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Zusammenfassung

Persönlichkeit wird als individuelle Verhaltensunterschiede definiert, die über die Zeit und über verschiedene Kontexte hinweg konsistent sind. Diese Konsistenz spiegelt die individuelle Variation wider, die wesentliche evolutive Prozesse wie Anpassung und Artbildung antreibt. Persönlichkeit kann daher evolutionäre Entwicklungen beeinflussen, indem sie auf Fitnesskomponenten wirkt, da die natürliche Selektion bestimmte Verhaltensphänotypen gegenüber anderen begünstigen kann. Folglich stellt Persönlichkeit nicht nur eine Ansammlung von Verhaltenstendenzen dar, sondern ein ökologisch relevantes Merkmal, das bestimmt, wie Individuen mit ihrer Umwelt interagieren und sich an diese anpassen.

Das Hauptziel dieser Dissertation war es, zu untersuchen, wie Persönlichkeit als treibender Faktor bei der adaptiven Radiation der Darwinfinken im Galápagos-Archipel wirken kann. Zu diesem Zweck wurden Verhaltensreaktionen entlang von drei der fünf Hauptachsen der Persönlichkeit – Aggressivität, Erkundungsverhalten und Mut (Boldness) – gemessen und deren ökologische Relevanz auf der Insel Floreana getestet. Jedes Merkmal wurde sowohl in kurzfristigen Haltungstests als auch in Freilandversuchen erfasst. Konkret wurde Aggressivität mittels eines Spiegeltests und einer simulierten innerartlichen Konfrontation (Playback) quantifiziert; das Erkundungsverhalten wurde durch einen neuartigen Arenatest und einen neuartigen Objekttest gemessen; und Mut wurde anhand

von Handhabungstests kurz nach dem Fang sowie einem Annäherungstest (Fluchtinitiationsdistanz, FID) bewertet.

Um die ökologische Validität dieser Merkmale weiter zu prüfen, wurden Zusammenhänge zwischen Reviergröße und sowohl Aggressivität als auch Erkundungsverhalten, zwischen Nahrungsverhalten und Erkundungsverhalten sowie zwischen dem Ausmaß menschlicher Aktivität und Mut untersucht. Alle drei Merkmale zeigten eine hohe Kontextkonsistenz mit signifikanten Korrelationen zwischen den in Gefangenschaft und im Freiland gemessenen Reaktionen. Bei der Untersuchung ökologischer Muster zeigte Kapitel 1, dass die Reviergröße bei beiden Arten negativ mit der Aggressivität korrelierte, wobei aggressivere Männchen kleinere Territorien besetzten. In Kapitel 2 wurde festgestellt, dass die artspezifische Nahrungsdiversität positiv mit dem Erkundungsverhalten korrelierte, was darauf hinweist, dass stärker erkundende Arten eine höhere Nahrungsdiversität aufwiesen. Kapitel 3 zeigte, dass sich der Mut zwischen Standorten mit unterschiedlichem Ausmaß menschlicher Aktivität signifikant unterschied: Vögel aus Gebieten mit höherer menschlicher Aktivität waren mutiger (kürzere FID).

Insgesamt zeigen diese Ergebnisse, dass Aggressivität, Erkundungsverhalten und Mut stabile Persönlichkeitsmerkmale bei Darwinfinken darstellen. Darüber hinaus verfeinern die Ergebnisse unser Verständnis der ökologischen Validität von Verhaltensphänotypen und unterstreichen ihre Rolle in evolutionären Prozessen als Triebkräfte adaptiver Radiation. Schließlich

betonen sie die Bedeutung der Integration verhaltensökologischer Ansätze in einen breiteren Rahmen, der Persönlichkeit mit Naturschutz verbindet, und liefern wertvolle Erkenntnisse für die Entwicklung effektiver Managementstrategien zur Erhaltung der Resilienz und des Anpassungspotenzials von Arten in sich wandelnden Umwelten.

Summary

Personality is defined as individual behavioral differences that are consistent over time and across contexts. This consistency reflects the individual variation that drives major evolutionary processes such as adaptation and speciation. Therefore, personality can influence evolutionary trajectories through its effects on fitness components, as natural selection may favor certain behavioral phenotypes over others. Consequently, personality is not merely a set of behavioral tendencies but an ecologically relevant trait that mediates how individuals interact with and adapt to their environments.

In this dissertation, the main goal was to investigate how personality can act as a driving factor in the adaptive radiation of Darwin's finches in the Galápagos Archipelago. To address this, I measured behavioral responses along three of the main five personality axes: aggressiveness, exploration, and boldness, and tested their ecological relevance on Floreana Island. Each trait was scored both during short-term captivity assays and during assays conducted in the wild. Specifically, aggressiveness was quantified using a mirror simulation test and a simulated conspecific intrusion (playback); exploration was measured through a novel arena test and a novel object test; and boldness was assessed using handling assays shortly after capture and a human approach assay (flight initiation distance, FID).

To further test the ecological validity of these traits, I examined associations between home range size and both aggressiveness and exploration, between

foraging behavior and exploration, and between levels of human activity and boldness. All three traits were consistent across contexts, showing significant correlations between responses measured in captivity and those obtained in the wild. When exploring ecological patterns, Chapter 1 revealed that home range size was negatively correlated with aggressiveness in both species, where more aggressive males occupied smaller territories. In Chapter 2, I found that species-level foraging diversity was positively correlated with exploration, indicating that more exploratory species had higher foraging diversity scores. In Chapter 3, boldness differed significantly between sites with contrasting levels of human activity, with birds from areas of higher human activity being bolder (shorter FID).

Together, these findings demonstrate that aggressiveness, exploration, and boldness represent personality traits in Darwin's finches, confirming their stability at the individual level. Moreover, the results refine our understanding of the ecological validity of behavioral phenotypes, emphasizing their role in evolutionary processes as drivers of adaptive radiation. Finally, they highlight the importance of integrating behavioral ecology into a broader framework that links personality to conservation, providing valuable insights for the development of effective management strategies aimed at sustaining species resilience and adaptive potential in changing environments.

General Introduction

Individual variation is a key driver of major evolutionary processes, such as adaptation and speciation (Bolnick et al., 2011; Wolf & Weissing, 2012). Although behavioral variation has long been recognized as an important component of ecological diversification (Dall et al., 2004; Sih et al., 2004; Réale et al., 2007), most studies of adaptive radiation have traditionally emphasized morphological and ecological traits—such as beak morphology, feeding specialization, or song divergence—while the role of personality as a driver of adaptive radiation has often been overlooked, receiving comparatively little attention (Gavrilets & Losos, 2009; Sommer-Trembo et al., 2024).

Animal personality refers to consistent among-individual differences in behavior, often conceptualized as an individual's response pattern to social or ecological conditions (Minderman et al., 2010; Stiegler et al., 2022; Stuber et al., 2022). These behavioral response norms must remain consistent across time and contexts to qualify as personality and are commonly assessed along five major axes: boldness, exploration, activity, aggressiveness, and sociability (Réale et al., 2007; Laskowski et al., 2022). A key component of personality research is the repeatability of behavioral traits, which quantifies the proportion of behavioral variance attributable to differences among individuals and provides the statistical basis for inferring consistent personality (Nakagawa & Schielzeth, 2010; Dingemanse & Dochtermann, 2013). Despite extensive laboratory and field studies, few have tested whether behavioral phenotypes measured under standardized captive conditions accurately reflect behavior

expressed in the wild (Herborn et al., 2010; McCowan et al., 2015). Captive-based assays—such as novel environment or open-field tests (Verbeek et al., 1994)—are valuable because they standardize testing conditions. Yet, responses may be confounded by factors unrelated to exploration, like recovery from handling stress or acclimation to captivity, among others (Niemelä & Dingemanse, 2014). Consequently, validating that individual differences are repeatable both within and across ecological contexts is essential for robust inferences about personality.

Natural selection may favor certain personality phenotypes over others (Dall et al., 2004; Réale et al., 2010), a process grounded in the demonstrated heritability of behavioral traits and their role in adaptive evolution (Sommer-Trembo et al., 2024). Personality can therefore influence evolutionary trajectories through its effects on individual fitness components such as reproductive success and survival (Dingemanse et al., 2004; Dingemanse & De Goede, 2004; Hall et al., 2015; Katsis et al., 2024). Moreover, selection of personality phenotypes may act indirectly through associations between behavioral types and ecological variables, including home range size (Wat et al., 2020; Naguib et al., 2022; Stuber et al., 2022; García-Loor et al., 2024), foraging behavior (Tebbich et al., 2009; Mettke-Hofmann et al., 2013; Herath et al., 2021; Gharnit et al., 2022; García-Loor et al., 2025), and responses to anthropogenic pressures such as urbanization (Blumstein, 2006; Atwell et al., 2012; Samia et al., 2015; Nepali et al., 2024). Collectively, these studies emphasize that personality is not merely a set of behavioral tendencies but an

ecologically relevant trait that mediates how individuals interact with and adapt to their environments.

Darwin's finches (subfamily Geospizinae) comprise 17 recognized species endemic to the Galápagos Islands and represent a classic model system for studying behavioral and evolutionary change, owing to the rapid adaptive radiation that has occurred over the past ~1.5 million years (Grant & Grant, 2002, 2014; Grant, 2017; Kleindorfer et al., 2022; Colombelli-Négrel et al., 2023). These species exhibit striking interspecific variation in beak size and shape, which underpins differences in foraging techniques and niche utilization (Lamichhaney et al., 2015, 2016; Kleindorfer et al., 2022). However, this diversity is increasingly threatened, with seven species listed as vulnerable and two as critically endangered (Freile et al., 2019). Despite the long-standing scientific interest in this group, research on their behavioral traits has only recently gained momentum. For example, emerging studies highlight the potential role of personality in shaping the adaptive radiation of Darwin's finches (García-Loor et al., 2024; Katsis et al., 2024; García-Loor et al., 2025). Exploration behavior has been linked to diet diversity, with more exploratory individuals exhibiting broader diets (Tebbich et al. 2009), a pattern consistent with recent findings that dietary generalists (Darwin's ground finches) are more exploratory in novel-environment tests than dietary specialists (Darwin's tree finches) (Katsis et al., 2024). Boldness during human handling also varies among species and study sites, and flight initiation distance (FID) is shorter in populations inhabiting islands without invasive predators or in urban areas

compared to those on predator-invaded or rural islands (Gotanda, 2020). Most recently, population-level FID distributions on Floreana Island shifted following the eradication of rodents and control of feral cats: in the absence of predators, finches increased the frequency of extreme FID responses (Common et al., in review). However, we still lack a cross-context validation for behavioral traits and a deeper understanding of personality in Darwin's finches.

In this dissertation, I investigate how personality can act as a driving factor in the adaptive radiation of Darwin's finches in the Galápagos Archipelago. Specifically, I focus on validating three of the five commonly recognized personality axes—aggressiveness, exploration, and boldness—across time and contexts, by comparing behavioral responses in short-term captivity assays and field assays. I also examine how these traits may be shaped by ecological conditions, testing for associations with environmental and species-level variables. For the short-term captivity assays, I used handling tests (back test and processing test) and a rapid-assessment cage, in which I conducted a novel environment test and a mirror stimulation test. For the field assays, I measured responses in a novel object test, a simulated conspecific intrusion (playback broadcast), and flight initiation distance (hereafter FID). In chapter 1, I test for cross-context validation of exploration (novel arena vs. novel object tests) and aggressiveness (mirror stimulation vs. conspecific intrusion tests) in two species: the critically endangered, range-restricted medium tree finch (*Camarhynchus pauper*) and the widespread small ground finch (*Geospiza fuliginosa*). I also examine whether aggressiveness and exploration predict

home range size, with the prediction that fast-exploring individuals would have larger home ranges, while more aggressive individuals would have smaller ones. In Chapter 2, I assess the consistency of exploration across contexts in six songbird species, including four Darwin's finch species (small ground finch, *G. fuliginosa*; medium ground finch, *G. fortis*; small tree finch, *C. parvulus*; medium tree finch, *C. pauper*; Galápagos flycatcher, *Myiarchus magnirostris*; and yellow warbler, *Setophaga petechia aureola*), by comparing responses in a novel environment test and a novel object test. Here, I predict a positive correlation between individuals' scores in the two assays. In relation to the neophobia threshold hypothesis, I further test whether species-level diversity in foraging techniques and substrates is associated with exploratory behavior, predicting that more exploratory species will exhibit greater foraging diversity. Finally, Chapter 3 evaluates the consistency of boldness across time and contexts in five finch species (small ground finch, *G. fuliginosa*; medium ground finch, *G. fortis*; cactus finch, *G.* scandens; small tree finch, *C. parvulus*; and medium tree finch, *C. pauper*; by comparing individuals' struggle responses during two handling assays with their FID scores in the field. I predict positive associations among these three measures, such that birds with stronger struggle responses will show shorter FIDs. In this chapter, I also test whether human activity influences boldness phenotypes, predicting the presence of bolder individuals at sites with greater human presence.

The overarching aim of these three chapters is to evaluate whether ecological variables are associated with patterns of individual behavioral differences

(personality) in Darwin's finches. Chapter 1 explores how aggressiveness and exploration relate to movement patterns and home range size; Chapter 2 examines the repeatability of exploration and its association with foraging behavior; and Chapter 3 validates boldness across time and contexts, as well as assesses its ecological relevance within the framework of urbanization and predator removal. Together, these studies provide an integrated perspective on how personality traits may shape adaptive variation and inform the conservation management of island songbirds.

Chapter 1

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Aggressive behavior as a predictor of home range size: findings from both range-restricted and widespread Darwin's finch species

Jefferson García-Loor, Mario Gallego-Abenza, Andrew C. Katsis, Verena Puehringer-Sturmayr, Diane Colombelli-Négrel, Çağlar Akçay & Sonia Kleindorfer

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Abstract

Information about an animal's home range (the geographical area in which it accesses resources for survival and reproduction) is vital broadly for understanding animal behavior and specifically for developing conservation management plans. Although personality traits—consistent individual differences in behavior across time and contexts—may affect an animal's home range size, we still lack a breadth of empirical studies across systems to fully appreciate this influence. Here, we tested the relationship between behavioral responses and home range size in two Darwin's finch species on Floreana Island: the critically endangered and range-restricted medium tree finch (*Camarhynchus pauper*) and the common and widespread small ground finch (*Geospiza fuliginosa*). Using a combination of rapid-assessment assays during both short-term captivity and in the field, we measured exploration and aggressiveness in males from both species. We then used radio telemetry to measure each bird's home range size over a week-long period. We predicted that 1) fast-exploring individuals would have larger home ranges, and 2) more aggressive individuals would have smaller home ranges. We found that medium tree finches had smaller home ranges than small ground finches, that exploratory behavior was positively correlated with home range size only in small ground finches, and that, in both species, individuals' aggressiveness was negatively correlated with home range size, whereby the more aggressive individuals occupied smaller home ranges. We conclude that behavioral responses that align with major personality traits can predict home range size, which may provide an important tool for the conservation and management of endangered species when, for example, selecting individuals with different personality profiles for reintroduction.

