ORIGINAL ARTICLE

Exploration behavior differs between Darwin's finch species and predicts territory defense and hatching success

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Abstract

Darwin's finch species in the Galápagos Islands are famously distinguished by their morphology but less attention has been given to behavioral differences between species. In this study, we compared behavior between four Darwin's finch species on Floreana Island: small ground finch (*Geospiza fuliginosa*), medium ground finch (*G. fortis*), small tree finch (*Camarhynchus parvulus*), and medium tree finch (*C. pauper*). After capturing birds using mist-nets, we measured three behavioral traits: (1) boldness during human handling, (2) exploration in a novel environment, and (3) aggressiveness towards their mirror image. First, we found that ground finches were bolder and more exploratory than tree finches, consistent with their distinct ecological niches on Floreana Island and with the theoretical prediction that diet generalists should be less wary of novelty. Second, we tested the ecological validity of these behavioral variables at the individual level by relating them to territory defense behavior and breeding success. We found that males that were more exploratory in the novel environment also reacted more aggressively to a simulated territory intruder and showed lower offspring hatching success during the breeding season. Hence, our findings support previous work showing behavioral differences between Darwin's finch species and also suggest pathways by which behavioral differences among individuals might influence fitness.

Significance statement

Closely-related species that overlap in their geographical range may differ in their morphology and/or behavior, allowing them to occupy different ecological niches. In this study, we explored behavioral differences between four Darwin's finch species on Floreana Island in the Galápagos Archipelago. We found clear interspecies differences in behavior, with the ground finches struggling more often during handling (boldness) and visiting more sectors in a novel environment (exploration) compared to the tree finches. After birds were released, we continued to observe a subset of male finches in the wild. An individual's exploration behavior significantly predicted both its aggressive response to a territory intruder (simulated using song playback) and offspring hatching success during the breeding season. This suggests that individual differences in exploration behavior can potentially be used as a proxy for territorial behavior in the wild and may also predict fitness outcomes.

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Introduction

When closely related species overlap in their geographical range, niche differentiation can help minimize competition by allowing each species to exploit different resources within the same habitat (Tokeshi 1999). Niche differentiation may manifest among species not only as differences in morphology (Tokeshi 1999), such as avian beak size (Pigot et al. 2016), but also as differences in behavior (Alatalo et al. 1987; Radespiel et al. 2003). An animal's behavioral phenotype potentially reflects how it uses its habitat—for example, during foraging (Toscano et al. 2016).

In ecosystems where multiple related species live in sympatry, interspecific comparisons may help us understand the extent to which niche differentiation shapes behavior at the species level (Radespiel et al. 2003; Kamenova et al. 2015).

The Darwin's finches (subfamily Geospizinae) provide an ideal model system for assessing behavioral differences between closely related species. All but one of the Darwin's finch species are endemic to the Galápagos Islands, with many islands containing multiple species living in sympatry (Grant 1986). Indeed, David Lack emphasized the importance of between-species comparisons in this system, writing: "It now seems probable that at least most of the seemingly non-adaptive differences in Darwin's finches […] would, if more were known, prove to be adaptive" (Lack 1983, p. xii). Darwin's finch species are distinguished both by their morphology and behavior, including distinct diets and foraging styles that are considered to have played an important role in the finches' diversification (Grant 1986; Kleindorfer et al. 2022). For instance, Darwin's tree finches (*Camarhynchus* spp.) are generally considered foraging specialists, with much of their diets comprising arthropods extracted from woody and leafy substrates (Tebbich et al. 2009). In contrast, the ground finches (*Geospiza* spp.) are better described as 'imperfect generalists': each species feeds on a wide variety of foods, including invertebrates and plant matter, but during critical periods will specialize on resources for which they are differentially adapted (De León et al. 2014). This aligns with the theoretical prediction that generalist species can coexist with specialists by adjusting their consumption towards less exploited parts of the resource spectrum (Wilson and Yoshimura 1994; Tokeshi 1999). Among the Darwin's finches, behavioral differences may help each species maintain its foraging niche, allowing ground finches to flexibly exploit a wider range of foods and so minimize resource overlap with tree finches.

Behavioral differences can occur between species, between populations of the same species, or between individuals within a population (Wilson 1998; Réale et al. 2007). In particular, research in recent decades has highlighted the importance of behavioral differences between individuals (Laskowski et al. 2022). Under the theoretical framework proposed by Réale et al. (2007), individual behavioral traits such as boldness, exploration, and aggressiveness influence one or more 'component traits' (e.g. parental style, dominance, foraging), which in turn influence 'composite traits' (survival, mating success, reproductive success) that contribute towards fitness. However, behavioral differences measured in captive or wild-caught individuals do not necessarily align with how animals behave in the wild: discrepancies could arise, for example, if individuals differ in their latency to recover from handling stress or to acclimate to captive conditions (Niemelä and Dingemanse 2014). Hence, we need to confirm that behavioral differences measured under artificial conditions are expressed and ecologically relevant in the wild (Niemelä and Dingemanse 2014). Ideally, response profiles from wild-caught individuals should be validated in those same individuals after release into the wild (e.g. Herborn et al. 2010; Cole and Quinn 2014; Colombelli-Négrel et al. 2022). For instance, individual aggressiveness is often quantified in captivity using a mirror stimulation test, which presents subjects with their mirror image to mimic the presence of a same-age and same-sex conspecific (e.g. Armitage 1986; Hall et al. 2015; Leitão et al. 2019). After subjects are released into the wild, individual differences in aggressiveness can then be validated by quantifying subjects' response to conspecific territory intrusions (e.g. Amy et al. 2010; Yoon et al. 2012; Colombelli-Négrel et al. 2022). How vigorously individuals defend their territory is ecologically relevant because it may reflect their ability to retain important resources or attract a mate (Cain et al. 2015; Krieg and Getty 2020).

To further support the ecological validity of individual behavioral differences, we can also estimate their effects on composite traits such as survival (Moiron et al. 2020) and mating and reproductive success (Sih et al. 2014; Masilkova et al. 2022; Clermont et al. 2023). In theory, selection should favor whichever behavioral traits maximize individuals' fitness, eventually leading to the erosion of behavioral variation within populations. This generally does not occur in practice, perhaps because the fitness consequences of behavioral phenotypes vary with environmental or social conditions (Dingemanse et al. 2004; Nicolaus et al. 2016). Ultimately, field tests exploring the fitness consequences of behavioral phenotypes will reveal selective pathways that shape their distribution within populations (Smith and Blumstein 2008).

