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Behavioral traits vary with intrinsic factors and impact local survival in Song Sparrows (Melospiza melodia)

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Behavioral traits vary with intrinsic factors and impact local survival in Song Sparrows (*Melospiza melodia*)

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ABSTRACT—Food acquisition is critical for individual fitness. Recent work has highlighted the importance of behavioral traits, such as boldness, for explaining variation in foraging abilities within populations. Greater flexibility in these behavioral traits might help populations persist in the face of environmental change; this may be particularly important for small populations that are more susceptible to local extirpation. We performed a winter-feeding experiment in an extensively studied island population of Song Sparrows (*Melospiza melodia*) to examine if intrinsic factors (age, sex, and inbreeding) explain variation in behavioral traits (neophobia, boldness toward predators, boldness toward competitors, and aggression) and how behavioral traits influence the probability of local survival for adults and of no dispersal and survival for juveniles. Our results showed that adults were less neophobic and bolder toward competitors than juveniles. This suggests that juvenile Song Sparrows might be more vulnerable to environmental changes than adults and may help explain why juvenile survival has been more strongly impacted by a new competitor on the island. Females were less neophobic than males, indicating that the sexes vary in their behaviors associated with resource acquisition, potentially due to constraints associated with reproduction in females. We found that the individual inbreeding coefficient did not appear to influence any of the behavioral traits examined here. Lastly, more neophobic adults were found to be more likely to survive to hold a territory the following breeding season, demonstrating the consequences of behavior on future fitness. These findings highlight that behavioral traits impact resource acquisition and fitness, and, thus, variation in these behaviors may play a critical role in understanding and predicting how populations respond to environmental change. *Received 25 August 2021. Accepted 26 February 2022.*

Key words: age, aggression, boldness, inbreeding level, neophobia, sex.

Características conductuales varían según factores intrínsecos e impactan sobrevivencia local en el gorrión *Melospiza melodia*

RESUMEN (Spanish)—La adquisición de alimento es crítica para la sobrevivencia individual. Trabajos recientes han destacado la importancia de características conductuales, como la osadía, para explicar la variación en capacidades de forrajeo al interior de poblaciones. Una mayor flexibilidad en características conductuales podría ayudar a las poblaciones a persistir de cara al cambio ambiental y esto podría ser particularmente importante para poblaciones pequeñas que son más susceptibles a extinciones locales. Llevamos a cabo un experimento de alimentación invernal en una población del gorrión *Melospiza melodia* que ha sido extensamente estudiada para examinar si factores intrínsecos (edad, sexo y endogamia) explican la variación en las características conductuales (neofobia, osadía ante depredadores, osadía ante competidores y agresión) y cómo las características conductuales influencian la probabilidad de sobrevivencia local para los adultos, y la no-dispersión y sobrevivencia para juveniles. Nuestros resultados muestran que los adultos fueron menos neofóbicos y más osados hacia competidores que los juveniles. Esto sugiere que los gorriones juveniles podrían ser más vulnerables a cambios ambientales que los adultos y esto podría ayudar a explicar por qué la sobrevivencia de los juveniles ha estado más fuertemente impactada ante un nuevo competidor en la isla. Las hembras fueron menos neofóbicas que los machos, indicando que los sexos varían en comportamientos asociados con adquisición de recursos, potencialmente debido a limitaciones asociadas con la reproducción en las hembras. Encontramos que el coeficiente de endogamia individual no parece influenciar ninguna de las características conductuales que examinamos aquí. Finalmente, los adultos más neofóbicos fueron más proclives a sobrevivir y asegurar un territorio en la siguiente temporada reproductiva, demostrando las consecuencias del comportamiento en la sobrevivencia futura. Estos hallazgos destacan que las características conductuales impactan la adquisición de recursos y, por ello, la variación en estas conductas podría jugar un papel crítico en nuestro entendimiento y capacidad de predecir cómo responden las poblaciones al cambio ambiental.

Palabras clave: agresión, edad, neofobia, nivel de endogamia, osadía, sexo.

An individual's ability to obtain food resources is critical for individual fitness and can have cascading effects on a population's stability and ability to withstand changing environments (Arcese and Smith 1988, Brittingham and Temple

1988, Sol et al. 2002, Richardson et al. 2019). Recent studies highlight the importance of behavioral traits in explaining why individuals within populations vary in their ability to acquire resources, particularly during periods when resources are limited, such as winter, when mortality is often higher (Smith et al. 1980, Schwabl-Benzinger et al. 1988, Arcese et al. 1992, Houston and McNamara 1993, Sutherland 1998, Smith and Blumstein 2008, Sih et al. 2012, Wolf and Weissing 2012). Moreover, individual performance during resource-limited periods can carry

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over to influence critical aspects of population dynamics including survival, natal dispersal, and reproduction (Brittingham and Temple 1988, Arcese 1989a, Houston and McNamara 1993, Sansom et al. 2009). Variation in behavior may be particularly important for small populations, as they are already vulnerable to extinction by stochastic processes and inbreeding depression (Amos and Balmford 2001, Furlan et al. 2012). Despite the importance of behavioral traits for individual fitness, population persistence, and range expansion (Duckworth 2008, Wolf and Weissing 2012, Cubaynes et al. 2014), studies quantifying variation in behavioral traits and their effects on future fitness remain rare, particularly in smaller, more vulnerable populations (Sih and Bell 2008). Examining behavioral variation within small populations may, therefore, be a critical first step in understanding how certain behaviors may contribute to population persistence in the face of shifting environments.