Keywords

Behavioral traits, telemetry, Darwin's finches, aggressiveness, home range.

Introduction

Understanding animal movement patterns is important when designing conservation strategies (Schofield et al. 2013; Bauer et al. 2015; Buechley et al. 2018). Both space use and occurrence patterns can vary across individual life stages and contexts, including, for example, during dispersal, migration, or reproduction (Cooper and Marra 2020; Pierce et al. 2021; Heath-Acre et al. 2022). The geographical area used by an individual, including the area in which it finds essential resources for survival and reproduction, is called its home range (Jahn et al. 2010; Abu Baker et al. 2017; Péron 2019). Home range size is not necessarily equivalent to territory size, which is the subset of an animal's home range that is actively defended against conspecifics (Odum and Kuenzler 1955; Anich et al. 2009; Burgos and Zuberogoitia 2020; Colombelli-Négrel et al. 2023). The factors influencing individual home range or territory size are multi-faceted, and may include age (Liu et al. 2020b), sex (Rivers et al. 2014; Alonso et al. 2020), pairing status (Mwangi et al. 2020; Sur et al. 2020) and breeding stage (Olsen et al. 2011; Liu et al. 2020a), habitat features (Hinam and Clair, 2008; Arbeiter and Tegetmeyer, 2011), resource availability (Karubian and Carrasco 2008; Kane et al. 2016; Rechetelo et al. 2016; Mwangi et al. 2020), and seasonal conditions (Jahn et al. 2010; van Overveld et al. 2020). Nevertheless, understanding how individual differences in behavior can influence home range size is vital for managing species' potential for occurrence and persistence.

Consistent individual behavioral differences (hereafter “personality”) describe an individual’s response norm to social and ecological conditions, and are often associated with home range size and habitat use (Minderman et al. 2010; Stiegler et al. 2022; Stuber et al. 2022). The response norms that constitute personality must be consistent across time and contexts, and are often measured across five main axes: boldness, exploration, activity, aggressiveness, and sociability (Réale et al. 2007; Laskowski et al. 2022). Selection may favor some personality phenotypes over others (Dall et al. 2004; Réale et al. 2010), which may be associated with home range size (Stuber et al. 2022). To date, the precise mechanisms linking personality with home range size are poorly understood and may depend on the life history of the animal. For example, more exploratory individuals with a higher tolerance for novelty may travel more widely, or across a wider range of habitats, in search of food and other resources. Only a few studies have explicitly tried to link personality traits with variation in home range size. In great tits (*Parus major*), less aggressive males had larger home ranges (Naguib et al. 2022), suggesting that having a large home range may trade off with investment into active territory defense. By contrast, in common brushtail possums (*Trichosurus vulpecula*), the correlation between exploration and home range size was positive in males but negative in females (Wat et al. 2020). Hence, although personality may influence home range size, the traits mediating this relationship may differ across species.

Home range size estimates can be used to develop action plans to protect endangered species (Sawyer, 2012; Morato et al. 2016; Plotz et al. 2016; Garcia-Heras et al. 2019). In many cases, target species can be elusive and difficult to track because they have low population density (Carrascal and Seoane 2009; Cosendey et al. 2016), occur over large areas (Fivaz and Gonseth 2014; Kearney et al. 2022), show migratory behavior (Hays et al. 2014; Arroyo et al. 2016), are poached (Tarjuelo et al. 2015; Borgerson 2015), or have experienced extreme habitat modification (McGowan et al. 2017; Mukul et al. 2019; Yan et al. 2021). Understanding the home range attributes of threatened species can help understand species presence and abundance and give insight into population connectivity and minimum resource requirements (Puehringer-Sturmayr et al. 2023), which is especially important in fragmented habitats. Applying principles of personality research to endangered species also has promising conservation outcomes, given the apparent association between personality and traits such as home range size and pairing success (Snekser et al. 2017; Seltmann et al. 2018). Hence, we need species-specific investigations to illuminate the relationships between personality, home range size, and parameters of biological fitness. This broader understanding of species' needs will assist the design and implementation of conservation management plans (Haage et al. 2017). Specifically, understanding how personality phenotypes mediate reintroduction success could be a useful tool when selecting individuals for reintroduction schemes (Gotanda 2020).

The Darwin's finches (subfamily *Geospizinae*) comprise 17 recognized species on the Galapagos Islands and are regarded as the fastest adaptive radiation of any terrestrial vertebrate (Grant and Grant 2002, 2014; Kleindorfer et al. 2022; Colombelli-Négrel et al. 2023). However, this diversity is currently threatened, with seven species categorized as vulnerable and two as critically endangered (Freile et al. 2019). Despite significant conservation interest in this unique and historically important study system, surprisingly few studies have investigated home range size in Darwin's finches. One recent study mapped the home ranges of five VHF-tagged medium ground finches (*Geospiza fortis*), a common species on Santa Cruz Island (Beausoleil et al. 2022). Across Darwin's finch species, exploration behavior has previously been linked with diet diversity, whereby more exploratory finch species (those that showed stronger interest in a novel object) also had a more diverse diet (Tebbich et al. 2009). Therefore, we expect more exploratory finches to have larger home ranges, as they can exploit resources from a wider range of habitat across the landscape.

In this study, we investigated the association between behavioral traits and home range size in two species of Darwin's finch: the critically endangered medium tree finch (*Camarhynchus pauper*), an island-endemic species that is range-restricted to a small area (24 km^2) of *Scalesia* forest in the highlands of Floreana Island (Dvorak et al. 2017; Peters and Kleindorfer 2018), and the small ground finch (*Geospiza fuliginosa*), a common and widespread species that occurs on most islands in the archipelago (Kleindorfer et al. 2019). We used a combination of rapid-assessment cage assays (novel environment test, mirror

stimulation test) and field assays (novel object test, response to broadcast of conspecific song) commonly used to measure both exploratory and aggressive behaviors in wild individuals (Réale et al. 2007; Bilby et al. 2022; Colombelli-Négrel et al. 2022; Katsis et al. 2023). We then tested for associations between the birds' behavioral phenotype and home range size, quantified using radio telemetry. Our first prediction was that fast-exploring Darwin's finches would have larger home ranges, aligned with what was found previously in male common brushtail possums (Wat et al. 2020). Our second prediction was that more aggressive Darwin's finches would have smaller home ranges, consistent with previous results in great tits and meadow voles (Spritzer et al. 2005; Naguib et al. 2022).

Methods

Study site and species

This study was conducted on Floreana Island in the Galapagos Archipelago in 2020 (Jan–Feb) and 2022 (Feb) during the onset of the heavy rains that usually trigger nesting activity in Darwin's finches. Both study sites, Cerro Pajas (-1.293479, -90.452012) and Asilo de la Paz (-1.314003, -90.455512), are located in the forest and woodland highlands at ~340 m above sea level (Fig. 1). The habitat is dominated by *Scalesia pedunculata* (family Asteraceae) and other tree species commonly used by Darwin's tree finches for foraging and nesting (Kleindorfer et al. 2022). Rainfall levels differed substantially between the two field seasons, with mean daily rainfall of 70 mm (range 0–105 mm) during

January and February 2020 and 1.5 mm (range 0–4 mm) during January and February 2022 (Galápagos Conservancy, https://www.galapagosvitalsigns.org, accessed 10 September 2022). We studied two Darwin's finch species: the medium tree finch (MTF) and small ground finch (SGF). The medium tree finch is endemic to the highlands of Floreana Island and is categorized as critically endangered by the International Union for Conservation of Nature (Freile et al. 2019), while the small ground finch occurs on almost all islands in the Galápagos Archipelago. Darwin's finch populations are currently threatened by native predators such as short-eared owls (*Asio flammeus galapagoensis*), introduced predators such as feral cats (*Felis catus*), and the introduced parasitic avian vampire fly (*Philornis downsi*) (Kleindorfer et al. 2021). In our study, sample sizes for Darwin's finch behavioral phenotype and home range size differed. This is because we conducted behavioral trials both at the time of capture and afterwards in the field (with different sample sizes for different assays, as described below), with only a subset of individuals selected for VHF tagging due to the limited number of tags available. (Table S1).

Mist-netting and radio-tagging

We used mist-nets to capture Darwin's finches at both study sites, following protocols used to observe Darwin's finches on Floreana Island since 2004 (Langton and Kleindorfer 2019). At the time of banding, each bird received a numbered aluminum band and a unique combination of between one and three color-bands. Shortly after capture, we measured subjects' exploration using a novel environment test and their aggressiveness using a mirror-stimulation test

(see below). We mist-netted 237 individuals from our two study species and used the first 20 MTF and first 15 SGF males for radio-tagging (in 2020: 10 MTF and 10 SGF; in 2022: 10 MTF and 5 SGF); we selected the first birds to maximize the number of field days for radiotelemetry observation. After measuring each bird's behavioral phenotype (see below), subjects were fitted with VHF radio tags (Lotek PicoPip Ag337) that send a radio signal to a receiver (Lotek Biotracker VHF 138 – 168 MHz) captured by an antenna (Lotek Yagi LiteFlex). The signal had a pulse length of 12 ms, and a pulse ratio of 30 ppm. The weight of the radio tags was 0.3 g, equivalent to 1.8% of the mean MTF body mass (~17 g) and 2.1% of the mean SGF body mass (~14.4 g). The radio tags were fitted to the birds' upper back following established protocols (Diemer et al. 2014), and subjects were released at their site of capture, typically within one hour after mist-netting?. .

Telemetry and home range size (HRS)

We located each tagged Darwin's finch during a period of 3–7 non-consecutive days (mean ± SE = 4.0 ± 0.2 days) until we obtained at least 20 fixes per bird, aiming that each GPS point was separated by a minimum of 30 min (some of them shorter) (Streby et al. 2015). We reached this threshold for 26 individuals (74% of tracked males) within four non-consecutive days of tracking. One additional bird fell short of this threshold (13 fixes) due to the loss of his transmitter. We retained this individual in our analysis, given that our results did not change when he was excluded. Radio telemetry tracking (hereafter 'tracking') was conducted in the morning between 06:00 and 12:00 GALT. In

total, we obtained 822 fixes from 35 males (20 during the 2020 season, 15 during the 2022 season; Fig. S1), with a mean ± SE of 23.5 ± 0.5 fixes per bird (range 13–27) and 5.5 ± 0.3 fixes per individual per day (range 1–12). We collected 464 fixes from 20 MTF (10 from 2020, 10 from 2022), with 23.2 ± 0.7 fixes (range 13–26) per individual and 358 fixes from 15 SGF (10 from 2020, 5 from 2022) with a mean of 23.9 ± 0.5 SE fixes per individual (range 13–27). The mean ± SE interval between fixes collected within the same day was 43.8 ± 0.9 min (range 22–314 min). We use the hrBootstrap function from the package '*adehabitatHR*' to estimate the number of fixes needed, where we observed how the trend starts to flattened after 13–14 fixes, which suggests that enough fixes were taken for the individuals (Fig. S7).

Novel environment test (exploration)

Exploration was measured during short-term captivity using a novel environment test (N = 44 MTF, 59 SGF; see Table S2 for summary based on species, pairing status, and year). After capture and processing, subjects were placed individually into a plastic release box (19 × 14 × 10 cm) for a standardized acclimation period (Bilby et al. 2022; Katsis et al. 2024). All finches tested in a given year experienced the same acclimation period: 5 min in 2020 and 1 min in 2022 (shortened to reduce waiting times for captured birds). This difference in acclimation period did not influence individuals' behavioral response, either in the novel environment test (t-test for *unique sector visits*: N = 101, t = 1,7, df = 65.2, P = 0.097) nor the mirror stimulation test (t-test for *mirror attacks;* N = 101, t = -0,9, df = 35.1, P = 0.387). After the door to the release box was raised,

the bird was allowed to enter the novel environment: a metal flight cage (75 × 44 × 42 cm) with three perches (one at height 6 cm and the other two at height 20 cm) (Fig. S2). The novel environment contained 13 discrete sectors that the subject could visit (three perches, four floor quadrats, four cage walls, the cage ceiling, and the release box). The novel environment test lasted 5 min, during which we recorded*: a)* the number of *unique sector visits,* and b*)* the number of *total sector visits* (including repeat visits). Although the repeatability of exploration has not been tested in Darwin's finches, the trait is known to be individually consistent across several songbird species, including great tits (*Parus major*; Thys et al. 2017), Australian zebra finches (*Taeniopygia castanotis*; McCowan et al. 2015), starlings (*Sturnus vulgaris*; Thys et al. 2017), and superb fairy-wrens (*Malurus cyaneus*; Hall et al., 2015). The novel environment test in our study was identical to that previously used by Katsis et al. (2023), who found that exploration was significantly repeatable in adult superb fairy-wrens. In a recent study, we demonstrated that exploration behavior differs between Darwin's finch species and predicts such factors as territory defense and offspring hatching success, supporting the ecological relevance of this trait (Katsis et al., 2024).

Mirror simulation test (aggressiveness)

We measured aggressiveness during short-term captivity using a mirror stimulation test. Immediately after the novel environment test, we remotely raised a curtain to reveal a mirror at one end of the flight cage (Bilby et al. 2022; Katsis et al. 2024) (Fig. S2). We expected male Darwin's finches to respond

aggressively to their mirror image, as they are highly territorial during the breeding season and will defend against conspecific intruders (Ratcliffe and Grant, 1983). Over a 3-min period, we then recorded a*) time near mirror*, the duration (in secs) spent within the three nearest sectors to the mirror, excluding time spent attacking the mirror; and b) number of *mirror attacks*, the number of times the subjects made physical contact with the mirror. In songbirds, proximity to and physical contact with the mirror is generally interpreted as an aggressive response (Leitão et al., 2019; Jones et al., 2022) and this response has been shown to be significantly repeatable in superb fairy-wrens (Katsis et al., 2023). The novel environment and mirror stimulation tests were recorded with a GoPro camera placed 50 cm outside the flight cage and behavior was scored using the software Solomon Coder v. beta 19.08.02 (András Peter, https://solomon.andraspeter.com).