In this study, we measured three behavioral traits in wild-caught Darwin's finch species on Floreana Island in the Galápagos Archipelago: (1) boldness during human handling, (2) exploration in a novel environment, and (3) aggressiveness towards their mirror image (variables defined in Table 1). We do not describe these behaviors as personality traits, as individual birds were not tested repeatedly and so we could not show the consistency of individual differences (Réale et al. 2007). First, we compared mean behavioral scores between Darwin's finch species. We predicted that ground finch species would be more exploratory than tree finches in the novel environment, consistent with their distinct ecological niches on Floreana Island and also with the theoretical prediction that diet-generalist species should be less wary of novel situations (*neophobia threshold hypothesis*; Greenberg 1983, 1990). Second, we continued to observe a subset of male Darwin's finches in the wild to assess the ecological validity of these measured behavioral traits at the individual level. We predicted that bolder, more exploratory, and more aggressive males would respond more strongly to a simulated intrusion in their home territory. We also assessed the potential fitness consequences of individual behavioral differences,

Table 1 Operational definitions for all behavioral variables recorded in Darwin's finches for this study. We performed handling tests (boldness), novel environment tests (exploration), and mirror stimulation tests (aggressiveness) using wild-caught finches, while territory defense trials were conducted with wild birds in their home territory

assay	variable	definition
handling tests	back-test response	number of struggles while held on its back for 30 secs
	processing response	number of measurement procedures (0–5) in which struggling occurred
novel environment test	unique sector visits*	number of unique sectors (1–13) visited in 5 min
	total sector visits*	number of sectors visited in 5 min, including repeat visits
	floor use	whether the bird spent 10 + secs on the floor of the novel environment (yes/no)
mirror stimulation test	time near mirror	time (secs) spent in the three sectors nearest the mirror
	attacked mirror	whether the bird made physical contact with the mirror (yes/no)
territory defense trials	latency to approach†	latency (secs) to begin approaching the speaker after playback began
	minimum distance†	minimum distance (m) from the speaker during playback
	time within 5 m†	proportion of time spent within 5 m of the speaker
	time within 1 m†	proportion of time spent within 1 m of the speaker
	flights†	number of flights during playback
	crosses†	number of flights that crossed over the speaker during playback
	vocalizations	number of vocalizations (songs, buzzes, or whistles) produced during playback

* variable contributed to *PC_Exploration*, our measure of exploration behavior

† variable contributed to *PC_Playback*, our measure of territory defense behavior

by testing whether a male's exploration score predicted its pairing status and breeding success.

Methods

Study sites and study species

From January to March 2020, we mist-netted Darwin's finches at three sites on Floreana Island in the Galápagos Archipelago, Ecuador. The two highland (humid zone) sites, located at Asilo de la Paz (1°18′46″S 90°27′16″W) and the base of Cerro Pajas (1°17′46″S 90°27′06″W), consisted largely of remnant *Scalesia pedunculata* forest. The one lowland (dry zone) site comprised dry scrubland dominated by palo santo trees (*Bursera graveolens)* in and around the township of Puerto Velasco Ibarra (1°16′28″S 90°29′13″W). Given its proximity to the township, the lowland study site experiences higher amounts of human disturbance than the two highland study sites (ACK et al. pers. obs.) and greater nest predation by introduced species such as black rats (*Rattus rattus*), house mice (*Mus musculus*), and feral cats (*Felis catus*) (O'Connor et al. 2010a). Conversely, the highlands experience higher rates of nest parasitism by the invasive avian vampire fly (*Philornis downsi*) (O'Connor et al. 2010a). Darwin's finches on Floreana Island have been color-banded and monitored since 2004 (Langton and Kleindorfer 2019). All new captures were fitted with a numbered aluminum leg-band and a unique combination of colored plastic bands. For this study, we targeted the five species

considered extant on the island: small ground finch (*Geospiza fuliginosa*), medium ground finch (*Geospiza fortis*), common cactus finch (*Geospiza scandens*), small tree finch (*Camarhynchus parvulus*) and medium tree finch (*Camarhynchus pauper*) (O'Connor et al. 2010b; Kleindorfer et al. 2019). In addition, we also caught individuals previously identified as genetic hybrids of *C. parvulus* and *C. pauper* (Kleindorfer et al. 2014). Due to their small sample sizes, common cactus finches and hybrid tree finches were excluded from all analyses; however, we summarize data from all species in Table S1 and Table S2. We placed mist-nets along roads and walking trails, which are generally the only accessible areas at our study sites. We monitored the mist-nets constantly and extracted birds as soon as they were captured.

Behavioral assays

Handling tests (boldness)

Response to human handling (suggested to be a measure of boldness; Réale et al. 2007) has been identified as a repeatable behavioral trait in several animal species, including bighorn sheep (*Ovis canadensis*; Réale et al. 2000), blue tits (*Cyanistes caeruleus*; Kluen et al. 2014), and superb fairy-wrens (*Malurus cyaneus*; Katsis et al. 2023). In this study, we conducted two different handling tests in adult finches. After capture, birds were placed in cotton bags and transported to a nearby banding station. During the 'back test' (Hessing et al. 1993; Hall

et al. 2015; Bilby et al. 2022), we held the subject in the bander's grip, tilted onto its back, and counted the number of times it struggled over a 30 s period (Fig. 1a). We called this variable *back-test response*. A struggle was characterized as a short, uninterrupted burst of wriggling or leg-kicking. Next, we took five morphological measurements: 1) tarsus length, using a sliding calliper; 2) head-bill length, using a sliding calliper; 3) tail length, using a ruler; 4) wing length, using a butt-ended ruler; and 5) body mass, using an electronic scale. As a second measure of boldness, we noted whether the subject struggled during each of these measurements and then assigned it a score on a discrete ordinal scale from 0 (did not struggle during any measurement) to 5 (struggled during all five measurements). We called this variable *processing response* (analogous to 'handling aggression' in Brommer and Kluen 2012; Kluen et al. 2014). As expected, these two measures of boldness were significantly positively correlated (Spearman's $\rho = 0.48$, $P < 0.001$). Sex was assigned based on a combination of morphometrics, plumage coloration, and the presence or absence of a brood patch (Price 1984; Grant et al. 1985; Grant 1990; Langton and Kleindorfer 2019) (see Supplementary Methods for details). We conducted handling tests for 152 small ground finches, 61 small tree finches, 25 medium ground finches, 24 medium tree finches, 8 common cactus finches and 5 hybrid tree finches (total $N = 275$ birds).

Novel environment (exploration) and mirror stimulation (aggressiveness) tests

A subset of captured birds ($N = 162$) undertook the novel environment and mirror stimulation tests, which measured exploration and aggressiveness, respectively. Réale et al. (2007, p. 295) defined exploration as "an individual's reaction to a new situation [including] behaviour towards a new habitat, new food, or novel objects." This trait is often measured by releasing animals into a novel arena and scoring their movements within that environment (an 'open field test' or 'novel environment test'; Verbeek et al. 1994). Although the consistency of exploration has not been tested in Darwin's finches, the trait is known to be repeatable across a number of songbird species, including great tits (*Parus major*; Dingemanse et al. 2012; Thys et al. 2017b), superb fairy-wrens (Hall et al. 2015; Katsis et al. 2023), Australian zebra finches (*Taeniopygia castanotis*; McCowan et al. 2015; Katsis et al. 2021), and starlings (*Sturnus vulgaris*; Thys et al. 2017a). Aggressiveness is an individual's agonistic response towards a conspecific (Réale et al. 2007); it can be measured in captivity using a mirror stimulation test, in which the subject's mirror image is mistaken for an unknown conspecific and provokes an agonistic response (Armitage 1986; Hall et al. 2015; Leitão et al. 2019).