Three behavioral traits commonly used to describe variation in personality among individuals are neophobia, boldness, and aggression (Sih and Bell 2008, Georgiev et al. 2013, Biondi et al. 2020). Neophobia is the aversion of an individual to novel situations, objects, or foods, and may reduce the likelihood of an individual encountering dangerous situations (Biondi et al. 2020). An individual who is less neophobic is more likely to approach a novel feeding source, risking predation, but potentially gaining a new resource. Alternatively, an individual who is more neophobic avoids risk by not approaching a new potential resource but does not gain resource benefits either (Biondi et al. 2020). Boldness describes the degree of tolerance an individual exhibits toward a threat (Biondi et al. 2020). For example, when foraging, a bolder individual might tolerate a potential predator to maximize food intake (Belgrad and Griffen 2016). Conversely, a shy (i.e., less bold), individual might avoid the predator, reducing risk of predation, but losing access to the food resource (Belgrad and Griffen 2016). Aggression is the degree of defense of a resource, typically against conspecifics (Sih et al. 2004, Evans et al. 2010). A more aggressive individual might defend a resource against a conspecific, dominating the resource at the risk of injury or predation. Alternatively, a less aggressive individual might flee from an interaction with a conspecific,

avoiding injury, but losing access to the resource (Georgiev et al. 2013).

Intrinsic factors, such as age, sex, and inbreeding level, may be correlated with variation in behavioral traits. The age of an individual has been shown to explain variation in behavior (Bergman and Kitchen 2008, Greggor et al. 2020), often with adults displaying higher levels of boldness, neophobia, and aggression than juveniles (Bildstein et al. 1991, O'Hara et al. 2017, Liang et al. 2020). Sex is known to play a role in behavior during foraging, with males typically being more aggressive and bolder than females (Smith et al. 1980, Holder et al. 1991, Rodríguez-Flores and Arriaga 2016, Saiyed et al. 2019). While it is hypothesized that males would be less neophobic than females, results have been inconclusive (Ensminger and Westneat 2012). Identifying links between inbreeding level and behavioral traits related to resource acquisition may be particularly informative given the negative impact that inbreeding depression can have on small and/or isolated populations (Keller 1998). For example, individuals that are more inbred might have greater difficulty acquiring territories (Höglund et al. 2002) or competing for resources (Välimäki et al. 2007).

Examining behavioral traits in relation to survival and dispersal can help determine if there are consequences of these behaviors on individual fitness and if there may be selection on particular behaviors (Belgard and Griffin 2016, Ward-Fear et al. 2018). Assessing these links in association with winter feeding may be particularly insightful because winter food acquisition can influence individual quality and survival, with carryover effects on breeding (Martin 1987, Arcese 1989a, Robb et al. 2008). Further, given that both behavioral traits and individual fitness can vary based on intrinsic state (e.g., age and sex; Smith et al. 1980, Arcese et al. 1992, Bergman and Kitchen 2008), assessing links between behavioral traits, intrinsic traits, and dispersal and survival will help to understand the consequences of behavior on future fitness and local population dynamics.

Our study took place on the small 6 ha island of Mandarte, off the coast of Vancouver, British Columbia, Canada, which is home to a resident population of wild Song Sparrows (*Melospiza melodia*). This population has been extensively studied for over 45 years, resulting in a wide range of knowledge about the population and a precise,

genetically corrected pedigree (Smith et al. 2006, Reid et al. 2014). Here, we asked the following questions: (1) Are intrinsic factors (age, sex, and inbreeding) linked to behavioral traits (neophobia, boldness, and aggression) during winter foraging? (2) Do behavioral traits influence the probability of dispersal and local survival? We addressed these questions using a series of experiments performed during winter, when both competition for food and mortality rates are high (Smith et al. 1980, Arcese and Smith 1988, Arcese et al. 1992). Adult Song Sparrows hold territories, have more experience with the system, and have been shown to be more dominant when foraging compared to juveniles (Smith et al. 1980, Arcese 1989b, Hyman et al. 2004); therefore, we expected adults to be bolder, more aggressive, and more neophobic than juveniles. Male Song Sparrows are more territorial and dominant than females (Smith et al. 1980, Arcese 1989b); therefore, we expected males to be bolder and more aggressive than females. Since females must acquire more resources over winter to prepare for egg-laying in the next breeding season (Lezana and Campos 2013), we expected females to be less neophobic than males. Due to the adverse effects of inbreeding on learning (Nepoux et al. 2015, Müller and Juškauskas 2018), and potentially the ability to acquire resources, we predicted that more inbred individuals would be less aggressive, less bold, and more neophobic. If winter survival and dispersal the following year are strongly tied to resource acquisition (Arcese 1989a), then we would expect that individuals who gain more resources (i.e., are less neophobic) will be more likely to not disperse and survive. Further, given that juvenile local survival is lower compared to adults on Mandarte (Smith et al. 1980, Arcese et al. 1992), we predict that this relationship will be stronger for juveniles compared to adults. Ultimately, this study will help fill in a knowledge gap as to how intrinsic traits of individuals may be correlated with behavioral traits and how these behaviors influence fitness, ultimately influencing population persistence in a small, isolated population of Song Sparrows.