Novel object test (exploration)

We measured exploration in the field as the neophilic response to a novel object placed in their habitat, adapting protocols previously used by Tebbich et al. (2009). First, we placed one of three different novel objects (30 × 50 cm double metal grid, 20 × 50 cm yellow bag, or 20 × 50 cm orange bag) in the field at height 2 m in natural vegetation. We placed small stones and branches to demarcate a 10-m radius around the novel object. Birds were alerted to the start of the trial using a bird whistle (Audubon, model number MT-PN-28905150) blown from a position 15 m from the novel object. The trial lasted 15 min and we scored birds' response to the novel object as the latency (in min) to approach

within 10 m of the novel object. To aid interpretation of this variable, we then inverted the latency score by subtracting each latency from the maximum possible value (15 min), so that higher scores indicated a higher level of exploration: that is, birds approaching in min 1 received a score of 15–1 = 14 (high exploration) and birds approaching in minute 14 received a score of 15–14 = 1 (low exploration). Of the 35 MTF and 100 SGF that approached the novel object in the wild during the field season in 2022 (García-Loor et al., unpublished data), 15 were color-banded and had previously been assayed using the novel environment test (8 MTF, 7 SGF) either in 2020 or 2022, allowing us to validate our measures of exploration across contexts.

Simulated conspecific intrusions (aggressiveness)

We measured aggressiveness in the field using simulated conspecific intrusions (song playback) in males' territories (15 MTF, 20 SGF). We targeted color-banded birds whose behavior we had previously measured in the novel environment and mirror stimulation tests. We prepared song playback tracks using conspecific songs recorded in 2020 with a good signal-to-noise ratio (Colombelli-Négrel et al. 2023). We used 9 unique playback tracks for the 15 MTF trials and 18 unique playback tracks for the 20 SGF trials. Each track had a duration of 3 min, comprising 1 min of playback followed by 1 min of silence and 1 min of playback. Each minute of playback contained six songs spaced at 10-sec intervals. We conducted all playback trials between 06:00 and 11:00 GALT, corresponding with the peak of song activity. After observing the male singing within 10 m from his nest, we placed the speaker (Sony XB12 Extra Bass

Portable Bluetooth Speaker, Sony Australia Limited or Soundcore Icon Mini Bluetooth Speaker, Anker Technology Ltd., United Kingdom; frequency response 20 Hz–20 kHz) and iPod on the ground 5 m from the nest and broadcast a randomly chosen playback track of a conspecific song (played at ~80 dB at 1 m; measured with a VLIKE VL6708 sound-level meter). One observer located ~10 m from the speaker narrated the trial into a directional microphone connected to a digital audio recorder. During the 3-min playback trial, we recorded the following behaviors: a) *time within 1 m*, the duration (in secs) spent within 1 m of the speaker; b) *minimum distance*, the minimum distance (in m) between the focal bird and the speaker; c) *flights*, the number of flights within 20 m of the speaker, and d) *crosses*, the number of flights over the speaker (Colombelli-Négrel et al. 2023).

Nest monitoring and pairing status

Although we started tracking only unpaired males, some subjects paired up during the observation period; therefore, we controlled for pairing status in our analysis and expected to find the same patterns of association between home range size and behavioral traits irrespective of pairing status. Nests were monitored following standardized protocols that were developed in 2004 on Floreana Island and maintained in the years since (Kleindorfer et al. 2021) (Kleindorfer 2007, O'Connor et al. 2010, Kleindorfer et al. 2014) (Kleindorfer 2007, O'Connor et al. 2010, Kleindorfer et al. 2014) (Kleindorfer 2007, O'Connor et al. 2010, Kleindorfer et al. 2014) (Kleindorfer 2007, O'Connor et al. 2010, Kleindorfer et al. 2014). The study areas were divided into 12 study

plots (each 200 × 100 m) that were systematically searched for singing males, nest building, and nest occupation. In addition, the pairing status of VHF-tagged males was confirmed by repeated observations at the nest during radiotracking, with males subsequently classed as paired (female seen lining the nest or incubating eggs) or unpaired (male sang without an observed female) (Kleindorfer et al. 2021). In total, we measured home range size for 35 males that were unpaired at the time of banding, of which 23 remained unpaired (15 MTF, 8 SGF) and 12 became paired (5 MTF, 7 SGF) within seven days (i.e., the duration of the radio tracking). In Darwin's finches, males build a display nest and sing at the nest to attract a female, but about 50% of singing males at a display nest can remain unpaired when monitored across one month (Kleindorfer et al. 2021).

Statistical analysis:

We performed statistical analyses using the software R version 4.1.1 (R Core Team 2022). To calculate male home range size (HRS), we used the package 'ctmm' version 1.2.0 to obtain the kernel density estimates at 95% range, considering the model type of the independent identically distributed (IID) process (Calabrese et al. 2016; Fieberg 2007; Signer et al. 2019). Principal component analysis (PCA) was executed using the function 'princomp' (R package 'stats' version 3.6.2). All the Spearman's correlation tests (as variables were not normally distributed) were executed using the function 'cor.test' ('stats' version 3.6.2). Linear models and generalized binary logistic regression were performed using the function 'lm' and 'glm' ('stats' version 3.6.2). We

based our model selection on AIC values, keeping the model with the lower value, when ΔAIC was > 2 points (Burnham and Anderson 2002); therefore, we include interactions in some models but not others. We checked for influential observations by calculating Cook's distance using the function 'cooks.distance' ('stats' version 3.6.2); we didn't find any highly influential observations, with all Cook's distance scores < 0.2. We determined variance inflation factor (VIF) using the function 'vif' from the R package 'car' (version 3.0-13; Fox and Weisberg, 2011), confirming that there were no collinearity issues in the model (highest VIF = 1.19).

a) Creation of PC_Aggressiveness variable

During the simulated territory intrusions, we measured four male response variables: time within 1 m, minimum distance, flights, and crosses. We used principal component analysis to reduce these four variables to one uncorrelated principal component (PC_Aggressiveness) with an eigenvalue of 3.08 and explaining 77% of total variance. Higher PC_Aggressiveness values indicated a more aggressive response to conspecific playback. To normalize the residuals in our linear model, all four variables were square-root-transformed prior to running the principal component analysis. Factor loadings for the four response variables were: *time at 1 m* (0.47), *minimum distance* (-0.52), *flights* (0.52), and *crosses* (0.49).

b) Validation of behavioral traits

For each behavior (exploration and aggressiveness), we compared two behavioral responses, both within and between assays, using Spearman's correlation tests (as variables were not normally distributed). For exploration, we tested the consistency of behavioral variables (1) within the novel environment test, comparing the number of *unique sector visits* vs *total sector visits*); and (2) across contexts, by comparing exploration in the novel environment (*unique sector visits*) with exploration towards a novel object in the field (*latency to approach to 10 m)*. For aggressiveness, we tested the consistency of behavioral variables (1) within the mirror simulation test, by comparing *time near mirror* between birds that did and did not contact the mirror (paired *t*-test and generalized binary logistic regression); and (2) across contexts, by comparing aggressiveness score from the mirror stimulation test (*time near mirror*) against the derived aggression scores obtained during the simulated conspecific intrusions (PC_Aggressiveness).

c) Behavioral traits and home range size (HRS)

We estimated the association between behavioral traits and HRS in both finch species, using both exploration (N = 34 individuals; 19 MTF, 15 SGF) and aggressiveness (N = 33 individuals; 19 MTF, 14 SGF). We log-transformed HRS values prior to analysis to normalize the model residuals. Since we predicted that more exploratory and less aggressive individuals would occupy larger home ranges, we included both behavioral scores and species in the main model [*lm(log10(HRS) ~ Exploration (unique sector visits) + Aggressiveness (time near mirror) + Species*]. In an alternative model, we also controlled for the

males' pairing status [*lm(log10(HRS) ~ Exploration (unique sector visits) + Aggressiveness (time near mirror) + Species + Status*].

Results

Mean ± SE home range size (level 95%) was 1.8 ± 0.4 ha (range 0.2–7.0) in MTF and 2.3 ± 0.6 ha (range 0.1–8.9) in SGF, with no difference between species (N = 35, t = -0.7, df = 23.4, P = 0.52). When considering both species together, paired males occupied smaller home ranges than unpaired males (paired t-test; N = 35, t = -3.1, df = 26.3, P = 0.004). Analyzing each species separately, paired and unpaired MTF males did not differ in the size of their home ranges (N = 20, t = -1.5, df = 17.8, P = 0.10), while unpaired SGF males had five times larger home ranges than paired males (N = 15, t = -2.7, df = 7.6, P = 0.03).

a) Validation of behavioral traits

Exploration variables within the novel environment test (*unique sector visits* and *total sector visits*) were strongly positively correlated in MTF (N = 44, r = 0.8, P < 0.001), in SGF (N = 59, r = 0.7, P < 0.001), and overall in both species (N = 103, r = 0.8, P < 0.001) (Fig. S3). Therefore, in future analyses we used unique sector visits as a proxy for exploration in the novel environment test. Across contexts, exploration of the novel environment (*unique sector visits*) and towards the novel object (*latency to approach to 10 m*) were significantly positively correlated when pooling data for both species (N = 15, r = 0.6, P =

0.032), but not when considering MTF (N = 8, r = 0.6, *P* = 0.106) or SGF (N = 7, r = 0.5, *P* = 0.263) separately (Fig. 2a).

For the aggressiveness variables measured in the mirror stimulation test, males from both species that attacked the mirror also spent more time near the mirror (N = 10, mean: 84.5 ± 15.1 SE; range 3–139.5) compared to males that did not attack the mirror (N = 55, mean: 44.8 ± 5.09 SE; range 0.4–132.5) (N = 65, *t* = 2.6, *df* = 11.1, *P* = 0.026). This pattern was also significant in the binary logistic regression model (*z = 3.707*, *P < 0.001*) (Fig. S4). Across contexts, aggressiveness towards the mirror (*time near mirror*) and towards conspecific playback (PC_Aggressiveness) were significantly positively correlated when pooling both species (N = 35, r = 0.4, *P* = 0.031), but not when considering MTF (N = 15, r = 0.5, *P* = 0.091) or SGF (N = 20, r = 0.3, *P* = 0.212) separately (Fig. 2b).

b) Behavioral traits and home range size (HRS)

In MTF, there was no significant association between HRS and exploration (*unique sector visits*, N = 19, r = 0.2, *P* = 0.486; *total sector visits,* N = 19, r = -0.1, *P* = 0.613). However, in SGF males, more exploratory birds in the novel environment had significantly smaller home ranges when considering *unique sector visits* as a measure of exploration (N = 15, r = -0.6, *P* = 0.033) (Fig. 3); but not when considering *total sectors visits* (N = 15, r = -0.43, *P* = 0.109).

Aggressiveness (*time near mirror*) was negatively associated with HRS in both species overall (N = 33, r = -0.5, P = 0.001), as well as in MTF (N = 19, r = -0.5, P = 0.017) and SGF (N = 14, r = -0.5, P = 0.050) separately. That is, males that spent longer near the mirror had smaller home ranges (Fig. 4). Our linear model showed that aggressiveness (*time near mirror*) was a significant predictor of HRS (t = -3.340, $P < 0.01$, $R^2_{adj} = 0.20$) over exploration (unique sector visits) or species (Table 2). In a separate set of models, pairing status did not significantly predict HRS and the negative relationship between aggressiveness (*time near mirror*) and HRS remained significant when pairing status was included in the model (t = -2.858, $P < 0.01$, $R^2_{adj} = 0.24$) (Table S3). We also found a near-significant negative trend between aggressiveness in the wild (*simulated conspecific intrusions*) and HRS when analyzing both species together (N = 20, r = -0.4, P = 0.098) (Fig. S6).

Discussion

In small ground finches and medium tree finches on Floreana Island, our measures of aggressiveness and exploration were consistent both within and across assay types, supporting the consistency of between-individual behavioral differences. Those differences, in turn, predicted individuals' home range size. Firstly, in both species, more aggressive males occupied smaller home ranges. Secondly, the association between exploration behavior and home range size differed between species: in medium tree finches, exploration did not predict home range size, while in small ground finches more exploratory males had

smaller home ranges. These different patterns may be related to differences in selection pressures for both species, since medium tree finches are a habitat-restricted specialist while small ground finches are a widespread generalist that occurs in most habitat types on the Galapagos Archipelago (Kleindorfer et al. 2022).

Home range size

To date, only one published study has used radiotelemetry to assess home range size in a Galapagos landbird. Beausoleil *et al.* (2022) used telemetry to estimate the home range of five medium ground finch (*G. fortis*) individuals (two males, three females) during the breeding season in a single year (2019). This study was undertaken in the lowlands of Santa Cruz Island at *El Garrapatero* beach (dry habitat) and reported home ranges that were about 10 times larger than those for small ground finches in the Floreana highlands. Clearly, many factors differed across the two studies, including study species, year, island, and habitat type. On Floreana Island, small ground finch home ranges are four times larger in the dry lowlands than in the humid highlands (García-Loor et al., unpublished data), suggesting that habitat and resource availability helps to shape individuals' movement patterns. In their medium ground finch study, Beausoleil *et al.* (2022) did not consider individual behavioral traits, which could perhaps have explained additional variation in subjects' home range size. The marked difference in home range size across studies underscores the need for island-specific information, especially for range-restricted species of conservation concern.

Exploratory behavior and HRS

Contrary to our predictions, more exploratory small ground finch males occupied smaller rather than larger home ranges. This finding conflicts with a previous study in common brushtail possums, in which more exploratory males had larger home ranges, although this association between exploration and home range size was sex-dependent (Wat *et al.* 2020). Future work should seek to understand the mechanisms that underlie these species-specific associations between behavioral traits and home range size. For example, one could measure the ontogeny of personality across life stages (Katsis et al. 2023) and how behavioral changes across an individual's lifespan influence its dispersal and spatial use patterns. Darwin's finches are socially monogamous and provide biparental care to offspring both during the nestling stage (Kleindorfer et al. 2022) and for about two weeks post-fledgling, after which time juvenile finches tend to flock and roost together (Schluter 1982; Beausoleil et al. 2022). During this formative period, juvenile social aggregations may affect individuals' foraging behavior and, hence, their long-term spatial behavior. Indeed, in captive Australian zebra finches (*Taeniopygia castanotis*), younger individuals develop similar foraging behavior to adults in close proximity through social learning (Farine et al. 2015). In addition to social factors, ecological factors such as predator abundance and food availability may also shape personality distributions at the population level, with shifting selection pressures across islands and seasons (Boag and Grant 1984).

Aggressive behavior and HRS

In both species, we found a negative association between male aggressiveness and home range size. Our results are aligned with previous findings in great tits (*Parus major*) and in meadow voles (*Microtus pennsylvanicus*), whereby individuals that were more aggressive, and hence less tolerant of intruders, occupied smaller home ranges (Spritzer et al. 2005; Naguib et al. 2022). If more aggressive males are better at outcompeting conspecifics, this may allow them to occupy high-quality patches that contain all required resources within a relatively small area. Conversely, less aggressive males may be forced to travel more widely to obtain the resources that they need. Future research should aim to identify the habitat characteristics that mediate differences in home range size. In addition, it would be informative to test whether females prefer to pair with aggressive males and, if so, whether this preference generates direct or indirect fitness benefits. From a physiological perspective, aggressiveness is linked to high testosterone levels (Wingfield et al. 1990; Smith et al. 2005). In socially monogamous bird species, both testosterone levels and agonistic behavior tend to decrease during offspring rearing phase, as observed in Lapland longspurs (*Calcarius lapponicus*) (Hunt et al. 1997). In Darwin's finches, males and females do not differ in their levels of the stress hormone corticosterone levels during the breeding season (Clark et al. 2018). Future work should examine the relationship between aggressiveness and hormone production across breeding stages in Darwin's finches, as previous studies have shown that opportunistic breeders, such as Darwin's finches, can regulate the

starting of their annual reproductive events based on weather conditions (Hau et al. 2004).