We conducted novel environment and mirror stimulation tests in the field, a short distance (~100 m) from the on-site banding station. Subjects were first placed individually in a plastic release box (dimensions 19 × 14 × 10 cm) and
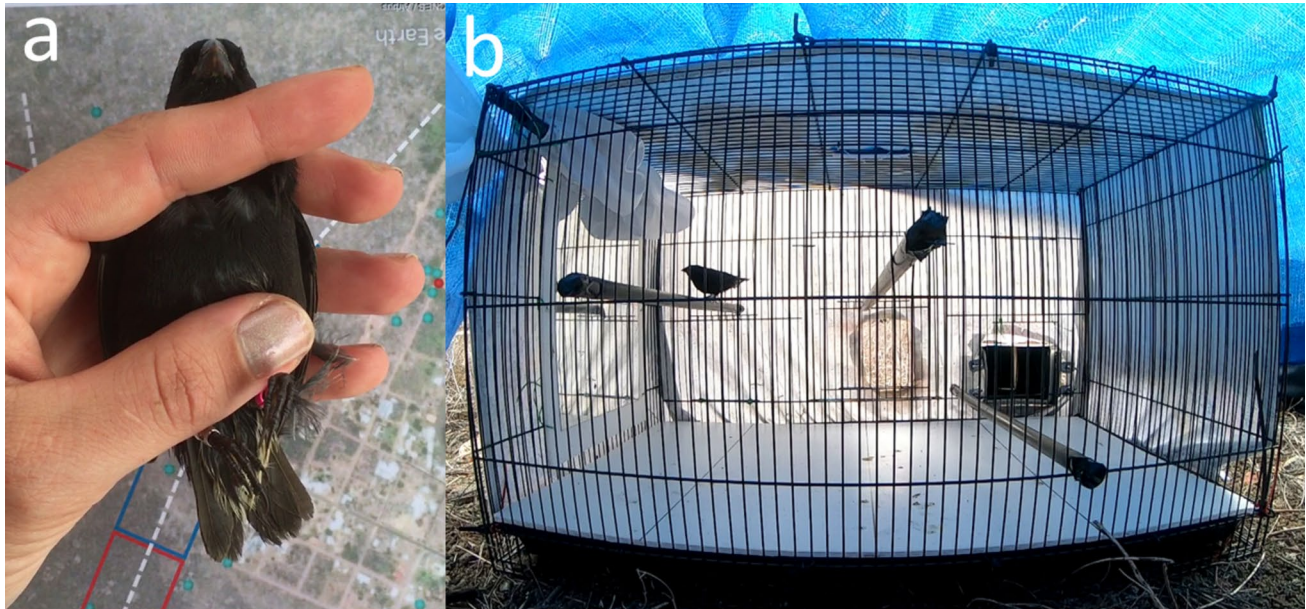

Fig. 1 Photographs of the behavioral assays used to measure behavior in this study. (**a**) An adult small ground finch tilted onto its back during the back-test handling test; and (**b**) the flight cage used for the novel environment and mirror stimulation tests, with the mirror revealed and a finch observing its mirror image

allowed 5 minutes to acclimate. The door from the release box was then raised, allowing the bird to directly enter the novel environment: a portable metal flight cage (75 × 44 × 42 cm) with three perches (one 6 cm high and the others 20 cm high) and the floorspace divided into four equal quadrants (Fig. 1b). The same cage was used for all trials. Subjects were initially given 180 s to emerge; if they did not emerge, they were forced into the flight cage by tapping on the release box. The cage was covered on all sides by an opaque fabric that visually isolated the bird from its surroundings, as well as a tarp for additional weather protection. On one side, we placed two cameras (GoPro Hero 7 Black) outside the cage to record the subject's movements. The cage was divided into 13 discrete sectors that the subject could visit: three perches, four floor quadrants, four cage walls, the cage ceiling, and the release box. We defined *total sector visits* as the number of sectors visited in 5 min following emergence (including repeats) and *unique sector visits* as the number of different sectors visited within the same period (Katsis et al. 2021). Hence, if a bird visited three different perches and twice landed on the front cage wall, then total sector visits was 5 and unique sector visits was 4. These two measures of exploration were significantly positively correlated (Spearman's $\rho = 0.80$, $P < 0.001$).

Following the 5-min novel environment test, we remotely raised a curtain to reveal a mirror (29 × 21 cm) at one end of the cage. We expected Darwin's finches to respond aggressively to their mirror image, as they are highly territorial and will defend against intruders in their territory (Ratcliffe and Grant 1983). We noted whether the subject made physical contact with the mirror (*attacked mirror*) and how long it spent near the mirror (i.e. in the three nearest sectors; *time near mirror*) over a 3-min period. As expected, these two measures of aggressiveness were significantly related, with birds that attacked the mirror also spending more time near the mirror (Mann-Whitney U = 274, $P < 0.001$).

At the end of the mirror stimulation test, the subject was recaptured by hand and released at its point of capture. Behaviors were manually scored from the recorded videos using the software Solomon Coder v. beta 19.08.02. All novel environment and mirror stimulation tests were conducted and scored by a single experimenter (ACK) to ensure consistency across trials. This scoring was not conducted blind to the subject's species and identity, as birds and their colorbands were visible in the videos. We conducted novel environment and mirror stimulation tests for 75 small ground finches, 46 small tree finches, 21 medium tree finches, 10 medium ground finches, 5 common cactus finches and 5 hybrid tree finches. Most tests ($N = 126$) were conducted in the morning between 06:45 and 12:00 GALT, although some took place in the early (12:00–13:10, $N = 6$) or late afternoon (15:50–18:20, $N = 30$). Birds were captured only for short periods (typically less than one hour) and released

after a single suite of behavioral assays. One small tree finch was missing aggressiveness data due to human error.

Territory defense trials

Male Darwin's finches defend their territories from conspecific intruders by displaying aggressively and chasing intruders from the area (Ratcliffe and Grant 1983, 1985). To quantify territory defense behavior in the field, we used conspecific song playback to simulate male intruders in the territories of male finches (females rarely respond to playback; Ratcliffe and Grant 1985). We targeted color-banded individuals whose boldness, exploration, and aggressiveness behavior we had measured or planned to measure. We conducted all playback experiments in January and February 2020, between 08:00 and 11:00 GALT to correspond with the peak of song activity. We tested 21 small ground finches, 16 small tree finches, and 11 medium tree finches (total $N = 48$ birds); we did not locate any territories belonging to medium ground finches. Most territory defense trials ($N = 31$) were conducted 1–15 days after the subject's capture for behavioral testing, although some trials took place 1–8 days before capture ($N = 9$) or on the same day ($N = 8$).