Methods

Study system

This study took place on Mandarte Island located off the coast of southwestern British Columbia, Canada, during late October 2013. Mandarte Island is a 6 ha islet with a population of Song Sparrows that remain on the island year-round, foraging predominantly on blackberry (*Rubus armeniacus*), Oregon grape (*Mahonia aquifolium*), nootka rose (*Rosa nootkatensis*), and red elderberry seeds (*Sambucus racemosa*) during the winter months (Smith et al. 2006, Johnson et al. 2018). Song Sparrows are sexually monomorphic, socially monogamous, and territorial (although territory defense decreases in the winter for resident populations). This population experiences very little adult predation with mortality primarily owed to overwinter exposure to cold (Smith et al. 1980, Arcese and Smith 1988, Evans et al. 2010, Scales et al. 2011, Nietlisbach et al. 2014, Germain et al. 2018). The Mandarte population of Song Sparrows has been annually monitored from April to July since 1975 and all individuals are individually color-banded, sexed, and followed throughout their entire lives (Tompa 1963, Smith et al. 2006, Johnson et al. 2018). Few immigrants (~1 on average) arrive each year to the island and all of them are caught in mist nets and banded. Food resources are lowest and Song Sparrows experience the highest mortality rates during the winter, with juvenile survival being impacted the greatest in extreme cold years (Smith et al. 1980, Arcese et al. 1992). During the winter, adults loosely associate with territories; however, juveniles travel around the island untied to a specific location. In 2013, there were 31 breeding females, and the total population size was 75 individuals (including breeding and nonbreeding females and males).

The Fox Sparrow (*Passerella iliaca*) is a recent colonist on Mandarte and is the only congeneric competitor species for Song Sparrows on the island. Fox Sparrows are native to British Columbia but were not observed on the island until 1975 (Drent et al. 1964, Tompa 1983), when they were first recorded breeding there, and became abundant in the 1980s (Johnson et al. 2018). Johnson et al. (2018) found that when the number of Fox Sparrows increased, Song Sparrow juvenile survival decreased, while the survival of adult Song Sparrows was not strongly impacted by Fox Sparrows. They found that this was primarily due to competition over wintering food resources, as Song Sparrows and Fox Sparrows have high diet overlap in this system, and Fox Sparrows, the
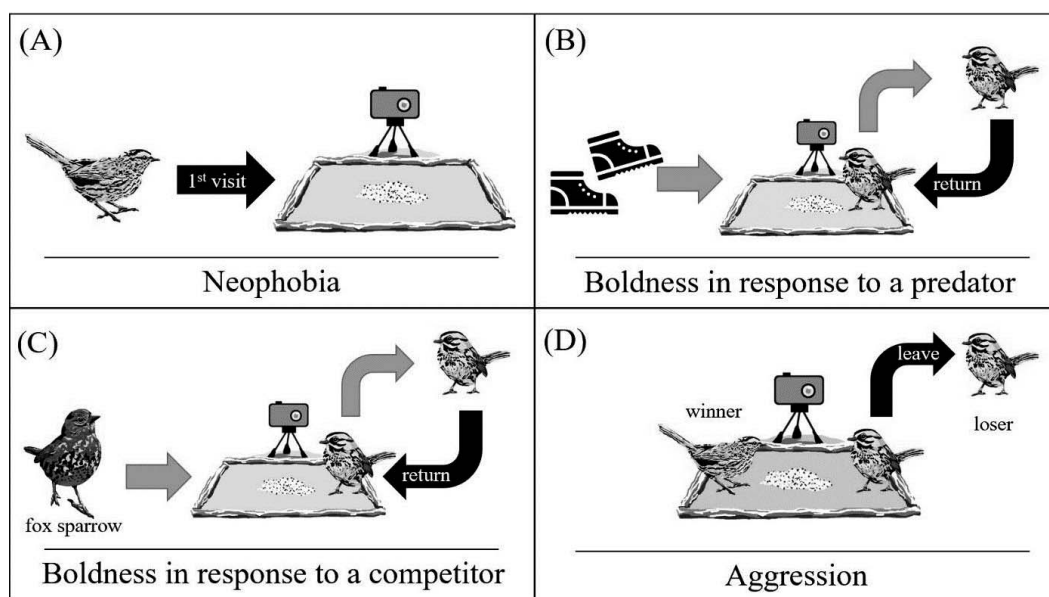
Figure 1. Behavioral traits assessed in Song Sparrows from Mandarte Island, British Columbia, Canada. (A) Neophobia measured as the latency of a Song Sparrow to first visit the feeding arena. (B) Boldness in response to a predator measured by the latency of a Song Sparrow to return to the feeding arena after being displaced by a human. (C) Boldness in response to a competitor measured by the latency of a Song Sparrow to return to the feeding arena after being displaced by a Fox Sparrow. (D) Aggression measured as the proportion of times a Song Sparrow stays in the arena (is a "winner") after chasing another Song Sparrow out of the arena out of the total number of interactions (including both being a winner and a "loser," defined as the one that leaves).

larger of the 2 species (~32 vs. ~24 g), are behaviorally dominant to Song Sparrows (Johnson et al. 2018). In 2013, there were 30 breeding female Fox Sparrows on Mandarte.