In both Darwin's finch species, paired males occupied smaller home ranges than unpaired males, which suggests that males may reduce their movements post-pairing to more vigorously defend their territory and/or guard their mating partner. However, in our study, it is difficult to disentangle the causality of this relationship: do male finches reduce their home ranges upon pairing, or are males with small home ranges more likely to secure a mate? Females may prefer males with smaller home ranges if, for example, these males are spending more time displaying at their nest, or if their smaller home ranges contain a greater proportion of high-quality habitat (e.g. Favaron et al. 2006).

Conservation implications

Understanding the movement patterns of threatened species can provide relevant information for conservation management (Puehringer-Sturmayr et al. 2023). From a foraging and habitat use perspective, generalist species occupy larger home ranges and tend to be more resilient under conditions of habitat loss, whereas specialist species are more vulnerable to habitat loss and generally experience a higher risk of extinction (Owens and Bennett 2000; Slatyer et al. 2013; Castañeda et al. 2019; Guerrero-Sanchez et al. 2022). The generalist small ground finch is a common and widespread species whose distribution has expanded in recent decades from the lowlands to the highlands on both Santa Cruz (Galligan and Kleindorfer 2010; Sulloway and Kleindorfer

2013) and Floreana Island (O'Connor et al. 2010; Kleindorfer et al. 2021). Its higher exploration scores in our study are consistent with the predictions of the neophobia threshold hypothesis, which proposes that more generalist species should be less wary of novelty (Greenberg 1983, 1990). The medium tree finch has a more specialist diet and is a range-restricted species endemic to the Floreana highlands, categorized as critically endangered (Freile et al. 2019; Kleindorfer et al. 2022). In the latter species, understanding movement patterns is essential for developing conservation strategies and management plans, especially given the limited habitat available to this species, representing only 26% (4599 ha) of the island, of which 5% (230 ha) is used for agriculture (Island Conservation and Galapagos National Park Directorate, 2020). In our study, medium tree finches were tagged only in the *Scalesia* forest that covers the island's central highland and generally remained in this area. However, the species is also currently establishing itself in the adjacent agricultural areas, outside of the protected land of Galapagos National Park, and future studies should aim to map the home ranges and movement patterns of these individuals in the agricultural zone.

Limitations of the study

One limitation of our study is that we do not have repeated testing of behavioral variables over time, which prevents us from calculating the temporal consistency of exploration and aggressiveness (Niemelä & Dingemanse 2018). Without data on within-individual behavioral variation, we cannot distinguish between phenotypic correlations that occur within and between individuals,

which risks under- or over-estimating the correlation between behavior and home range size (Niemelä and Dingemanse 2018). Nevertheless, we provide some evidence that between-individual behavioral differences are consistent across contexts (i.e. across two different assays measuring the same purported personality trait) for both exploration and aggressiveness, partially satisfying the definition of personality as "consistent between-individual differences in behaviour across time and/or contexts" (Sánchez-Tójar et al. 2022).

Conclusion

This study found within- and between-context support for consistent behavioral differences in exploration and aggressiveness behavior in two Darwin's finch species studied across two years. Our measurements of behavioral traits, which align with two major personality axes (exploration and aggressiveness), predicted individuals' home range size. In both species, males that were more aggressive (spent more time near the mirror during a mirror stimulation test) had smaller home ranges. The relationship between exploration and home range size differed between species, which may be related to differences in foraging ecology between the small ground finch (a fast-exploring generalist) and medium tree finch (a slower-exploring invertebrate specialist). From a conservation perspective, using our understanding of home range size to inform conservation management will be of increasing importance as we attempt to redress the impacts of the Anthropocene (Lewis and Maslin 2015) and biodiversity crisis (Koh et al. 2004; Rodríguez-Rodríguez and

Martínez-Vega 2022). On Floreana Island, the Galapagos National Park Directorate has begun implementing a large-scale eradication program of introduced mammals to reverse the island's significant biodiversity losses (Hanson and Campbell 2020). Therefore, having baseline data on the Darwin's finches' behavioral and spatial ecology prior to the eradication creates opportunity to compare changes in personality structure, breeding success, and movement patterns after removal of invasive predators (Banko et al. 2019).

Table 1. Summary of home range sizes (ha) in male medium tree finches (MTF) and small ground finches (SGF). The table shows sample size (n), mean ± SE, and range (min to max) of home range sizes, grouped by species (MTF, SGF), pairing status (paired, unpaired) and year (2020, 2022). * In 2022, all monitored males built a nest, but none found a breeding partner during the four-week study period.

	All			***2020***			***2022***		
	n	**Mean ± SE**	**Range**	**n**	**Mean ± SE**	**Range**	**n**	**Mean ± SE**	**Range**
MTF				10	0.9 ± 1.9	0.2–1.9			
Unpaired	15	2 ± 0.5	0.2–7	5	0.7 ± 0.3	0.2–1.9	10*	2.7 ± 0.7	0.4–7.0
Paired	5	1.1 ± 0.3	0.2–1.7	5	1.1 ± 0.3	0.2–1.7			
	All			**2020**			**2022**		
	n	**Mean ± SE**	**Range**	**n**	**Mean ± SE**	**Range**	**n**	**Mean ± SE**	**Range**
SGF				10	1.4 ± 0.6	0.1–6.8			
Unpaired	8	3.7 ± 1.1	0.8–9	3	3 ± 1.9	0.8–6.8	5*	4.1 ± 1.4	0.9–8.9
Paired	7	0.7 ± 0.2	0.1–1.8	7	0.7 ± 0.6	0.1–1.8			

Table 2. Output from linear models testing the effects of personality and species (medium tree finch, MTF, or small ground finch, SGF) on home range size (log-transformed). 'Unique sector visits' is a measure of exploration during the novel environment test (with higher values indicating greater exploration) and 'time near mirror' is a measure of aggressiveness during the mirror stimulation test (with higher values indicating greater aggressiveness).

	Estimate	***Std. Error***	***t***	***p***
(Intercept)	0.056	0.371	0.151	0.881
Unique Sector Visits	0.080	0.076	1.056	0.300
Time Near Mirror	-0.015	0.005	-3.340	**0.002**
Species (SGF)	0.138	0.351	0.392	0.698

Figure 1. We conducted our study in the highlands of Floreana Island (dark mark in top-left inset), one of the southern islands of the Galapagos Archipelago. Our two study sites were Cerro Pajas and Asilo de la Paz (black dots).

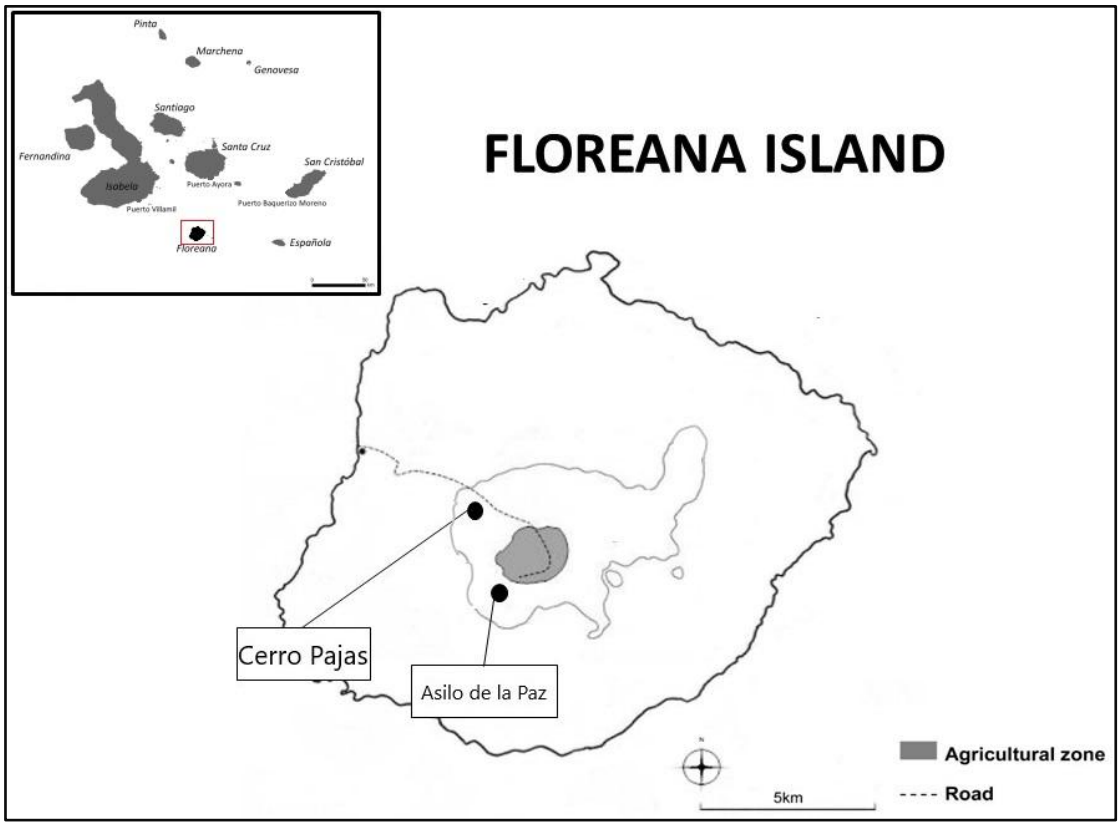
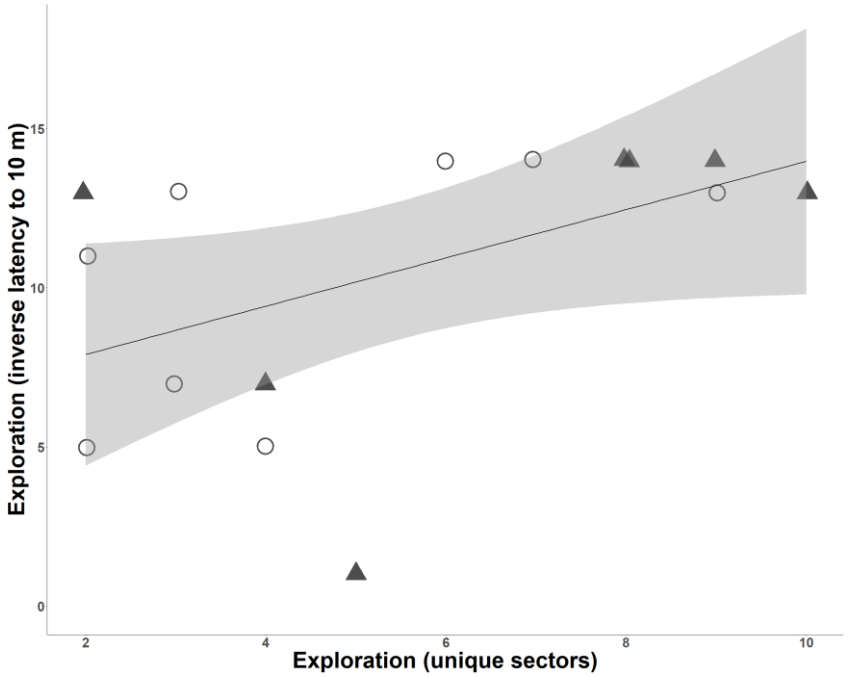


Figure 2. Behavioral variables measured in the same individuals across contexts in medium tree finches (open circles) and small ground finches (filled triangles). a) Exploration in the novel environment test (number of unique sectors visites) correlated positively with exploration in the novel object test (inverse latency to approach to 10 m), when considering both species together (r = 0.6, N = 15, *P* = 0.03). b) Aggressiveness during the mirror simulation test (*time near mirror*) correlated positively with aggressiveness during a simulated territory intrusion (*playback response*, PC_Aggressiveness) when considering both species together (r = 0.4, N = 35, *P* = 0.04).

a) Cross-context validation for exploration



b) Cross-context validation for aggressiveness

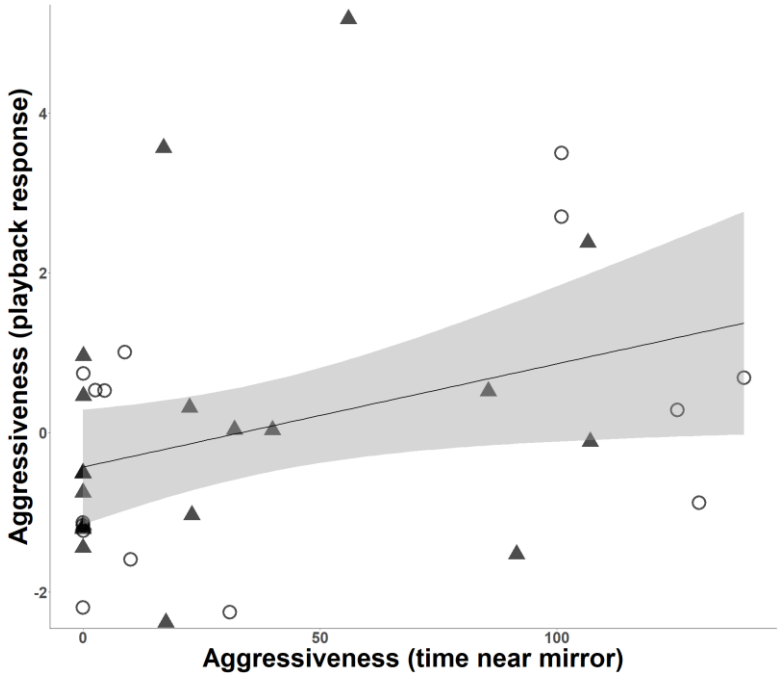


Figure 3. The relationship between exploration and home range size (log-transformed) differed between Darwin's finch species. The number of *unique sectors visits* during a novel environment test (a) did not predict home range size in medium tree finches, and (b) was negatively associated with home range size in small ground finches. 95% confidence intervals are shown in grey.