We generated our playback stimuli using conspecific songs recorded in 2020. We created 35 unique playback stimuli from 35 individuals (14 small ground finches, 10 small tree finches, 11 medium tree finches) (see Supplementary Methods for details). Each playback track comprised 1 min of song playback, then 1 min of silence, then 1 min of song playback (total 3 min). The 1-min song playback periods each contained six repetitions of a single song type recorded from a male finch. In Darwin's finches, males produce a single song consisting of one syllable repeated many times (Colombelli-Négrel and Kleindorfer 2021; Colombelli-Négrel et al. 2023); thus, the playbacks simulated a lone intruding male. We then transferred these playback tracks to an Apple iPod (Apple Inc., USA).

Once we entered a male finch's territory, we placed the iPod and playback speaker in the branches of a shrub or tree at a height of 1–1.5 m in the center of the territory. We then started a randomly-chosen playback track (played at ~80 dB at 1 m) corresponding with the subject's species. Two observers (within ~10 m of the speaker) narrated the experiment into a microphone. For each subject, we recorded seven response variables during the playback period: latency to approach, minimum distance, time within 5 m, time within 1 m, flights, crosses, and vocalizations (defined in Table 1). We never started playback until the male was observed within 20 m of the speaker and never tested neighbours on the same day or with the same stimulus. Playback tracks were randomly assigned to each subject with the condition that the stimulus bird was not recorded closer than

1 km from the subject's territory. To minimize observer bias, playback trials were conducted blind to the subjects' boldness, exploration, and aggressiveness scores.

Monitoring breeding success

During the breeding season, unpaired male Darwin's finches build a display nest in their territory and sing at the nest until chosen by a female (Grant 1986). After mating, the female lays 3–4 eggs and incubates them for a period of ~ 12 days, during which the male delivers food to her (Grant 1986). After hatching, the mother broods the nestlings and both parents deliver food (Kleindorfer et al. 2021), until fledging occurs 13–16 days posthatch (Grant 1986). Major sources of nest failure are nest abandonment and egg predation during the incubation period (O'Connor et al. 2010a) and nestling predation and avian vampire fly parasitism during the nestling period (O'Connor et al. 2010a, c).

During the first two months of the 2020 breeding season (January and February), we searched for Darwin's finch nests at our three study sites and monitored the breeding success of male finches whose behavior we had previously measured. Upon discovering a suitable male, we observed his nest for ~ 20 min to determine if he was paired with a female or unpaired; we then revisited the nest at least every three days to check on his pairing status. If the male became paired, we continued to regularly monitor the breeding pair to determine the success of their nesting attempt. We established offspring stage (eggs or nestlings) either by directly accessing the nest with a ladder or by observing the parents' incubation or provisioning behavior with binoculars, following a standardized protocol (Kleindorfer et al. 2021). Monitoring ended when the outcome of the nesting attempt was known (i.e. nest abandoned or taken over, offspring died, or offspring fledged). For each male finch, we determined its (1) pairing status (unpaired or paired), (2) hatching success (eggs did not hatch, eggs hatched), and fledging success (nestlings fledged, nestlings did not fledge). We monitored breeding success for $N = 23$ small ground finches, 13 small tree finches, and 13 medium tree finches (total $N = 49$ birds). Some males ($N = 5$) were observed at two nests during the monitoring period and we analysed their most successful outcome.

Statistical analysis

All statistical analyses were performed in R v. 4.1.2 (R Core Team 2021). Principal component analyses were performed on the correlation matrix using the *princomp* function in the package 'stats' v. 4.2.3. Zero-inflated models were fitted using the package 'glmmTMB' v. 1.1.6 (Brooks et al. 2017) and included a single zero-inflation parameter applying to all observations (*ziformula = ~1*). ANOVAs were performed based on Type II sums of squares using the *Anova* function in the package 'car' v. 3.1-1 (Fox and Weisberg 2018). Post hoc pairwise comparisons were performed using the *pair* function in the package 'emmeans' v. 1.8.5 (Lenth 2022), with *P*-values Holm-adjusted to account for multiple testing.

Species differences in boldness, exploration, and aggressiveness

To derive a single exploration score for each subject, we used principal component analysis to reduce total sector visits and unique sector visits to a single principal component (*PC_Exploration*) with an eigenvalue of 1.73 and which cumulatively explained 86.3% of variance (eigenvectors 0.71, 0.71). Higher principal component scores for *PC_Exploration* indicated that the subject was more exploratory (i.e. visited more total and unique sectors) in the novel environment.

For the handling tests, we assessed species differences in *back-test response* and *processing response* (see Fig. S1 and Fig. S2 for histograms) using separate zero-inflated Poisson (ZIP) models. For the novel environment test, we tested for species differences in *PC_Exploration* using a linear model. For the mirror stimulation test, we used a GLM (with binomial distribution) to test whether some species were more likely to attack the mirror, and a zero-inflated GLM (with Gaussian distribution) to test for species differences in time spent near the mirror (this response variable was square-root-transformed to normalize the model residuals). In all models, we included sex and species as fixed effects and used ANOVAs to assess whether the removal of each fixed effect caused a significant change in model fit. Because handling assays were conducted by four different experimenters, the boldness models also included Handler ID as an additional fixed effect. For models in which 'species' significantly improved model fit, we conducted post hoc pairwise comparisons between species.

Three of our study species (small ground finch, small tree finch, medium tree finch) occurred at multiple study sites, which may be subject to different environmental selection pressures. To test whether boldness, exploration, and aggressiveness differed between study sites, we conducted separate analyses for each species (see Supplementary Methods for statistical details). Additionally, to test whether the three behavioral traits were related to each other, we tested for correlations between exploration (*PC_Exploration*) and each measure of boldness and aggressiveness (see Supplementary Methods for statistical details).

Relationship between behavioral traits and territory defense in the wild

Using principal component analysis, we reduced six of our seven territory defense variables to one uncorrelated principal component (*PC_Playback*) with an eigenvalue of 3.24 and explaining 54% of variance (Table S3). Higher *PC_Playback* scores indicated a more aggressive response to the simulated intruder (shorter latency to approach, shorter minimum distance, more time spent within 5 m, more time spent within 1 m, more flights, and more crosses). We excluded the seventh variable (vocalizations) because it did not contribute significantly to the retained principal component (Björklund 2019). We used the R package 'PCAtest' v. 0.0.1 (Camargo 2022) to assess the correlational structure of our dataset and the distinctness of each principal component (see Supplementary Methods for statistical details).