Experimental design

We assessed behavioral traits using winter feeding arenas to create a novel foraging environment. Winter feeding arenas allowed us to assess multiple behavioral traits because, due to decreased food availability associated with winter, birds are incentivized to approach, forage, and compete for food (Smith et al. 1980). We created the feeding arenas (arenas, hereinafter) by clearing and marking a roughly 30 cm square area with sticks and then placing 250 ml of commercial bird seed within the arena (Johnson et al. 2018). Arenas were set up at 8 sites distributed across the island and monitored daily for 4 d using video cameras. Cameras ran continuously between 0800 and 1800 h in 40–150 min segments, depending on camera battery life. Seed was refreshed in the morning and then periodically replenished as needed throughout

the day. The experiment ran 24–27 October 2013. Once the study was complete, the videos were reviewed in the lab. Each time a bird entered the frame we noted the time (hh:mm:ss), the individual's color band combination, the behavior (e.g., enter, forage, chase, leave), whether the bird was inside or outside of the marked arena, and the time the individual left the arena.

Behavioral traits

We measured neophobia, boldness, and aggression from the camera footage (Fig. 1 graphically shows how each trait was measured). We assessed neophobia as the latency of an individual to approach the novel arena and camera for the first time and interact with the commercial bird seed source (Fig. 1A; only including hours when the arenas and cameras were active; An et al. 2011). No food supplements had been supplied to the natural population in approximately 10 years, therefore, we considered the food, arena, and the cameras to present a novel foraging environment. We assessed boldness as the latency of an

Table 1. Observed range, mean, and median and associated sample sizes of Song Sparrow behavioral traits in Mandarte Island, British Columbia, Canada.

Behavioral trait	Metric	Range (min–max)	Mean	Median	n	Male	Female	Adult	Juvenile
Neophobia	Latency to approach (h)	0.44–34.45	13.50	16.25	30	17	13	16	14
Boldness in response to a predator	Latency to return (min)	0.58–11.03	5.93	4.83	10	5	5	3	7
Boldness in response to a competitor	Latency to return (min)	0.03–7.55	1.31	0.37	14	6	8	9	5
Aggression	Proportion of wins	0–1	0.50	0.53	15	9	6	8	7

individual to return to the arena after a startle test, measured in 2 different contexts—with humans (a potential predator) and Fox Sparrows (a competitor). Boldness in response to a predator was performed by a human approaching the arena, startling all of the birds away, and then measuring latency for the same individual Song Sparrow, who was flushed by the human, to return to the arena (Fig. 1B). After the predator startle tests, we noted whether a Fox Sparrow approached the arena before the Song Sparrows because, due to high competition, we predicted that Song Sparrows might further delay their return (Johnson et al. 2018). Boldness in response to a competitor was measured when a Fox Sparrow entered the arena, startling a Song Sparrow out of the arena, and then measuring the latency for that same Song Sparrow to return (Fig. 1C). Here, time was measured from when the individual Song Sparrow left the arena to the time when that same individual returned. To control for any effects of learning that might occur over multiple trials, we only included the first time that an individual participated in each of the startle tests. Due to the nature of our study (which behaviors we evaluated, short sampling duration, and free-roaming individuals) we did not have sufficient sample size to assess repeatability in our boldness metrics or neophobia. We suggest that future studies could focus on repeatability to understand whether these behaviors are fixed or flexible for individuals.

We assessed aggression as whether an individual won (chased another bird out of the arena) or lost (was chased out of the arena) when it was in the arena with another conspecific (Fig. 1D). Due to our experimental setup, we could not control which individuals interacted in aggressive interactions and in which order. Therefore, to account for multiple interactions with multiple individuals, we evaluated aggression as the proportion of successful interactions over the duration of the 4 d period.

To assess if the proportion of times won was an accurate representation of individual behavior, we assessed the repeatability of aggression for individuals using the *rptR* package and a binomial error distribution (Stoffel et al. 2017). We found evidence for repeatability (15 individuals, median samples per individual is 6, $n = 137$, scale approximation $R = 0.638$, $P < 0.05$). This suggests that individuals are consistent in their aggressive behavior and that the proportion of times an individual won is an accurate representation of this behavioral trait.