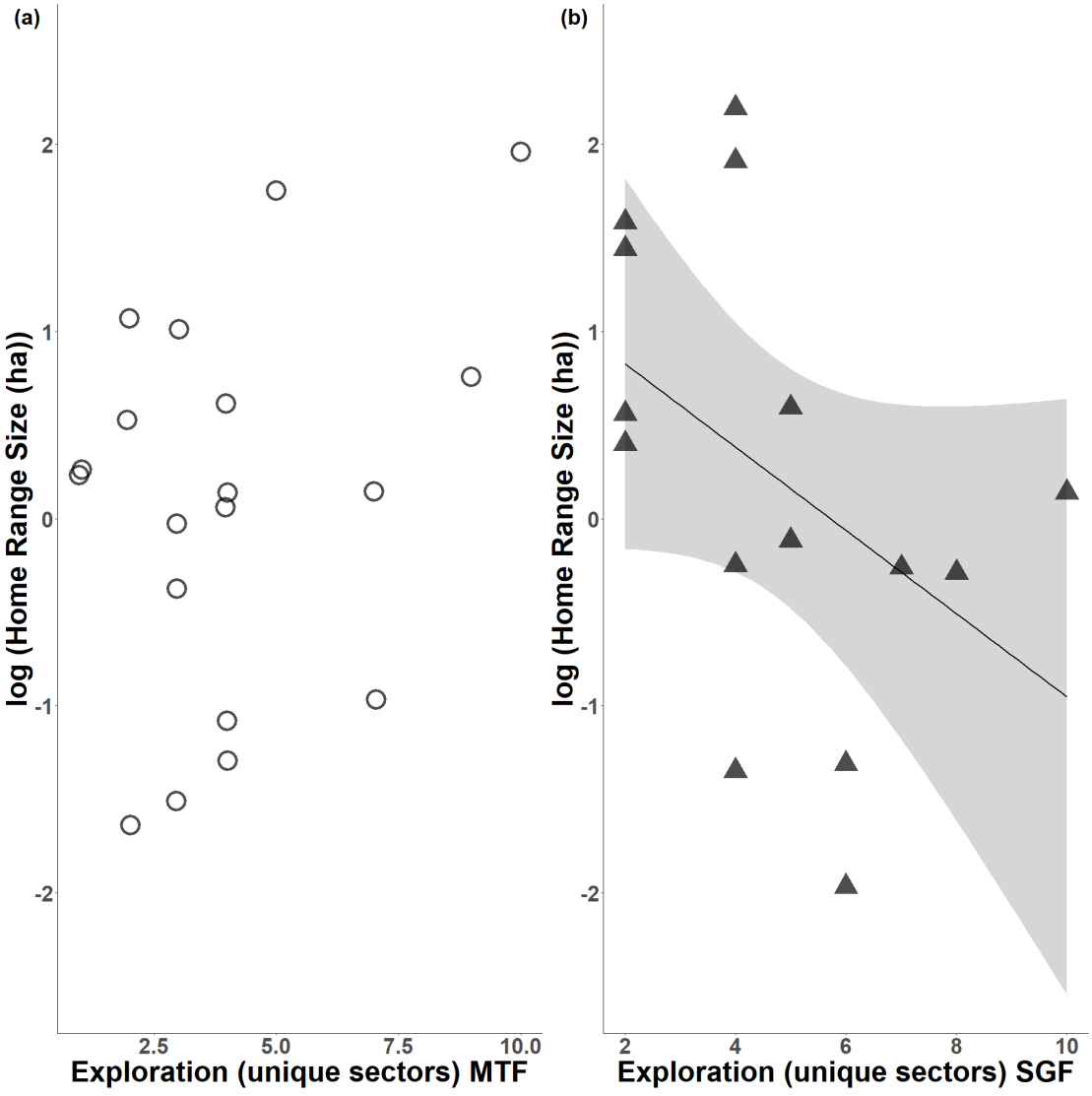
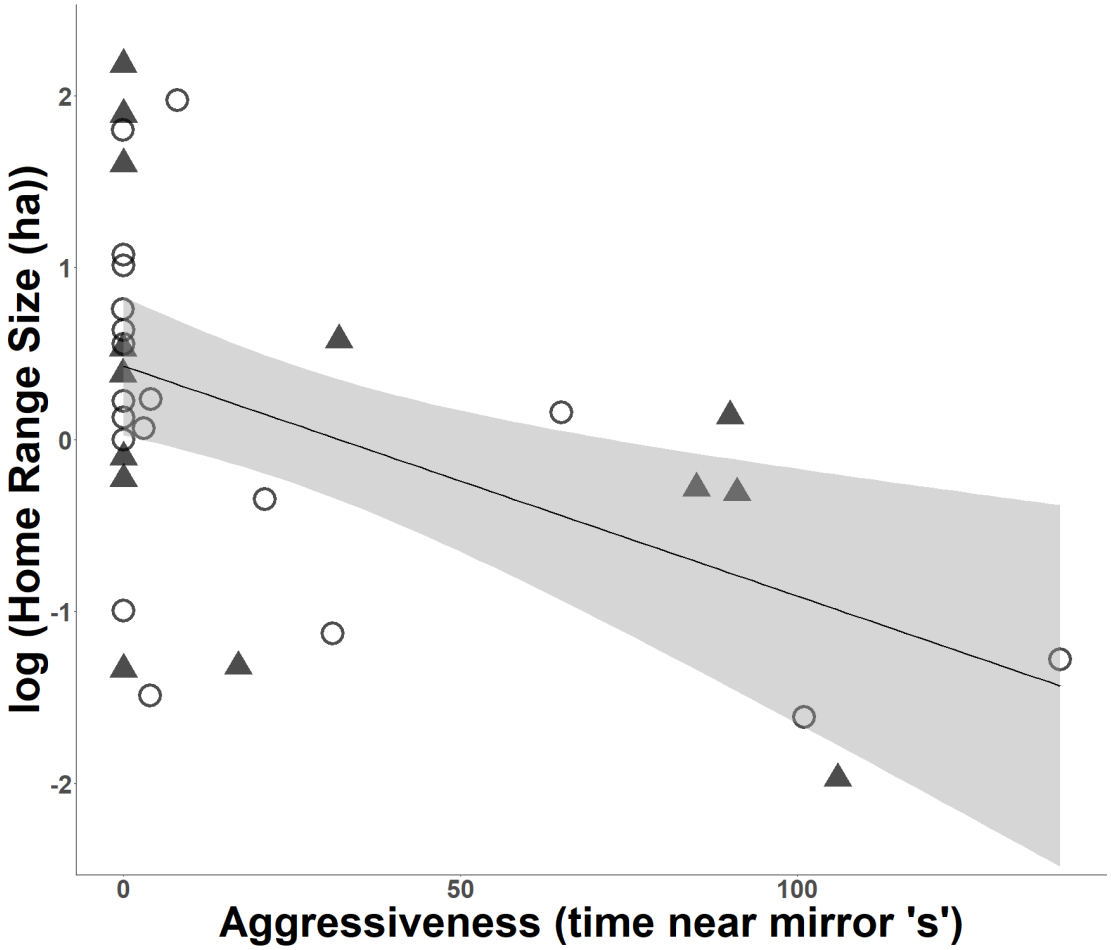


Figure 4. Aggressiveness in the mirror stimulation test (*time near mirror, in secs*) was negatively associated with home range size (log-transformed) in medium tree finches (open circles) and small ground finches (filled triangles) (r = -0.5, N = 33, *P* = 0.001). 95% confidence intervals are shown in grey.



Chapter 2

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Exploration behavior is consistent and associated with foraging behavior in island songbirds

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Abstract

According to the neophobia threshold hypothesis, species with greater dietary specialization should be less exploratory. Few studies have measured the repeatability of exploration behavior of individually marked animals in the wild, so we lack a robust test of the neophobia threshold hypothesis. We tested this hypothesis across six landbird species, including four Darwin's finches, in a species assemblage renowned for its foraging diversity. First, we tested whether color-banded individuals showed consistent exploration behavior across two different contexts: (1) in response to a novel environment, during short-term captivity, and (2) in response to a novel object in the field. Second, to test the predictions of the neophobia threshold hypothesis, we correlated foraging diversity for each species (diversity of foraging substrates and techniques, calculated using the Shannon diversity index) against its mean exploration score. We found that individual differences in exploration behavior in the novel environment were significantly repeatable across a two-year period (consistent over time) and also correlated with individual differences in exploration towards the novel object (consistent across contexts). Specifically, individuals that visited many sectors in the novel environment also approached the novel object in the field more quickly. At the species level, foraging substrate diversity was positively associated with the proportion of birds to approach the novel object, and species with higher foraging technique diversity were quicker to approach the novel object. These findings are consistent with the neophobia threshold hypothesis. Furthermore, our results suggest that consistent behavioral differences in exploration can shape population-level patterns of foraging diversity.

Key Words:

Darwin's finches, foraging diversity, Galapagos, neophilia, novel arena.

Introduction

Individuals, populations, and species may differ in the diversity of their diets and foraging strategies (Eccard et al., 2020; Stephens & Krebs, 1986; Toscano et al., 2016). Ultimately, diversity in foraging behavior can produce evolutionary change and adaptive radiations (Araújo et al., 2011; Gavrilets & Losos, 2009). Hence, understanding variation in individual traits associated with foraging can help us understand selection pathways that result in novel evolutionary trajectories. Animal personality refers to individual differences in behavioral responses that are consistent across time and contexts (Sih, Bell, Johnson, et al., 2004; Sih, Bell, & Johnson, 2004; Réale et al., 2007; Laskowski et al., 2022). Understanding which personality traits are associated with foraging behavior first involves establishing the consistency of target traits, including cross-context comparisons of behavioral assays in an ecological setting, and population-level assessments of foraging behavior (Dall et al., 2004; Toscano et al., 2016). Réale *et al.* (2007) proposed five broad personality axes (exploration, activity, boldness, aggressiveness, and sociability) and suggested several assays that could be used to measure each axis across different contexts/conditions, ultimately with the view to test their functional relevance.

Exploration, defined as an individual's behavioral response to a novel stimulus or situation (Réale et al., 2007), is a widely studied personality trait that can have consequences for individual survival and reproductive success (Dingemanse et al., 2004; Dingemanse & De Goede, 2004; Hall et al., 2015; Katsis et al., 2024b). Previous studies suggest that exploration phenotypes can predict the degree of foraging specialization, both at the individual level (e.g. in eastern chipmunks, *Tamias striatus*; Gharnit *et al.*, 2022; in common brushtail possums, *Trichosurus vulpecula*; Herath *et al.*, 2021) and at the species level (Webster & Lefebvre, 2000; Greenberg & Mettke-

Hofmann, 2001; Tebbich et al., 2009; Mettke-Hofmann et al., 2013). This positive association between exploration and foraging diversity is potentially explained by the neophobia threshold hypothesis (Greenberg, 1990; Greenberg & Mettke-Hofmann, 2001), which posits that more exploratory (less neophobic) species are more likely to investigate new resources and integrate them into their diets.

Exploration has widely been tested both in the wild and in captivity, although surprisingly few studies have assessed whether phenotypes measured in captivity are representative of how individuals behave in the wild (but see Herborn *et al.*, 2010; McCowan *et al.*, 2015). While captive-based assays, such as novel environment or open-field tests (Verbeek et al., 1994), allow researchers to standardize testing conditions across trials, behavioral responses may be confounded by factors unrelated to exploration, such as subjects' latency to recover from handling stress or to acclimate to captive conditions (Niemelä & Dingemanse, 2014). Hence, we need to validate that individual differences in exploration remain consistent when measured across different contexts.

Darwin's finches are a useful model system for studying evolutionary change, in part due to the rapid adaptive radiation that this group have undergone over the last ca. 1.5 million years, with 17 species currently extant on the Galápagos Islands (Grant & Grant, 2014a; Grant, 2017; Kleindorfer et al., 2022; Colombelli-Négrel et al., 2023). This radiation exhibits dramatically different beak sizes and shapes that are associated with different foraging techniques and niche utilization (Lamichhaney et al., 2015, 2016). In a previous study, Darwin's finch species with more generalist diets were also more likely to approach novel objects in the wild, suggesting a positive correlation between exploration and foraging diversity (Tebbich et al., 2009). Similarly, we

recently found that Darwin's ground finches, which are dietary generalists, were more exploratory in a novel environment test compared to Darwin's tree finches, which are dietary specialists (Katsis et al., 2024b). However, we still lack a cross-context validation for exploration behavior in Darwin's finches.

In this study we aimed, first, to assess the consistency of exploration behavior across contexts in six songbird species on Floreana Island, including four Darwin's finch species. Specifically, we compared the responses of color-banded individuals in two different exploration assays: (1) a novel environment test, conducted during short-term captivity, and (2) a novel object test, conducted in the field by placing a novel object in their territory. We predicted a positive correlation between individuals' exploration of the novel environment (number of total and unique sector visits) and exploration of a novel object (latency to approach the novel object in the field). Second, we tested whether the diversity of foraging techniques and foraging substrates used (hereafter referred to as foraging diversity) was associated at the species level with exploration behavior (Tebbich et al., 2009). To do this, we correlated each species' mean exploration score with its diversity of substrates and techniques used during foraging (we did not measure dietary diversity per se). Foraging technique and substrate (i.e., how and where birds forage) have been proposed to be linked with exploration behavior, as foraging behavior is the behavioral pathway to accessing dietary items (Tebbich et al., 2009). We predicted that more exploratory species would show greater foraging diversity, consistent with the predictions of the neophobia threshold hypothesis.

Methods

Study site and species

We conducted our study in 2020 (Jan–Feb) and 2022 (Feb–Mar) on Floreana Island in the Galápagos Archipelago, at two highland sites (Cerro Pajas, 1° 17' 36.5"S, 90° 27' 07.2"W, Asilo de la Paz, 1° 18' 50.4"S, 90° 27' 19.8"W) and one lowland site, in and around the township of Puerto Velasco Ibarra (1° 16' 50.7" S, 90° 28' 50.0" W). The study was conducted along twelve 200-m transect plots that have been monitored in the highlands as part of a long-term monitoring program that began in 2004 (Langton & Kleindorfer, 2019). We quantified exploration (novel environment test and novel object test) and foraging behavior in six native passerine species: the small ground finch (SGF; *Geospiza fuliginosa*), medium ground finch (MGF; *G. fortis*), small tree finch (STF; *Camarhynchus parvulus*), medium tree finch (MTF; *C. pauper*), Galápagos flycatcher (GFC; *Myiarchus magnirostris*), and yellow warbler (YW; *Setophaga petechia aureola*). The first five species are endemic to the Galápagos Islands, while the yellow warbler is an endemic subspecies. The medium tree finch is an island-endemic restricted to Floreana Island and categorized as Critically Endangered (CR) by the International Union for Conservation of Nature (Freile et al., 2019). The vegetation at both highland sites (Cerro Pajas and Asilo de la Paz) is dominated by *Scalesia pedunculata* (family Asteraceae). The lowland site includes the town of Puerto Velasco Ibarra and the surrounding uninhabited scrubland that is dominated by palo santo (*Bursera graveolens*) and acacia (*Parkinsonia aculeata*). Based on data obtained from the website "*Galapagos Vital Signs*" (Galapagos Conservancy, https://www.galapagosvitalsigns.org), rainfall levels varied markedly between the two field seasons, during January and February 2020, mean rainfall was 70 mm (range 0–105 mm), whereas in the same period of 2022, mean rainfall was considerably lower at 1.5 mm (range 0–4 mm) (García-Loor et al., 2024). All three

study areas are commonly used by Darwin's finches, yellow warblers, and Galápagos flycatchers for foraging and nesting, although ground finches are more common in the lowlands and tree finches are more common in the highlands (Dvorak et al., 2017; Kleindorfer et al., 2022; Lawson et al., 2023).