To test which behavioral traits predict a bird's territory defense response, we used linear models with territory defense (*PC_Playback*) as the dependent variable and one behavioral measure (*processing response*, *back-test response*, *PC_Exploration*, *attacked mirror*, or *time near mirror*) as the predictor variable. These five models included species, study site and (for boldness models) Handler ID as additional fixed effects, and we used ANOVAs to test which fixed effects improved model fit.

Correlations between exploration and fitness

To test the relationship between exploration score and fitness, we used three binomial GLMs with pairing status (unpaired, paired), hatching success (eggs did not hatch, eggs hatched), and fledging success (chicks did not fledge, chicks fledged), respectively, as the response variables. All three models included species (small ground finch, small tree finch, medium tree finch) and male exploration score (*PC_Exploration*) as fixed effects, and we used ANOVAs to test which of these fixed effects improved model fit. We initially included an interaction term (species × exploration) as an additional fixed effect but this was non-significant ($P > 0.05$) and subsequently removed from all models. We used Akaike's information criteria to confirm that the inclusion of the interaction term did not improve model fit (see Supplementary Methods). When testing the relationship between exploration and pairing status, we included all male Darwin's finches for which we had exploration scores and nest observations ($N = 49$). When testing the relationships between exploration and hatching/fledging success, we narrowed our dataset to include only paired males with known nesting outcomes ($N = 26$).

Results

Species differences in boldness, exploration, and aggressiveness

In the handling tests, both measures of boldness were predicted by species (ANOVA: *processing response*: $\chi^2_3 = 17.37$, $P < 0.001$; *back-test response*: $\chi^2_3 = 15.08$, $P = 0.002$). Post hoc pairwise comparisons showed that, during processing, the ground finches struggled during more measurement procedures than the tree finches (adjusted $P < 0.036$ for all species comparisons, Table 2). During the back test, small ground finches struggled fewer times than medium tree finches (adjusted $P = 0.005$) (Table 2). Sex predicted neither measure of boldness, while Handler ID

Table 2 Post hoc pairwise comparisons for boldness and exploration between four Darwin's finch species (small ground finch = SGF, medium ground finch = MGF, small tree finch = STF and medium tree finch = MTF)

comparison	estimate	SE	t	P
(a) *Processing response (N = 262)*				
SGF–MGF	-0.28	0.17	-1.65	0.197
SGF–MTF	0.68	0.25	2.77	**0.022**
SGF–STF	0.38	0.15	2.51	**0.036**
MGF–MTF	0.96	0.28	3.37	**0.005**
MGF–STF	0.67	0.21	3.16	**0.008**
MTF–STF	-0.29	0.27	-1.09	0.275
(b) *Back-test response (N = 262)*				
SGF–MGF	-0.48	0.19	-2.52	0.058
SGF–MTF	-0.64	0.19	-3.34	**0.005**
SGF–STF	-0.26	0.16	-1.65	0.299
MGF–MTF	-0.16	0.24	-0.64	0.598
MGF–STF	0.22	0.22	1.04	0.598
MTF–STF	0.38	0.20	1.89	0.236
(c) *Exploration (PC_Exploration) (N = 152)*				
SGF–MGF	0.14	0.38	0.37	1.000
SGF–MTF	1.28	0.28	4.54	**< 0.001**
SGF–STF	1.43	0.22	6.66	**< 0.001**
MGF–MTF	1.13	0.44	2.57	**0.034**
MGF–STF	1.29	0.40	3.20	**0.007**
MTF–STF	0.16	0.30	0.52	1.000

(a) *Processing response* (considered as boldness), the number of measurement procedures in which the subject struggled; (b) *back-test response* (considered as boldness), the subjects' number of struggles during a 30 s back test; and (c) *PC_Exploration* (exploration of a novel environment), with higher values indicating that the subject visited more total and unique sectors of the assay cage in 5 min. Each model included species and sex as fixed effects, with pairwise comparison results averaged across sex. The two boldness models also included Handler ID as a fixed effect. *P*-values are Holm-adjusted to account for multiple testing, and statistically significant (< 0.05) values are marked in bold

predicted *back-test response* but not *processing response* (Table S4).

In the novel environment test, exploration was predicted by species (ANOVA: $F_{3,147} = 17.59$, $P < 0.001$). Post hoc pairwise comparisons showed that the ground finches were more exploratory than the tree finches (adjusted $P < 0.034$ for all species comparisons; Table 2, Fig. 2, Fig. S3). In addition, ground finches were generally more likely than tree finches to use the floor of the novel environment cage (Table S5). Sex did not predict exploration score (Table S4).

In the mirror stimulation test, attacking the mirror was generally rare, occurring in only 0–24% of subjects by species (Table S2). Species did not differ in their likelihood of attacking the mirror ($\chi^2_3 = 3.35$, $P = 0.340$) nor in their time spent near the mirror ($\chi^2_3 = 2.06$, $P = 0.560$). Sex predicted neither measure of aggressiveness (Table S4).

In small and medium tree finches, study site predicted boldness and exploration but not aggressiveness (see Supplementary Results, Fig. S4). Specifically, small tree finches were bolder at Cerro Pajas than at Puerto Velasco Ibarra (*back-test response*: $t = -2.62$, $P = 0.026$) and medium tree finches were bolder at Cerro Pajas than at Asilo de la Paz

(*back-test response*: $t = -1.98$, $P = 0.048$). Small tree finches ($t = -2.58$, $P = 0.040$) and medium tree finches ($t = -3.48$, $P = 0.003$) were both more exploratory at Cerro Pajas than at Asilo de la Paz.

All three behavioral traits (exploration, boldness, and aggressiveness) were correlated with each other, although this result was not consistent across all variables (see Supplementary Results, Table S6, Fig. S5). Specifically, exploration (*PC_Exploration*) was positively associated with one boldness variable (*processing response*: $N = 152$, $\rho = 0.18$, $P = 0.027$) and with one aggressiveness variable (*attacked mirror*: $N = 151$, $U = 689.5$, $P = 0.018$). The relationship between exploration and *time near mirror* was quadratic, with exploration highest among birds that spent an intermediate duration near the mirror ($F_{1,148} = 16.19$, $P < 0.001$).