Intrinsic factors

We examined 3 intrinsic factors to assess if they link to behavioral traits—age, sex, and inbreeding. For age, we grouped individuals as juveniles (hatched that year) and adults (hatched any time before the current year). Our study included 14 juveniles and 16 adults (Table 1). The adults were 1–4 years old. Individuals were sexed using genetic sexing techniques (for details see Postma et al. 2011). In short, if a nestling survived 6 d in the nest, then a blood sample was taken, and a CHD marker was used to determine if the individual was male or female. Our study included 17 males and 13 females (Table 1). To evaluate the level of which an individual is inbred, we used their inbreeding coefficient (*f*, the degree to which the individual's parents shared the same alleles by descent from a common ancestor) calculated using a genetic pedigree (for details see Sardell et al. 2010, Reid et al. 2014, Nietlisbach et al. 2017). In short, genetic paternity was verified using up to 170 microsatellites, with 99.7% certainty, and maternity was assigned with 100% certainty, and proofed with observed maternal behavior. An inbreeding coefficient of 0 indicates that individuals are outbred (e.g., the offspring of an immigrant–resident pairing), and the closer the

value to 1, the more inbred an individual. The inbreeding coefficient values for the individuals used in this study ranged from 0 to 0.17 (Supplemental Material).

Probability of local survival and no dispersal

To understand how behavioral traits might impact individual fitness, we examined if behavioral traits influenced the probability that an individual would not disperse and survive to establish a territory and breed on the island the following year. This metric has different implications depending on the age of the individual. For adults, dispersal from Mandarte is rare (Smith et al. 2006). Once an adult has established a territory, it typically maintains a territory until it dies; however, on rare occasions it can also be evicted from a territory and become a nonbreeding floater (Arcese 1989b). In the case of juveniles, individuals may die, disperse off island, or survive. If they do not disperse and survive, they may not establish a new territory and become a floater, or they can establish a new territory and reproduce on Mandarte (Wilson and Arcese 2008). Some instances of juvenile emigration off of Mandarte to local islands have been observed (Arcese 1989a), but other surveys have found none (Wilson and Arcese 2008). That being said, emigration cannot be distinguished from mortality in this system. Juvenile local survival (from independence to age year 1) on Mandarte is 0.23 and 0.31 for females and males, respectively, which is approximately half of those of adults (0.42 and 0.55 for females and males, respectively, 1993–2018; Reid et al. 2021). Hereinafter, when referring to this process, for adults we will say "local survival" and for juveniles we will say "they did not disperse and survived." In April of each year a systematic survey is conducted on the island where all Song Sparrow individuals are resighted and territories mapped (Smith et al. 2006). From this data, for each individual observed in our study, we determined if they did not disperse, survived, and established a territory to breed in the 2014 breeding season.

Analyses

Intrinsic factors and behavioral traits—To determine if intrinsic factors explained variation in behavioral traits, we created a model set for each of the 4 behavioral traits. In each model set, we included 1 model for each of our intrinsic factors. While these individual traits may interact to influence behavioral response, we only included 1 trait per model, rather than an interaction between terms, owing to small sample size (Table 1). For the neophobia models, we used time to first arrival as the response variable with a generalized linear model (GLM) and a Gamma distribution because these data are continuous and non-zero (hours, including partial h). For each of the boldness models we used latency to return (minutes, including partial min) as the response variable with a GLM and a Gamma distribution. In the human startle test, we also included a fixed effect of whether a Fox Sparrow returned to the food before the Song Sparrow (1) or not (0). For the aggression models, we used a GLM with a beta distribution (*betareg* package; Cribari-Neto and Zeileis 2010), with the proportion of interactions won out of all interactions as the response variable. For each behavioral trait, we created single term models for each intrinsic factor: sex, age, and inbreeding. Using those models, we estimated the beta parameter and 95% confidence interval for each factor (Cumming and Finch 2005, Nakagawa and Cuthill 2007). For our results we described a factor to have "strong support" if the 95% CI did not overlap zero, the factor had "moderate support" if the estimate is away from zero, but the 95% CI unevenly overlapped zero (up to 85% CI did not overlap zero), and the factor had "no support" if the estimates centered on zero or if 95% CI were large and overlapping zero. To evaluate model fit for specific models we reported marginal R^2 values.

Probability of local survival and no dispersal— Due to limited sample size for boldness and aggression (Table 1), we focused this part of the analysis on examining the impact of neophobia on the probability of adult local survival and the probability that a juvenile did not disperse and survived. We constructed models for adults and juveniles separately. For each model the response variable was whether an individual established a territory the following breeding season or not (1: held a territory in 2014; 0: did not hold a territory in 2014) and we used a GLM with a binomial error distribution. For adults, we created 3 models: a single term model with a fixed effect of sex, a single term model with a fixed effect of neophobia,

Table 2. Song Sparrow behavioral traits in Mandarte Island, British Columbia, Canada. Parameter beta estimates and 95% confidence intervals (lower CI, upper CI) from models examining the effects of intrinsic factors on (A) neophobia, (B) boldness in response to a competitor, (C) boldness in response to a predator, and (D) aggression. Values in bold have strong support or moderate support.