Mist-netting

During the field seasons in 2020 and 2022, we mist-netted, color-banded, and measured exploration behavior from our six study species. At the time of banding, each bird received a uniquely numbered aluminum band and a unique combination of between one and three color-bands. Novel environment tests (see below) were performed within 30 mins after capture. All birds were then released at their site of capture, typically within one hour.

Exploration of wild-caught birds: novel environment test

During short-term captivity, we measured subjects' exploration behavior using a novel environment test . First, each subject was placed individually into a plastic release box (19 × 14 × 10 cm) for a standardized acclimation period: 5 min in 2020 (N = 152) or 1 min in 2022 (N = 94) (acclimation time was shortened in 2022 to reduce subject waiting times). After the door to the release box was raised, the bird was allowed to enter the novel environment: a metal flight cage (75 × 44 × 42 cm) with three perches (one at a height of 6 cm and the other two at a height of 20 cm). 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. The novel environment contained 13 discrete sectors that the subject could visit: three perches, four floor quadrants, four cage walls, the cage ceiling, and the release box. The novel environment test lasted 5 min, during which we scored*: a)* the number of *unique sector visits,* and b*)* the number

of *total sector visits* (including repeat visits to the same sector). This assay used similar protocols to a previous study that found significant repeatability of exploration scores in adult superb fairy-wrens (*Malurus cyaneus*) (Katsis et al., 2023). Novel environment tests were recorded with a GoPro camera placed 50 cm outside the flight cage and behavior was scored by one of two experimenters (JG-L and ACK) using the software Solomon Coder v. beta 19.08.02 (András Peter, https://solomon.andraspeter.com). In total, we conducted 246 trials of the novel environment test (SGF = 89, MGF = 12, STF = 70, MTF = 44, GFC = 3, YW = 28) with 237 individuals (8 individuals undertook repeated trials; mean number of trials per bird = 1.04 ± 0.01 SE, range = 1–3) (see Fig. S3 for additional details).

Exploration in the wild: novel object test

During February 2022, we conducted novel object trials in the field, following protocols previously used by Tebbich *et al.* (2009). First, we placed one of three different novel objects (30 × 50 cm double metal grid, 20 × 50 cm yellow bag, or 20 × 50 cm orange bag) in the field at a height of 2 m in natural vegetation. Using small stones and branches, we demarcated a 10-m radius around the novel object. The birds were alerted to the start of the trial using a bird whistle (Audubon, model MT-PN-28905150), which was blown from a distance of 15 m from the novel object. Each trial lasted 10 min, during which we scored birds' response to the novel object as their latency (in min) to approach within 10 m and within 3 m of the novel object. We scored response to the novel object as: (1) *response 10 m*, the number of individuals per species to approach to 10 m divided by the total number of individuals of all species that approached to 10 m (proportion, species-level measure); (2) *response 3 m*, the number of individuals per species to approach to 3 m divided by the total number of conspecifics that approached to 10 m (proportion, species-level measure), (3) *latency*

to 10 m, the time (in secs) for an individual to approach within 10 m (n = 262), and (4) *latency to 3 m*, the time (in secs) for an individual to approach from 10 m to within 3 m (only individuals that approached within 3 m, n = 57) (Table S1). To aid interpretation of latency to 10 m, we inverted the latency score by subtracting each latency from the maximum possible value (10 min), so that higher scores indicated more exploratory behavior: that is, birds approaching the novel object during the first minute received a score of 10–1 = 9 (high exploration) and birds approaching during the ninth minute received a score of 10–9 = 1 (low exploration). In total, we conducted 48 novel object trials and measured exploration for 267 individuals that approached during these trials (SGF = 99, MGF = 6, STF = 39, MTF = 33, GFC = 21, YW = 69) (see Fig. S3 for additional details). Of these, 44 individuals were color-banded (SGF = 8, STF = 3, MTF = 5, YW = 28) and had previously been assayed using the novel environment test in 2020 or 2022. No color-banded medium ground finches or Galápagos flycatchers were observed during the novel object trials

Foraging diversity

We collected 320 first-foraging observations during January and February in 2020 and 2022 from our six study species (SGF = 166, MGF = 25, STF = 67, MTF = 30, GFC = 6, YW= 26). For each observation, we noted the bird's foraging technique (bite, chip off, grasp, glean, peck, probe, pry, sally) and foraging substrate (air, dead bark, dead leaf, flower, fruit, grass, green leaf, ground, lichen, live bark, moss), following long-term protocols from our study population (Kleindorfer et al., 2022). We collected foraging data along 200-m transects, which were each traversed 3–7 times per year. On a given day, we used only the first observation per individual to avoid pseudo-replication (Kleindorfer et al., 2022).

Statistical analysis

We performed statistical analyses using the software R version 4.1.1 (R Core Team 2022). Univariate linear mixed models (LMMs) were implemented using the package lme4 version 1.1-33 (Bates et al., 2015) and lmerTest version 3.1-3 (Kuznetsova et al., 2017), and bivariate LMMs using the package MCMCglmm version 2.35 (Hadfield, 2010). We extracted χ^2 and *P* values from the ANOVA table of deviance using Type III χ^2 tests in the package car version 3.0-12 (Fox & Weisberg, 2018). Results are reported as estimate ± SE (Bates et al., 2015). All figures were created using ggplot2 version 3.5.1 (Wickham, 2009).

a) Consistency of exploration over time

We assessed individual-level adjusted repeatability (R) (Nakagawa & Schielzeth, 2010) of novel environment exploration (unique sector visits and total sector visits) using LMMs with individual ID (band number) as the random effect and included year, species, and sex as fixed effects. Model fit was assessed using the package DHARMa version 0.4.4 (Hartig, 2017). 'Total sector visits' was log-transformed to fulfill the assumption of normality of residuals. We calculated repeatability using the package rptR version 0.9.22 (Stoffel et al., 2017) with individual ID as the grouping variable. The significance of R was tested using likelihood ratio tests against the null hypothesis that R = 0, and we calculated 95% confidence intervals with parametric bootstrapping (1000 iterations). We included individuals that were only assayed once, as all observations contribute to the estimate of total variance (Martin et al., 2011). We did not assess the repeatability of novel object exploration over time, as no color-banded individuals were observed more than once.

b) Consistency of exploration across contexts

Given the strong positive correlation between unique sector visits and total sector visits (see also Katsis *et al.*, 2024), we used principal component analysis to reduce these variables to a single principal component (*PC_Exploration*) with eigenvalue 1.68 that explained 84% of the variance (factor loadings for both variables = 0.71). Principal component analysis was executed using the function 'princomp' (R package 'stats' version 3.6.2).

To assess the consistency of exploration across contexts, we used two bivariate LMMs that included exploration of the novel environment (*PC_Exploration*) as their first response variable and exploration of the novel object (inverse latency to 10 m or latency to 3 m, respectively) as their second response variable. A Gaussian error distribution was assumed for all factors. These models included sex and species as fixed effects, and individual ID as a random effect. Year of the novel environment test was omitted as a fixed effect, as the models did not converge when this variable was included. The two types of exploration assay were conducted on different days; therefore, we set within-individual covariances to zero (i.e., rcov = ~idk(trait):units, Scenario 4 in Table 2 of Dingemanse & Dochtermann (2013)). Because there were no repeated measures for response to the novel object, we fixed its variance to zero. The prior used was moderately informative (nu = 1.002) and parameter-expanded (Houslay & Wilson, 2017), as convergence and effective sample size were improved compared to a weakly informative (nu = 0.002) and non-parameter-expanded prior. We ran the MCMC for 1,000,000 iterations ('nitt') with 75,000 burn-in and a thinning interval of 300. Effective sample sizes were > 2000 for all models. Autocorrelation was assessed using the function 'autocorr' to ensure it was < 0.1 for each run. We ran each model three times with the same prior structure to confirm that the Gelman-Rubin

statistic (Gelman & Rubin, 1992) was approximately 1 for all models, indicating proper model convergence. If the 95% credible intervals did not cross zero, the among-individual correlation between exploration scores was considered statistically significant. This analysis included individuals that were only tested with one of the exploration assays, as all observations contribute to estimates of total variance. To assess whether correlations between PC_Exploration and inverse latency to 10 m were being driven by the most frequent species in our dataset (yellow warbler), we conducted two additional bivariate models that limited analysis to yellow warblers only and Darwin's finches only, respectively.

c) Exploration and foraging diversity

We calculated foraging diversity per species using the Shannon diversity indices for foraging technique and foraging substrate, using the function 'diversity' in the package vegan version 2.5-7 (Dixon, 2003) (Table S2). We tested the species-level association between exploration towards a novel object (proportion response 10 m, proportion response 3 m, mean inverse latency 10 m, mean latency to 3 m) and both foraging diversity index scores (technique and substrate) using a Spearman's correlation test with the function 'cor.test' ('stats' version 3.6.2).

Results

a) Consistency of exploration over time

Both measures of exploration during the novel environment test were significantly repeatable, although 95% confidence intervals crossed zero for unique sector visits (unique sector visits: R = 0.37 ± 0.25, 95% CI = 0.00–0.80, P = 0.037; total sector visits: R = 0.80 ± 0.11, 95% CI = 0.53–0.95, P = 0.023) (Fig. 1). These results indicate

that approximately 37% of the variance in unique sector visits and 80% of the variance in total sector visits could be explained by individual identity. Species differed in their exploration behavior (unique sector visits: $\chi^2 = 63.02$, $P < 0.001$; total sector visits: $\chi^2 = 93.47$, $P < 0.001$), and fewer total sectors were explored in 2022 compared to 2020 ($\chi^2 = 18.21$, $P < 0.001$) (Table S1).

b) Consistency of exploration across contexts

Both exploration variables in the novel environment (unique sector visits and total sector visits) were positively associated ($r_S = 0.82$, N = 246, $P < 0.001$) (Fig. 2). Among individuals, exploration in the novel environment (PC_Exploration) was positively correlated with exploration in the novel object test (inverse latency to 10 m) (all species pooled: estimate = 0.69, 95% CrI = [0.44 – 0.98], N = 43) (Table 1a, Fig. 3a). That is, individuals that visited many sectors in the novel environment also approached the novel object in the field more quickly. We found the same pattern when we analyzed only yellow warblers (estimate = 0.54, 95% CrI = 0.13–0.98, N = 29) and a non-significant positive trend when analyzing only Darwin's finches (estimate = 0.47, 95% CrI = -0.03–0.99, N = 15) (Table S2, Fig. S1). PC_Exploration was not significantly correlated with latency to 3 m, our second measure of exploration in the novel object test (estimate = 0.43, 95% CrI = -0.10–0.94, N = 19) (Table 1b, Fig. 3b).

c) Exploration and foraging diversity

At the species level, we found that the proportion of individuals to approach the novel object to within 10 m was highest in small ground finches and yellow warblers, and to within 3 m was highest in medium tree finches and Galápagos flycatchers (**Table S3**). Foraging technique and substrate diversity were highest in small ground finches and medium tree finches (see **Table S4**).

We also found species-level correlations between exploration in the novel object test and foraging diversity, where the proportion of individuals per species approaching within 3 m of the novel object was significantly positively correlated with the diversity of foraging substrates (r_S = 0.83, N = 6, *P* = 0.042) (Table 2, Fig. 4a). Likewise, the mean latency from within 10 m to 3 m of the novel object was significantly negatively correlated with foraging technique diversity: that is, species that approached the novel object more quickly had more diverse foraging techniques (r_S = -0.83, N = 6, P = 0.042) (Table 2, Fig. 4b). There were also near-significant trends for species with a higher proportion of individuals approaching 10 m to have more diverse foraging techniques (r_S = 0.77, N = 6, P = 0.072) and for species with shorter latency to 3 m to forage on more diverse substrates (r_S = -0.77, N = 6, P = 0.072) (Table 2).

Discussion

In this study of six landbird species on Floreana Island, we aimed to assess the individual consistency of exploration behavior within and across contexts and to compare exploration and foraging diversity at the species level. We found that individuals' exploration of a novel environment was both repeatable over time and correlated with exploration when measured in a different context (a novel object test conducted in the field). This finding provides an important foundation for designing and implementing behavioral assay protocols that minimize wildlife handling. Such field assays are particularly useful for endangered or sensitive species, such as the medium tree finch, where excessive capture and handling of individuals is impractical or inadvisable. In addition, we found a species-level correlation between exploration and foraging behavior, as predicted by the neophobia threshold hypothesis, with more

exploratory species using a greater diversity of foraging techniques and substrates (see also Tebbich et al., 2009).

Individuals showed consistent exploration behavior in behavioral assays conducted in captivity (novel environment test) and in the wild (novel object test). Previous studies in captive songbirds have reported mixed evidence for the consistency of exploration across contexts. For example, juvenile great tits (*Parus major*) were individually consistent in their exploration of artificial trees in a room and in their approach to novel objects across three different assays in a controlled observation room (Verbeek et al., 1994). Conversely, captive house sparrows (*Passer domesticus*) showed no association between their exploration of a novel environment and their neophobic response towards a novel object (Kimball & Lattin, 2023). In general, we cannot necessarily assume that different measures of exploration will directly correlate with each other, and there is growing evidence that there may be repeatability within certain exploratory contexts (e.g. towards novel environments, rather than objects or foods) but not across contexts (Greggor et al., 2015). Nevertheless, we found a significant positive correlation between exploration in a novel environment and towards a novel object, even with, in some cases, a two-year interval between the two assay types.