Relationship between behavioral traits and territory defense in the wild

Among our five behavioral variables, only exploration (*PC_Exploration*) significantly predicted an individual's

Fig. 2 Exploration of a novel environment (*PC_Exploration*) in four Darwin's finch species: small ground finch (SGF, $N = 75$ birds), medium ground finch (MGF, $N = 10$), small tree finch (STF, $N = 46$) and medium tree finch (MTF, $N = 21$). Red markers show mean ± SE with raw data overlaid. Higher *PC_Exploration* values indicate that the bird visited more total and unique sectors during the novel environment test. Bars indicate statistically significant differences between species based on post hoc pairwise comparisons, with Holm-adjusted *P*-values
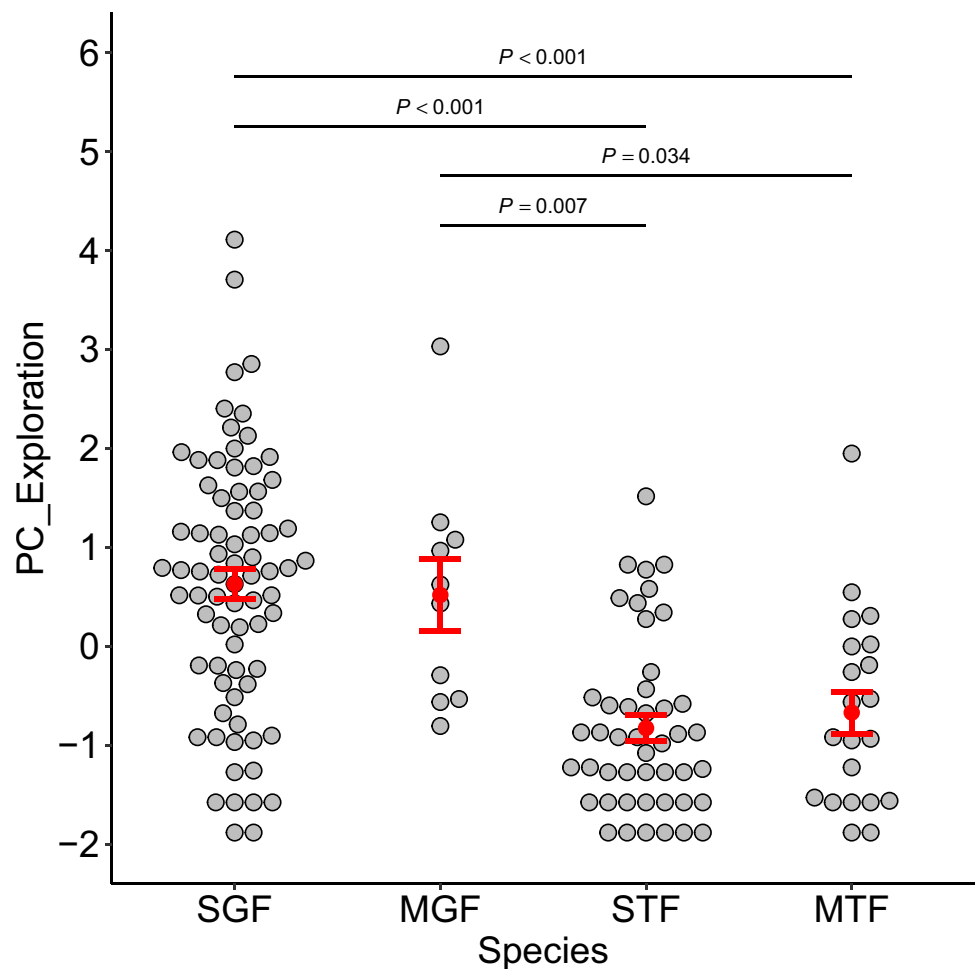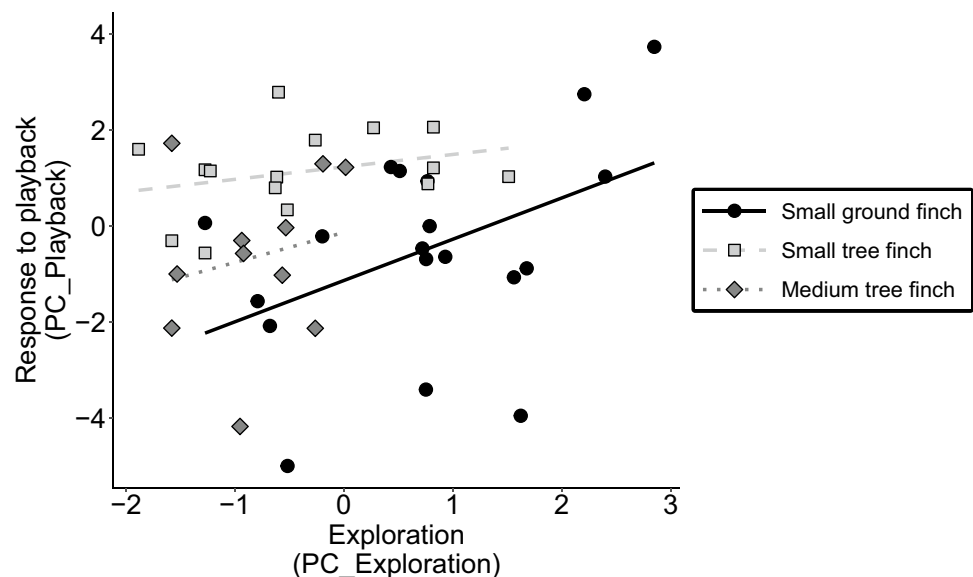
Table 3 Output from linear models testing the relationship between five behavioral variables (representing boldness, exploration, or aggressiveness) and territory defense behavior (*PC_Playback*)

Fixed effect	df	F	P
(a) *Boldness: Processing response*			
Species	2	7.85	**0.001**
Study site	2	3.46	**0.041**
Handler ID	1	0.88	0.354
Processing response	1	1.04	0.314
Residuals	41		
(b) *Boldness: Back-test response*			
Species	2	7.78	**0.001**
Study site	2	3.10	0.056
Handler ID	1	0.54	0.465
Back-test response	1	1.00	0.323
Residuals	41		
(c) *Exploration: PC_Exploration*			
Species	2	11.83	**< 0.001**
Study site	2	4.75	**0.014**
PC_Exploration	1	7.50	**0.009**
Residuals	39		
(d) *Aggressiveness: Time near mirror*			
Species	2	9.42	**< 0.001**
Study site	2	4.95	**0.012**
Time near mirror	1	3.18	0.082
Residuals	39		
(e) *Aggressiveness: Attacked mirror*			
Species	2	7.86	**0.001**
Study site	2	4.10	**0.024**
Attacked mirror	1	0.53	0.473
Residuals	39		

Higher *PC_Playback* scores indicate a more aggressive territory defense response. Statistically significant ($P < 0.05$) results are marked in bold

territory defense response (Table 3). Specifically, more exploratory birds had higher *PC_Playback* scores ($F_{1,39} = 7.50$, $P = 0.009$; Fig. 3), indicating that they were quicker to approach the intruder playback, approached more closely, spent more time within 5 m and within 1 m of the speaker, undertook more flights, and crossed over the speaker more often during the playback period.