Intrinsic factor	Beta estimate	Lower CI	Upper CI
(A) Neophobia: latency to approach			
Age	**0.47**	**−0.05**	**0.99**
Sex	**0.40**	**−0.14**	**0.93**
Inbreeding	−1.31	−6.30	3.58
(B) Boldness in response to a competitor: latency to return			
Age	**1.43**	**0.15**	**2.89**
Sex	0.35	−1.26	2.08
Inbreeding	−10.85	−34.27	9.23
(C) Boldness in response to a predator: latency to return			
Age	−0.36	−1.53	0.65
Sex	0.46	−0.54	1.45
Inbreeding	1.49	−10.70	12.89
(D) Aggression: proportion of wins			
Age	0.10	−1.31	1.52
Sex	0.49	−0.96	1.94
Inbreeding	1.91	−12.98	16.81

and a model with fixed effects of sex, neophobia, and their interaction. For juveniles we created 2 single-term models: 1 with a fixed effect of sex and 1 with a fixed effect of neophobia. We could not include the model with the interaction between neophobia and sex for juveniles due to insufficient spread of the data. Furthermore, for the purposes of simplification, we did not evaluate inbreeding for either age group, due to a lack of pattern observed in preceding analyses. We used the same model evaluation technique described above and

all analyses were performed in program R 3.6.3 (R Core Team 2020).

Data on behavioral traits of Song Sparrow from Mandarte Island, British Columbia, Canada, and intrinsic factors used in the study are available in the online Supplemental Material.

Results

Intrinsic factors and behavioral traits

Intrinsic factors explained variation in neophobia and boldness in response to a competitor, but not boldness in response to a predator or aggression (Table 2). Sex and age were both important intrinsic factors explaining variation in neophobia, and age was the only intrinsic factor that explained variation in boldness in response to a competitor (Table 2). Inbreeding received no support for explaining variation in any of the behavioral traits examined here (Table 2).

Neophobia—Adults were less neophobic than juveniles, approaching the novel food resource more quickly (Fig. 2A, Table 2A, approximate R^2 = 0.05). Furthermore, females were less neophobic than males (Fig. 2B, Table 2A; approximate R^2 = 0.04). In both cases the 95% CI unevenly overlapped zero (Table 2A) and the 85% CI did not overlap zero (β_{age} = 0.47, 85% CI = 0.09–0.85; β_{sex} = 0.40, 85% CI = 0.01–0.79), suggesting these factors had moderate support.

Boldness in response to a competitor—Adults were bolder than juveniles (Table 2B, approximate R^2 = 0.23), returning faster after being startled by a competitor than juveniles (Fig. 2C).
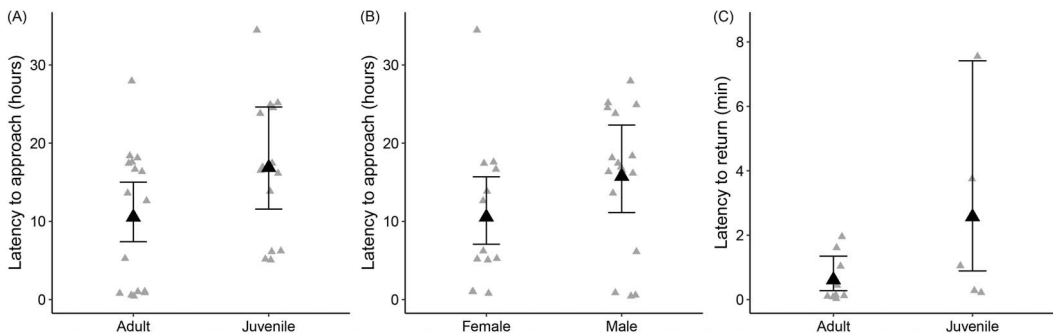

Figure 2. Song Sparrows from Mandarte Island, British Columbia, Canada, varied in their latency to approach the arena (i.e., neophobia) based on (A) age and (B) sex and in (C) their latency to return after being startled by a competitor (boldness in response to a competitor) based on age. Black triangles and error bars represent model predicted estimates and 95% confidence intervals. Small gray triangles are the raw data.

Table 3. Song Sparrow behavioral traits in Mandarte Island, British Columbia, Canada. Parameter beta estimates and 95% confidence intervals (lower CI, upper CI) from models examining the effects of neophobia on the probability of (A) adult local survival and (B) that a juvenile did not disperse and survived. Values in bold have moderate support.

Factor	Beta estimate	Lower CI	Upper CI
(A) Adult			
Neophobia	**0.09**	**−0.03**	**0.23**
Sex	−0.51	−2.59	1.48
Neophobia × sex	0.01	−0.28	0.30
(B) Juvenile			
Neophobia	−0.03	−0.16	0.09
Sex	0.18	−2.05	2.55

The 95% CI for the beta estimate did not overlap zero suggesting that age had strong support (Table 2B).

Probability of local survival and no dispersal— Adults that were more neophobic had a higher probability of local survival than those that were less neophobic (Table 3A, Fig. 3A; approximate $R^2 = 0.09$). Here, the 95% CI unevenly overlapped zero (Table 3A) and the 85% CI did not overlap zero (β = 0.09, 85% CI = 0.00–0.19), suggesting that the effect of neophobia on local survival had moderate support. Juveniles did not show a relationship between the neophobia and the

probability that an individual did not disperse and survived (Table 3B).