In a previous study, Tebbich et al. (2009) demonstrated a correlation between foraging diversity and exploration across eight Darwin's finch species, showing that more generalist species (i.e. with broader dietary diversity) were also more exploratory towards a novel object in the field. In our study, we similarly found a positive species-level correlation between exploration and diversity of foraging techniques and substrates in four Darwin's finches and two other songbird species. This may indicate

that exploratory species are more likely to investigate new resources and integrate them into their foraging niche, as predicted by the neophobia threshold hypothesis (Greenberg, 1983). Classical resource partitioning theory emphasizes how species can occupy distinct niches through different means of resource use (Pianka, 1974; Schoener, 1974). While diet is often used as a measure of niche separation, partitioning can also be reflected in the substrates on which animals forage or the specific techniques they use to access resources (Macarthur & Levins, 1967). In our study, we did not record which food items were consumed, as this is often difficult or impossible to see in the field. However, we hypothesize that there is an association between foraging substrates and techniques and the dietary items consumed. For instance, specific foraging techniques such as 'pry' and 'chip off' are closely tied to the extraction of subsurface invertebrates from within woody substrates; species that rarely use these techniques would have limited access to such food items (Kleindorfer et al., 2022). Among Neotropical flycatcher species, for example, foraging technique was a strong predictor of dietary diversity (Sherry, 1984). In a comparative study of 252 European bird species, there was a positive relationship between habitat specialization and dietary specialization, although this relationship was driven largely by non-passerines (Reif et al., 2016). Height of foraging may also be an important factor linking exploration and foraging substrate, if different species forage at different strata (e.g. bare ground versus live bark) based on their exploration phenotypes. In particular, Darwin's finch species differ in their likelihood of foraging on the ground (Kleindorfer et al., 2022) and those that avoid ground foraging would be less likely to encounter ground-based plants and invertebrates. Future studies testing the neophobia threshold hypothesis could address this limitation by correlating foraging height and diet, for example, with exploration explicitly measured in a foraging context (e.g. food neophobia; Marples *et al.*, 2007). Our study was conducted at three sites (two

highland, one lowland) on Floreana Island that likely differed in their habitat quality and/or food availability, which may have influenced individuals' foraging behavior at each site (Lyons, 2005; Powell et al., 2015). Our sample sizes in this study were insufficient to meaningfully compare foraging variation between sites, and we acknowledge that species-level differences in foraging diversity could be partly explained by the habitat inhabited by each species.

In general, there is evidence that exploratory phenotypes are associated with innovative behavior, including in foraging tasks (Biondi et al., 2010; Forss et al., 2017; Greenberg, 2003). For example, Carib grackles (*Quiscalus lugubris*) that solved a novel problem-solving task ("innovators") had higher exploration scores and were less neophobic than non-solvers ("non-innovators") (Overington et al., 2011). Therefore, the broader foraging niches of generalist species may be driven in part by their more exploratory phenotypes. In our study, small ground finches and medium tree finches exhibited the highest diversity of foraging techniques. Small ground finches have a generalist diet and are the most recently evolved of Darwin's finches (Petren et al., 1999), with a broad distribution across the archipelago. The medium tree finch, a critically endangered island endemic (Kleindorfer, Common, & Sumasgutner, 2021), had the second highest foraging diversity score, and feeds variously on invertebrates, fruits, seeds, and flowers (Kleindorfer et al., 2022; Tebbich et al., 2009). Understanding the colonization histories of these two species may help explain their more exploratory behavior and, hence, their greater foraging diversity, particularly if their populations on Floreana Island were established by exploratory colonist individuals. This is consistent with the observation that small ground finches have only in the last century expanded into the highlands of Floreana and Santa Cruz Islands (Dvorak et al., 2017; Galligan & Kleindorfer, 2010; Kleindorfer, Common, O'Connor,

et al., 2021; O'Connor et al., 2010). Likewise, the medium tree finch possibly evolved from a colonist population of large tree finches (*C. psittacula*) from Isabela Island (Grant & Grant, 2014b; Peters & Kleindorfer, 2018), whereby the colonist (presumably more exploratory) individuals from Isabela Island expanded into new foraging niches on Floreana Island. Such patterns would align with previous research on exploration and its relationship with dispersal and colonization events (Cote et al., 2010; Liebl & Martin, 2012), indicating that species with these traits tend to be more successful at expansion and establishment.

Understanding differences in foraging behavior and their association with behavioral phenotypes can give crucial insights into the ecological needs of individuals and populations (Morris & Mukherjee, 2007) and may help us identify the factors influencing adaptive capacity, predator-prey interactions, and site fidelity (Schirmer et al., 2019; Harris et al., 2020; Herath et al., 2021; Pereira et al., 2024). From a conservation point of view, understanding a population's behavioral heterogeneity may help us predict its resilience and adaptive capacity following major disturbances, such as drought or habitat loss. These behavioral differences are also relevant for the design of conservation interventions, such as captive breeding or translocation (Sinn et al., 2014; May et al., 2016; Germano et al., 2017). For example, if the endangered species in a translocation program exhibits low exploration, it would be important to ensure that individuals are released into a habitat that is as similar as possible to their original site, allowing them to utilize a comparable foraging niche. Meanwhile, fast-exploring species with broader foraging niches and more diverse suites of foraging techniques may survive better and show greater site fidelity in their new location, regardless of any habitat differences (De Azevedo & Young, 2021). Despite these benefits, animal personality remains an underutilized tool in conservation programs

(MacKinlay & Shaw, 2023), though progress is being made to redress this (Berger-Tal & Blumstein, 2024). Understanding habitat use patterns and foraging behavior of threatened species is essential for implementing effective conservation management strategies (Puehringer-Sturmayr et al., 2023).

Floreana Island represents a special case study in conservation management, given the recent implementation of a feral mammal eradication program in 2023, led by the Galápagos National Park Directorate with the support of various non-governmental and partner organizations. This eradication will be followed across the next decade by the reintroduction of 12 locally extinct species to Floreana Island, including five landbird species (Island Conservation and Galapagos National Park Directorate, 2020). This ecological restoration will provide an unprecedented opportunity to measure changes in the exploration behavior and foraging diversity of resident species following the reintroduction of competitor and predator species, and hence evaluate adaptive pathways that facilitate coexistence and drive competitive outcomes. In this way, the adaptive radiation of Darwin's finches can now be viewed from the perspective of individual behavioral differences that may shape the use of foraging niches before, during, and after the reintroduction of competitor species. The congruence between our findings and those of Tebbich et al. (2009) suggests that the species-level association between exploration behavior and foraging diversity is robust. This creates a framework for understanding how species' behavioral phenotypes might shape their foraging niches, allowing trophically similar species to co-occur while minimising overlap in their resource use.

Table 1. Output from bivariate LMMs showing variances (diagonals, in bold), covariances (below diagonals) and correlations (above diagonals) between exploration of a novel environment (PC_Exploration, unique and total sector visits) and exploration of a novel object: (a) inverse latency to 10 m and (b) latency from 10 m to 3 m. Lower and upper bounds of 95% credible intervals are shown in parentheses. Study species including in the model were small ground finch, small tree finch, medium tree finch, and yellow warbler. There were no Galápagos flycatchers or medium ground finches that took part in both exploration assays.

a) Inverse latency to 10 m		
	PC_Exploration	Inverse latency
PC_Exploration	**0.60 (0.21, 0.99)**	0.69 (0.44, 0.98)
Inverse latency	1.52 (0.80, 2.14)	**8.68 (7.20, 10.40)**
b) Latency from 10 m to 3 m		
	PC_Exploration	Latency
PC_Exploration	**0.52 (< 0.01, 0.95)**	0.43 (-0.10, 0.94)
Latency	0.74 (-0.22, 1.72)	**6.22 (3.64, 9.26)**

Table 2. Species-level correlations (N = 6) between foraging diversity (Shannon diversity index) and four measures of exploration in the novel object test: % response to 10 m, % response to 3 m, latency (secs) to 10 m, and latency (secs) to 3 m. Statistically significant values are shown in bold.

Novel object test	***Foraging Technique (Shannon diversity index)***	***Foraging Substrate (Shannon diversity index)***
Response 10 m	(r_S = 0.77, *P* = 0.072)	(r_S = 0.54, *P* = 0.266)
Response 3 m	(r_S = 0.49, *P* = 0.329)	**(rs = 0.83, *P* = 0.042)**
Latency 10 m	(r_S = -0.26, *P* = 0.623)	(r_S = -0.14, *P* = 0.787)
Latency 3 m	**(r_S = -0.83, *P* = 0.042)**	(r_S = -0.77, *P* = 0.072)

Figure 1. Scatterplots comparing individuals' exploration behavior in their first versus second trials of a novel environment test. We quantified exploration as (a) unique sector visits, the number of cage sectors visited over 5 mins; and (b) total sector visits, the total number of sectors visited, including repeat visits, over 5 mins. For both variables, higher scores indicate a more exploratory response to the novel environment. For individuals with repeat testing (N = 8), first trials were conducted in 2020 and second trials in 2022.

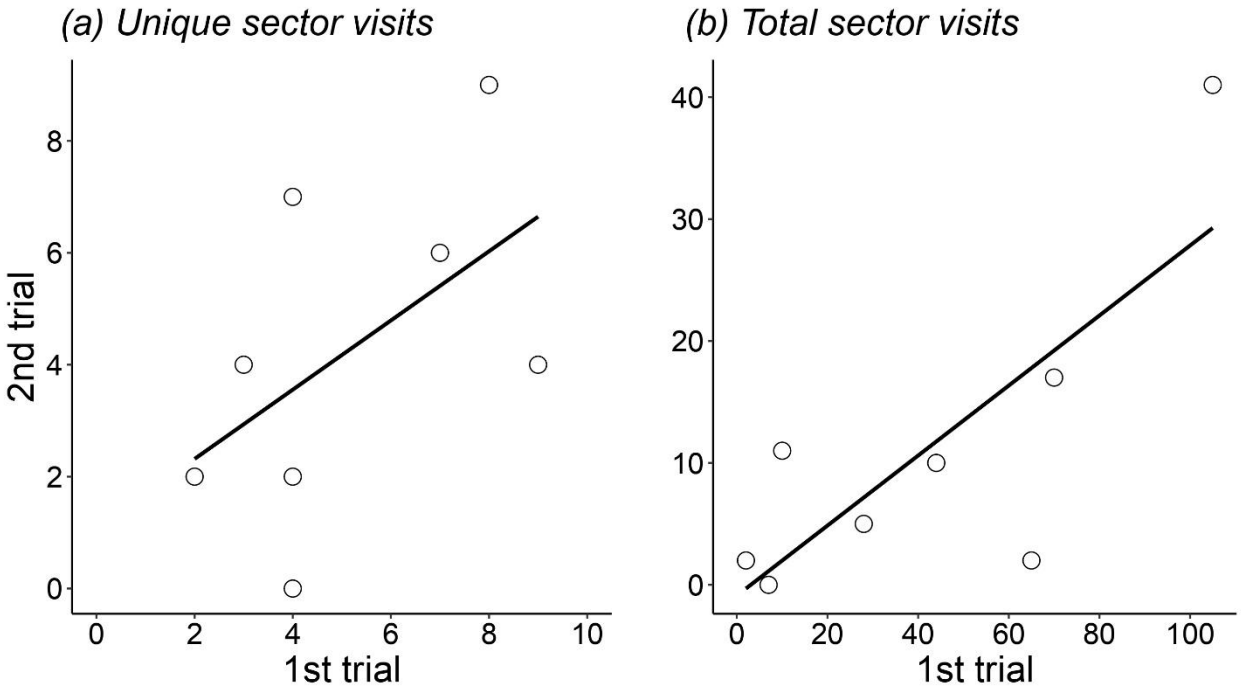


Figure 2. Correlation between the two exploration variables (total sector visits, unique sector visits) measured during the novel environment test. Species abbreviations: small ground finch (SGF), medium ground finch (MGF), small tree finch (STF), medium tree finch (MTF), Galápagos flycatcher (GFC), and yellow warbler (YW).

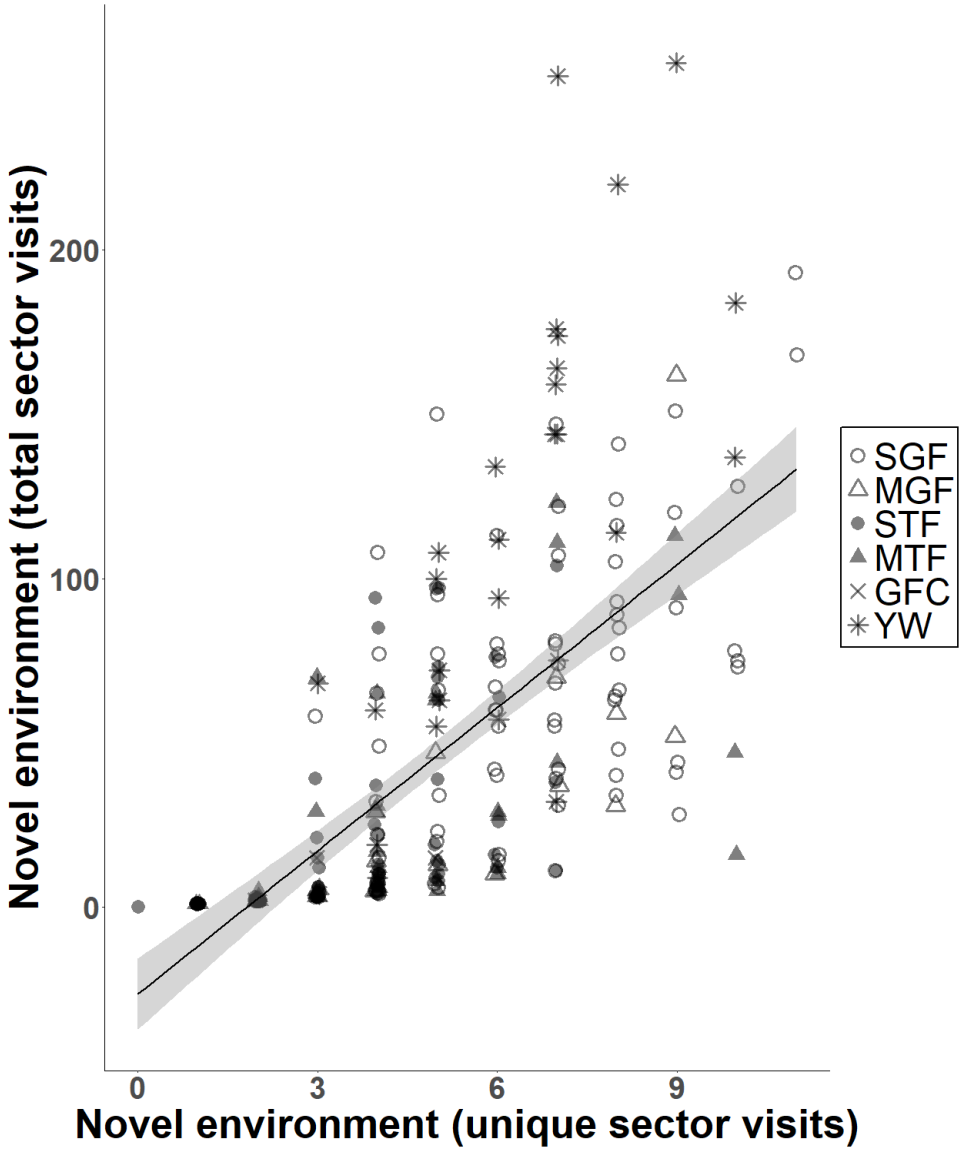


Figure 3. Correlation estimates (mean ± 95% CrI) between exploration during a novel environment test (PC_Exploration) and exploration during a novel object test (inverse latency to 10 m or latency to 3 m). For both models, higher PC_Exploration scores indicated that the individual visited more total and unique sectors visited during the novel environment test. (a) Higher values for inverse latency to 10 m indicated greater exploration, and (b) higher scores for latency to 3 m indicated lower exploration. Study species included in the models were small ground finch, small tree finch, medium tree finch, and yellow warbler. There were no Galápagos flycatchers or medium ground finches that took part in both exploration assays. In (a), the correlation estimates do not overlap with 0, indicating that among-individual differences in exploration during the novel environment test and the novel object test were significantly positively correlated.