Correlations between exploration and fitness

There were no significant interactions between species and exploration (Table S7). When non-significant interactions were removed from the models, species predicted hatching success but not pairing status or fledging success (Table S7). A male's exploration (*PC_Exploration*) did not significantly predict its pairing status ($\chi^2_1 = 3.36$, $P = 0.067$; Fig. 4a). Among paired males, more exploratory birds showed significantly lower hatching success ($\chi^2_1 = 4.70$, $P = 0.030$; Fig. 4b) but did not differ in their fledging success ($\chi^2_1 = 0.39$, $P = 0.532$; Fig. 4c).

Discussion

In this study, we measured three behavioral traits (boldness, exploration, and aggressiveness) in four Darwin's finch species on Floreana Island. At the species level, ground finches (*G. fuliginosa* and *G. fortis*) were bolder and more exploratory than tree finches (*C. parvulus* and *C. pauper*), consistent with our prediction that niche differentiation among sympatric species should result in behavioral differences. We also sought to validate the obtained behavioral measures at the individual level by correlating the behavior of wild-caught birds with their territory defense and breeding success in the
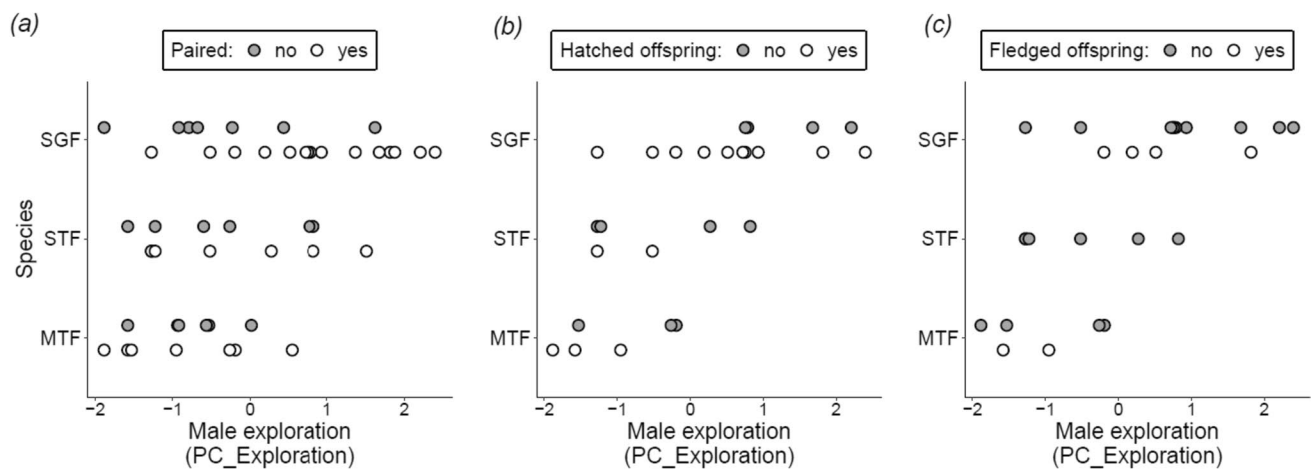
Fig. 3 Scatterplot showing the positive relationship between exploration of a novel environment (*PC_Exploration*) and aggressiveness in the wild (response to a simulated territory intrusion, *PC_Playback*) in small ground finches, small tree finches and medium tree finches on Floreana Island. Separate regression lines are shown for each species. Higher *PC_Exploration* scores indicate that the bird visited more total and unique sectors during the novel environment test, while higher *PC_Playback* scores indicate a stronger response to the territory intruder

Fig. 4 Dot plots showing the relationships between exploration (*PC_Exploration*) and three measures of breeding success, in three Darwin's finch species (SGF = small ground finch, STF = small tree finch, MTF = medium tree finch). (**a**) A male's exploration score did not predict its pairing status (GLM: $\chi^2_1 = 3.36$, $P = 0.067$); (**b**) more exploratory males had lower offspring hatching success (GLM: $\chi^2_1 = 4.70$, $P = 0.030$); and (**c**) a male's exploration score did not predict its likelihood of fledging offspring (GLM: $\chi^2_1 = 0.39$, $P = 0.532$). Higher exploration scores indicate that the bird visited more total and unique sectors during the novel environment test

wild. We found that exploratory males reacted more strongly to simulated territory intrusions in the field, supporting the ecological relevance of exploration when measured in wild-caught individuals. An individual's exploration score did not significantly predict its pairing status; however, among paired males, exploration was negatively associated with hatching success, suggesting a potential pathway by which behavioral traits might influence fitness.

Darwin's finch species differed in their exploration behavior, with ground finches visiting more sectors of the novel environment on average than tree finches. These species-level differences in behavior, alongside better documented differences in morphology (Grant 1986; Grant and Grant 2006), may be the result of niche differentiation, allowing closely related sympatric species to coexist with minimal overlap in their resource utilization (Tokeshi 1999). This result is also consistent with the predictions of the neophobia threshold hypothesis (Greenberg 1983, 1990), which proposes that species with more generalist diets—in this case, the Darwin's ground finches (Tebbich et al. 2009; De León et al. 2014)—should be less wary of novelty. A prior field study by Tebbich et al. (2009) also supported this hypothesis, reporting a positive species-level relationship between neophilia and diet diversity across nine Darwin's finch species. The mechanisms driving this relationship are unclear, but two broad explanations are possible: (1) more exploratory species like the ground finches are more likely to investigate new resources and integrate them into their foraging niche, or (2) diet-generalist species like the ground finches are more likely to encounter new resources and so become better accustomed to novelty. Because encountering more diverse foods does not necessarily imply more

diverse consumption, future studies should test the neophobia threshold hypothesis more explicitly by collecting cross-species data on food neophobia (aversion to novel foods) and dietary conservatism (aversion to incorporating novel food into one's regular diet) (Marples et al. 2007). Other factors that potentially explain behavioral variation among species include differences in metabolic rate and life history (Careau et al. 2009; von Merten and Siemers 2012), as predicted by the pace-of-life syndrome hypothesis (Réale et al. 2010).

During the novel environment test, ground finches were much more likely than tree finches to use the floor sectors of the flight cage, which would have contributed to their higher exploration scores. One interpretation of this result is that how finch species explore the novel environment reflects how they explore their natural environment—that is, the same neophobia that prevents tree finches from foraging on the forest floor (fewer than 10% of foraging attempts; Kleindorfer et al. 2022) may also suppress use of the cage floor. Of course, this is not the only possible explanation, and it would be useful to show that the differences in exploration in our study are not purely driven by tree finches' aversion to ground use. When we only consider the exploration variable 'total sector visits', which does not penalize subjects for avoiding the floor sectors, we find that ground finches are still more exploratory than tree finches in three out of four comparisons (Table S8, Fig. S6). In addition, preliminary data from four Floreana landbird species (small ground finch, small tree finch, medium tree finch, and yellow warbler, *Setophaga petechia aureola*) suggest that more exploratory birds in the novel environment test are also quicker to approach a novel object suspended in the field at a height of 2 m (JG-L et al., unpublished data). Taken together, these results suggest that interspecies differences in

exploration persist even in contexts where ground use is not a relevant factor.