Discussion

From our study of behavioral traits and intrinsic factors of a wild population of Song Sparrows, 4 key points emerged. First, adult Song Sparrows were bolder toward competitors and less neophobic than juveniles. This suggests that adults were less risk-averse than juveniles; they were more willing to risk encountering an interspecific competitor to gain resources and to explore new resources, potentially resulting in greater resource acquisition compared to juveniles. Second, females were less neophobic than males. This suggests that males and females might experience different pressures that impact foraging, leading to females being more willing to engage in risk to acquire new food resources. Third, inbreeding did not influence any of the behavioral traits examined here. This suggests that either inbreeding does not impact neophobia, boldness, or aggression, or we were unable to detect these impacts. Finally, more neophobic adults were found to survive the winter to establish a territory, or remain on current territory, and breed the following year, suggesting that avoiding risk may benefit future survival and reproduction on Mandarte. Overall, these results
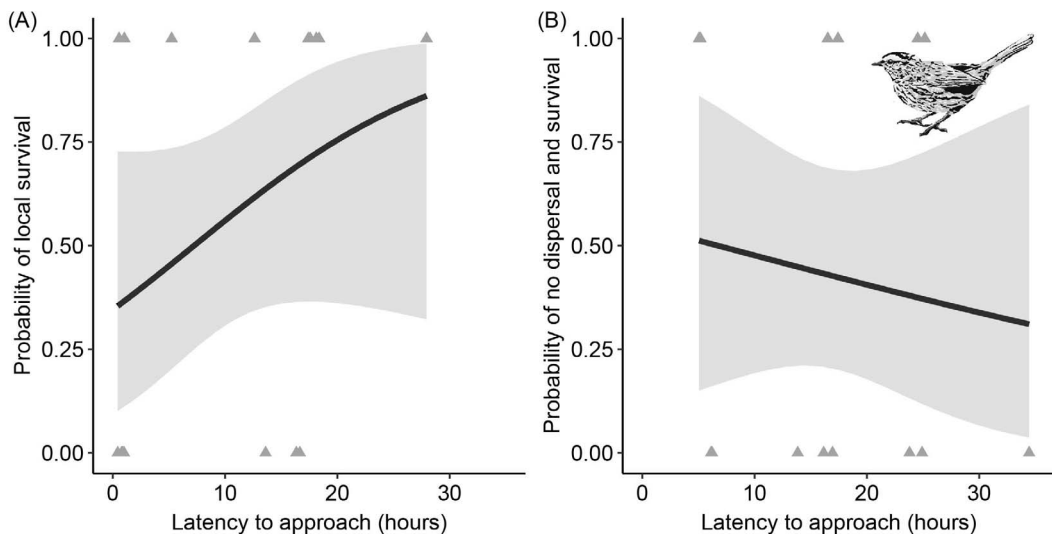

Figure 3. Song Sparrow behavioral traits in Mandarte Island, British Columbia, Canada. Model predicted relationship between neophobia and the probability of (A) adult local survival and (B) that a juvenile did not disperse and survived. The light gray areas around each line represent the 95% confidence intervals, small gray triangles are the raw data.

suggest that intrinsic factors can alter behaviors associated with foraging and impact local survival, as well as play a crucial role in the expression and variation of behaviors within a population.

Age differences in resource acquisition

Interspecific competition can greatly impact resource acquisition, with potentially profound population-level consequences in areas with introduced species or where populations are already near the tipping point of extirpation (Nishikawa 1985, Alexander et al. 2016, Van Zuiden et al. 2016, Lambert et al. 2019, Schleuning et al. 2020). On Mandarte, adults were bolder toward their Fox Sparrow competitors than were juveniles. Fox Sparrows compete with Song Sparrows for winter food resources and the increase in Fox Sparrows over time has resulted in decreased overwinter survival for juvenile Song Sparrows, but no impact on adult survival (Johnson et al. 2018). Our results suggest that the differential impacts of Fox Sparrows on adult and juvenile Song Sparrows may arise, in part, due to differences in boldness between the age classes. When faced with a larger competitor, juvenile Song Sparrows take longer to return to foraging, compared to adult Song Sparrows, potentially attributing to their reduced survival as the number of competitors increases.

Inconsistent with other studies (O'Hara et al. 2017, Sherratt and Morand-Ferron 2018), we found that adults were less neophobic than juveniles. Neophobia represents a trade-off between costs associated with exploration and overavoidance. While some studies show that the incentives to engage in riskier behavior decline with age (Greenberg and Mettke-Hofmann 2001, Crane and Ferrari 2017), others suggest that neophobia is a learned behavior and the amount of risk associated with novelty in a given environment influences neophobia (Greenberg 1992, 2003). For example, individuals that are exposed to greater risk when exploring new areas or resources will be more neophobic than those exposed to less risk (Sherratt and Morand-Ferron 2018). Thus, if juveniles are exposed to greater risks during exploration than adults and neophobia is a learned behavior, then one would predict adults would be less neophobic than juveniles (Greggor et al. 2020), as we found. On Mandarte, predation pressure on adults and juveniles is low

(Smith et al. 2006), and instead, the main risks to birds outside the nest may be competition. The age-based differences observed in how Song Sparrows respond to Fox Sparrows may lead to juveniles being more risk averse to avoid novelty and competitive interactions, compared to adults.

