 vs 11	-1.44	1.62	-0.89	0.38	(-4.62, 1.74)
_cons	-2.94	1.37	-2.14	0.03	(-5.63, -0.25)
ID					
Var(_cons)	6.72	5.82	-	-	(1.23, 36.69)

Table A2.3 (b). Marginal contrasts of vocalizations between locations.

Contrast	**df**	**Chi^2**	**$P > Chi^2$**
Location			
(NFLA vs. EVER)	1	2.60	0.11
(PSSF vs. EVER)	1	0.00	0.96
Joint	2	3.15	0.21

Table A2.3 (c). Marginal contrasts of vocalizations by location within period.

Contrast	**df**	**Chi^2**	**$P > Chi^2$**
Location@Period			
(NFLA vs EVER) 1	1	3.32	0.07
(NFLA vs EVER) 2	1	0.70	0.40
(PSSF vs EVER) 1	1	0.23	0.63
(PSSF vs EVER) 2	1	0.18	0.67
Joint	4	4.09	0.39

Table A2.3 (d). Marginal contrasts of vocalizations by period within each location.

Contrast	**df**	**Chi^2**	**$P > Chi^2$**
Period@Location			
(2 vs 1) EVER	1	0.00	1.00
(2 vs 1) NFLA	1	1.38	0.24
(2 vs 1) PSSF	1	1.97	0.16
Joint	3	3.33	0.34

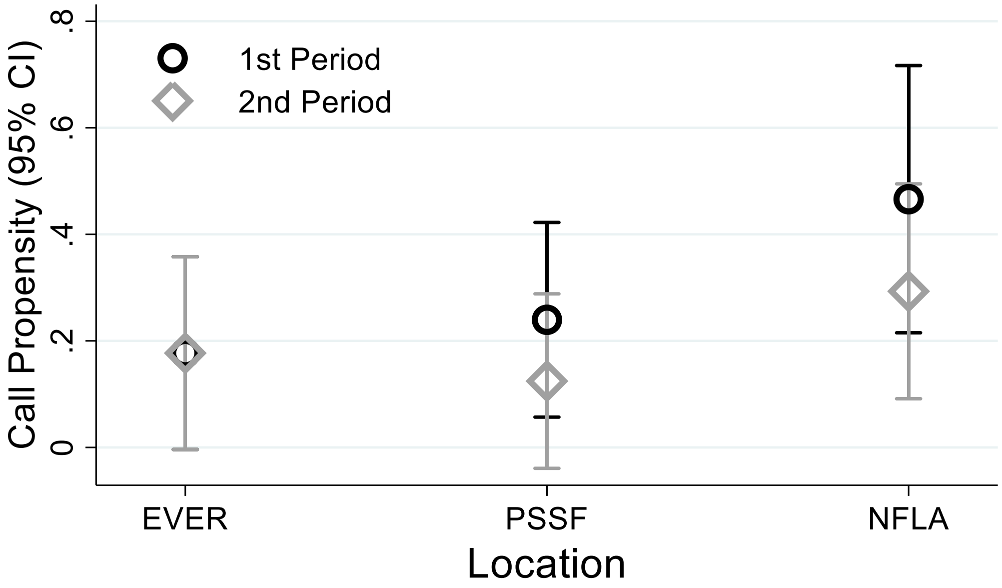


Figure A2.3. Marginal predicted mean probability that birds gave any calls (1 = called, 0 = did not call) during testing, with 95% confidence intervals, for nuthatches tested at the three locations and in each of the two time periods. See text for location abbreviations.