Darwin's finch species also differed in their boldness, with ground finches struggling during more measurement procedures (i.e. showing a stronger *processing response*) than tree finches. Small and medium ground finches are largely ground-based foragers that regularly exploit anthropogenic food sources (De León et al. 2019; Kleindorfer et al. 2022). This may lead them to interact more often or more directly with humans, or with introduced ground-level predators such as cats and black rats, which could drive adaptive changes in their boldness. Living in proximity to human development has previously been associated with 'proactive' traits such as boldness, exploration, and aggressiveness, both in Darwin's finches (Gotanda 2020) and more generally in other bird and mammal species (Miranda et al. 2013; Tryjanowski et al. 2016; Holtmann et al. 2017; Thompson et al. 2018).

Tree finch behavior differed significantly between our two highland study sites, with birds at Cerro Pajas being more exploratory than those at Asilo de la Paz. Although only 2 km apart, these study sites diverge in several key environmental factors that could potentially drive differences in finch behavior. First, Asilo de la Paz experiences more human disturbance than Cerro Pajas, being a frequently visited tourist site and adjacent to Floreana Island's main agricultural zone (Ruiz-Ballesteros and Brondizio 2013). Second, during the breeding season, Cerro Pajas finches suffer more intense parasitic pressure by the invasive avian vampire fly: although the parasite is ubiquitous in highland nests, fledging success in the 2020 season was 32% at Asilo de la Paz (from 44 nests monitored) and 0% at Cerro Pajas (from 72 nests monitored), with most nestling mortality caused by parasitism (SK et al., unpublished data). Because we only measured behavior at three study sites during a single season, this result is merely suggestive. Understanding how environmental factors influence behavior at fine spatial scales would require more intensive sampling of finch behavior at a larger number of study sites. On nearby Santa Cruz Island, small ground finches also vary in their morphology and foraging strategy across a relatively small geographic area, which suggests that local environmental conditions can drive morphological and behavioral variation even within contiguous populations (Kleindorfer et al. 2006; Sulloway and Kleindorfer 2013).

Our three behavioral measures were correlated with each other, such that more exploratory birds were also bolder and more aggressive. These results are broadly suggestive of the proactive–reactive axis, a behavioral syndrome whereby 'proactive' individuals are characterized as bold, fast-exploring, and aggressive, while 'reactive' individuals are shy, slow-exploring, and non-aggressive (Koolhaas et al. 1999; Coppens et al. 2010). However, we cannot conclude that such a behavioral syndrome exists without repeated testing of individuals. Our wild birds were captured only for short periods (typically less than one hour) and released after a single suite of rapid-assessment assays. Without data on within-individual behavioral variation, we cannot statistically distinguish between phenotypic correlations that occur within and between individuals, respectively (Niemelä and Dingemanse 2018). This could lead to under- or overestimates of the correlation between average trait values: for example, between exploration and boldness (Niemelä and Dingemanse 2018). Another potential difficulty is the serial nature of our assay schedule, whereby aggressiveness was always measured immediately after exploration. To support the presence of a behavioral syndrome, these assays should ideally be conducted independently and in a randomized order to ensure that they do not influence each other's outcomes.

Although behavioral phenotypes have previously been linked with fitness (Moiron et al. 2020), it is seldom clear how these effects are mediated. In our study, more exploratory Darwin's finch males responded more aggressively to simulated territory intrusions in the wild. This finding connects differences in exploration behavior with territory defense, an ecologically relevant component trait that likely has fitness consequences. Several prior studies in great tits have shown similar relationships between behavioral type and territory defense, with fast-exploring birds responding more aggressively to conspecific playback by staying longer near the loudspeaker and singing longer songs (Amy et al. 2010; Snijders et al. 2015). However, a different pattern was found in superb fairy-wrens, whereby birds with more extreme exploration phenotypes (i.e. fast or slow explorers, rather than moderate explorers) defended their territories more aggressively (Colombelli-Négrel et al. 2022). These contrasting results suggest that relationships between behavioral traits and territory defense vary across species.

Only one of our three measures of breeding success was significantly predicted by the male's behavioral phenotype: more exploratory males, once paired, showed significantly lower hatching success. This could indicate that behavioral traits linked with high exploration scores, such as aggressive territory defense, come at the expense of other reproductively important behaviors. African penguins (*Spheniscus demersus*) provide similar support for such a trade-off, whereby parents that defend their nest vigorously also raise slower-growing chicks (Traisnel and Pichegru 2018). In this study, we did not attempt to identify any causal factors that connect exploration behavior with lower hatching success, although several explanations are possible: for example, exploratory males may be less vigilant of potential predation threats, choose riskier nest sites, or provide less food to the incubating female. Future work would benefit from an increased sample of observed nests, particularly from the underrepresented tree finches, to confirm this link between male behavior and offspring hatching success, and to disentangle any species-level differences. Measuring an additional suite of component traits

(e.g. foraging efficiency, nest provisioning) and composite traits (e.g. survival) would also help illuminate any pathways connecting exploration and fitness. It would be particularly interesting to examine differences in long-term partner fidelity based on behavior (e.g. Sun et al. 2022), since females may have incentive to divorce more exploratory partners if they consistently perform poorly during nesting. Male exploration score did not predict fledging success in our sample, perhaps because avian vampire fly parasitism was so extreme at some study sites (e.g. at Cerro Pajas) that offspring died regardless of their parents' behavior. This would obscure any relationship between exploration and fledging success that may otherwise exist in the parasites' absence.

In this study, we found clear behavioral differences between Darwin's finch species, with ground finches being bolder during human handling and more exploratory in a novel environment compared to tree finches. Differences in exploration between species were consistent with the predictions of the neophobia threshold hypothesis, given that ground finches have more generalist diets than tree finches and are, therefore, expected to be less neophobic. In three Darwin's finch species, males that were more exploratory in the novel environment also defended their territory more aggressively, supporting the ecological relevance of our behavioral assays. Among paired males, high exploration scores were also negatively associated with hatching success: this suggests that exploratory males who defend their territories more aggressively may do so at the expense of breeding success, although this trade-off is still to be confirmed. Future research should test the repeatability of these behavioral traits in individual Darwin's finches and investigate their influence on foraging behavior and fitness outcomes.

Data availability All datasets generated or analysed for this study are included in the article's supplementary material.

Declarations

Ethical approval All fieldwork and experimental procedures were conducted with approval from the Flinders University Animal Welfare Committee (E480-19) and the Galápagos National Park Directorate (Dirección del Parque Nacional Galápagos) (PC-02–20). All applicable international, national, and/or institutional guidelines for the use of animals were followed.

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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