Sex differences in neophobia

Our study showed that females are less neophobic, or more willing to explore novel food resources, than males. This could arise due to different pressures experienced by the sexes. Differential energetic costs associated with reproduction may exert pressure on females to take more risks to acquire more resources. For example, female Song Sparrows that allocate more effort toward reproduction are less likely to survive to the following year (Tarwater and Arcese 2017), indicating that reproduction takes a toll on them over winter. Therefore, due to potentially poorer body condition associated with the previous breeding season (Balbonín et al. 2012) or the need to prepare for the physical taxation of the next breeding season (Houston et al. 1983), females may be more likely to seek out new food resources than males. Moreover, female Song Sparrows on Mandarte are less dominant than males at supplementary food sources (Smith et al. 1980), which further suggests that females might have to seek out new resources and rush in when they find a new opportunity before males arrive, in order to meet their daily energetic requirements. Males may also be able to afford to stay and defend one place (Wingfield 1994), rather than incur risks associated with leaving their territory in search of novel food sources. Being more risk averse may be one factor that contributes to higher male overwinter survival compared to females (Germain et al. 2018).

Inbreeding

Inbreeding level has been shown to have negative impacts on an individual's ability to compete for resources (Thompson et al. 2000, Välimäki et al. 2007) and territory-holding ability (Höglund et al. 2002). Here, we did not find a link between inbreeding level and behavioral traits. This could either be because inbreeding is less important for driving variation in winter food acquisition in Mandarte Song Sparrows, or it is

important, but we were unable to detect a link due to small sample size. On Mandarte, in studies with larger sample sizes than ours, inbreeding levels were found to impact the probability of local survival and lifetime reproductive success in females (Tarwater et al. 2018) and, during extreme years, inbreeding negatively impacted survival (Keller et al. 1994). Given the known adverse effects of inbreeding levels on this population and others, and that studies linking behavioral traits to inbreeding level in general are rare and have mixed results (Müller and Juškauskas 2018, Herdegen-Radwan 2019), we recommend future studies continue to explore these links.

Probability of local survival and no dispersal

Behavioral traits have been shown to influence different aspects of reproduction including pairing success, nesting productivity, and biomass of offspring (Garamszegi et al. 2008, Colchester and Harrison 2016, Arroyo et al. 2017). Here we found that more neophobic adults were more likely to survive the winter to establish or maintain a territory the following breeding season; however, neophobia did not impact the probability that a juvenile did not disperse, survived locally, and established a territory the following year. This suggests that it is beneficial for adults, who have previously held territories, to exhibit less exploratory behavior and limit their exposure to potential threats (i.e., competition and predation; Nietlisbach et al. 2014, Biondi et al. 2020). This pattern could result from links between territory quality, survival, and food acquisition. For example, an individual who held a high-quality territory, where food density is higher (Germain et al. 2015), may be more likely to acquire the resources they need while staying on their general territory. In contrast, an individual who held a low-quality territory may need to leave their territory, exhibiting more exploratory and less neophobic behaviors to gain resources, potentially exposing themselves to more risk and putting themselves at a fitness disadvantage (i.e., later laying dates and producing offspring that are less likely to recruit; Germain et al. 2015). That being said, adults switch territories opportunistically at any time of year, regardless of territory quality (Arcese 1987, Germain and Arcese 2014), and while links between breeding territory quality and fitness are

known (Germain et al. 2018) less is known about the quality of the territories in the winter. Therefore, more work should be done to clarify links between individuals, neophobia, and adult local survival. For juveniles, our results suggest that exploratory behavior alone does not play a large role in the probability that they do not disperse, survive, and acquire a territory the following breeding season. Instead, studies have shown that other factors, including dominance at feeders in the summertime, interspecific and intraspecific competition, maternal age, and natal morphological traits influence the probability that a juvenile Song Sparrow does not disperse, survives, and acquires a territory on Mandarte (Arcese and Smith 1985, Arcese 1989b, Smith et al. 2006, Johnson et al. 2018, Tarwater et al. 2018).

The profound impacts of animal behavior on adaptability, individual fitness, and population persistence are increasingly being acknowledged (Wolf and Weissing 2012). Our work illustrates that in this small, island population, behavioral traits differ based on intrinsic factors, these behaviors influence how animals acquire resources and interact with colonist species, and variation in these behaviors has fitness consequences. While it is widely acknowledged that variation between individuals has a large impact on sources of variation across population studies (Cam and Monnat 2000, Cam et al. 2002, Reid et al. 2003, Duckworth 2008), there is still much to learn about how and why individuals vary and the impact this can have on individual fitness and population persistence. Given threats to species and small populations in particular, performing studies on behavioral traits and fitness impacts is critical for understanding persistence in a changing world.

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