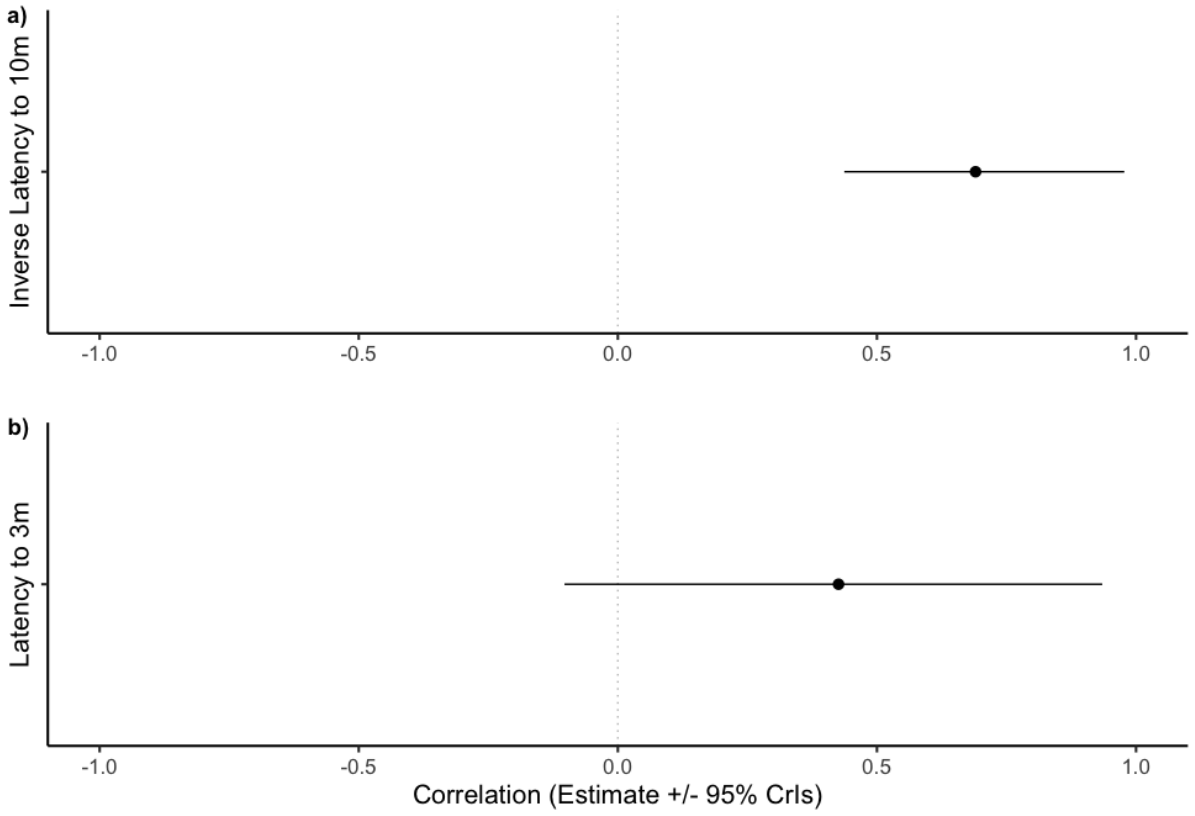
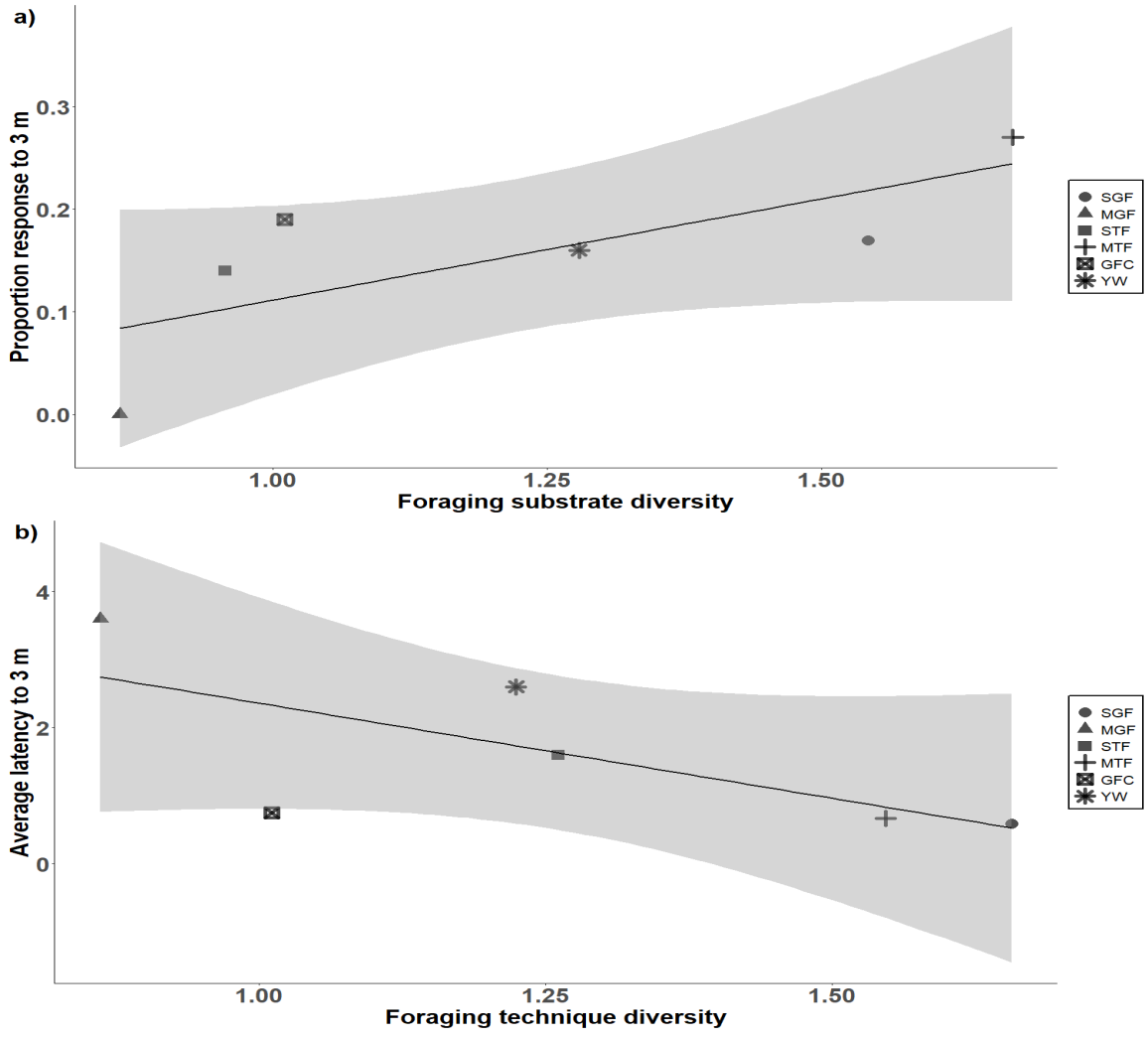


Figure 4. Species-level correlations between exploration behavior and diversity of foraging (Shannon diversity indices) in six landbird species on Floreana Island. (a) Positive correlation between foraging substrate diversity and proportion response to 3 m (the proportion of individuals per species that approached within 3 m of the novel object during the novel object test). (b) Negative correlation between foraging technique diversity and the mean latency to 3 m (mean latency to approach within 3 m of the novel object after entering the 10-m zone) during the novel object test. Species with more diverse foraging techniques approached the novel object faster than species with less diverse foraging techniques. Species abbreviations: small ground finch (SGF), medium ground finch (MGF), small tree finch (STF), medium tree finch (MTF), Galápagos flycatcher (GFC), and yellow warbler (YW).



Chapter 3

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Boldness is consistent over time and across contexts in five Darwin's finch species

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Abstract

Boldness can be measured as an animal's response to a non-novel risky situation, such as the presence of a predator. To be considered a personality trait, individual differences in boldness should be consistent both over time and across contexts. One common measure of boldness is flight initiation distance, which is considered a proxy for antipredator behaviour. Generally, flight initiation distance tends to be shorter in urban animals compared to non-urban animals, which may reflect either a plastic response to anthropogenic factors or selection for bolder phenotypes. In this study, we measured the boldness response of five Darwin's finch species on Floreana Island, Galápagos, using three behavioural assays across two contexts: 1) two rapid-assessment handling assays conducted during short-term captivity (554 back tests and processing tests); and 2) a field-based human approach assay to measure flight initiation distance (606 trials, including 77 color-banded individuals that also underwent handling assays). We calculated the consistency of boldness scores within and across assay types and then compared boldness between study sites with low and high levels of human activity. Our three measures of boldness showed high individual-level repeatability (back-test response R = 0.89, processing response R = 0.81, flight initiation distance R = 0.49), indicating that boldness is a personality trait in these species. Further, individuals that struggled more during our two handling assays also tolerated closer human approaches in the wild (back test R2 = -0.49, processing test R2 = -0.46), validating boldness as a consistent trait across contexts. As we predicted, birds from sites with higher levels of human activity were bolder (shorter flight initiation distances). We conclude that boldness is a measurable and ecologically relevant personality trait in Darwin's finches and that anthropogenic environments may shape behavioural traits in ways that could drive long-term evolutionary changes.

Keywords:

Anti-predator behaviour, handling assay, flight initiation distance, personality, repeatability, urbanization.

Introduction

Boldness is an animal's response to a non-novel, risky situation, such as the presence of a predator (Réale et al., 2007). This personality trait has been widely measured across multiple taxonomic groups, including fish (Moran et al., 2016), amphibians (Kelleher et al., 2018), reptiles (Carazo et al., 2014), mammals (Réale et al., 2000), and birds (David et al., 2012; Kerman et al., 2016). While bolder individuals may have higher reproductive success (Smith and Blumstein, 2008), boldness can come at a cost, as bolder birds are more vulnerable to predation due to their tendency to take greater risks (Lu et al., 2012). Although boldness has been shown to be repeatable at the individual level in a range of species (Hedrick and Kortet, 2012; Highcock and Carter, 2014; He et al., 2017; Bubac et al., 2018; Harris et al., 2020), we are just beginning to understand its potential role in ecological and demographic processes. For example, boldness is known to covary with life history factors such as age and sex (Patrick et al., 2013, 2017; Vakili et al., 2025) and may mediate trade-offs between exploration and exploitation during foraging (Patrick et al., 2017).

Among the most widely used measures of boldness is flight initiation distance (FID) (Blumstein, 2006; Díaz et al., 2013), which is the distance at which an animal moves away from an approaching threat, usually a human (Blumstein, 2006; Cooper and Frederick, 2007; Cooper and Blumstein, 2015). Individual differences in FID are repeatable over time in multiple taxa, including burrowing owls (*Athene cunicularia*) (Carrete and Tella, 2010), barn swallows (*Hirundo rustica*) (Møller, 2014), king penguins (*Aptenodytes patagonicus*) (Hammer et al., 2022), greylag geese (*Anser anser*) (Katsis et al., 2025), and feral horses (*Equus ferus caballus*) (Cabrera et al., 2017). Flight initiation distance has also been used to assess tolerance to anthropogenic disturbance (Blumstein and Fernández-Juricic, 2004; Merrall and

Evans, 2020; Díaz et al., 2013; Abou-Zeid et al., 2024). Because FID is widely studied, it can be used to measure individual responses to disturbance across environmental gradients, including high-risk versus low-risk habitats (Rodríguez-Prieto et al., 2011; Andersson et al., 2014; Shuai et al., 2024).

Boldness varies along urban gradients across species, with bolder animals more likely to inhabit urban environments (Blumstein, 2006; Samia et al., 2015; Nepali et al., 2024). For example, urban dark-eyed juncos (*Junco hyemalis thurberi*) were significantly bolder than their rural counterparts, suggesting that bolder phenotypes may be favoured by selection in urban habitats (Atwell et al., 2012). However, selection is not the only possible mechanism by which urban birds might display bolder phenotypes. Individual greylag geese reduced their FID when visiting a site with high levels of human foot traffic (Katsis et al., 2025), suggesting that boldness can be behaviourally plastic despite the consistency of among-individual differences. Alternatively, individuals with bolder phenotypes may choose to settle in areas with higher levels of human disturbance, while shyer individuals choose to settle in more rural sites (the personality-matching choice hypothesis; Edelaar et al., 2008). This has been reported in dunnocks (*Prunella modularis*), where individuals showed strong fidelity to their breeding territories, suggesting preferences to environments with specific features (Holtmann et al., 2017). Thus, FID offers an accessible method to better understand animal risk-taking in the context of human presence.

Darwin's finches (subfamily Geospizinae) in the Galápagos Islands provide an ideal model for studying behavioural and evolutionary changes due to their rapid adaptive radiation, which has produced 17 species over approximately 1.5 million years (Grant and Grant, 2014; Grant, 2017). These species exhibit marked interspecific differences

in beak size and shape, which are associated with foraging techniques and niche utilization (Lamichhaney et al., 2016, 2015; Kleindorfer et al., 2022). Previous studies have demonstrated that boldness during human handling differs across species and study sites (Katsis et al., 2024). Furthermore, finches from urban areas and islands without invasive predators exhibit shorter FIDs than those from rural areas and islands with invasive predators, respectively (Gotanda, 2020). Most recently, the population-level distribution of FIDs in Darwin's finches shifted following the onset of rodent removal and feral cat control on Floreana Island. In the absence of predators due to removal measures, Darwin's finches increased the proportion of extreme FID responses in the population (Common et al., 2025). While there is strong and consistent evidence that FID changes in predictable ways across a variety of ecological settings, we lack cross-context validation for boldness in Darwin's finches.

In this study of five Darwin's finch species on Floreana Island, we aimed to assess (1) the consistency of boldness behaviour both over time and across contexts, and (2) differences in boldness across sites that vary in levels of human activity, to better understand potential selection pathways related to boldness. To assess the consistency of boldness across contexts, we compared individuals' struggle responses during two types of human handling assay (back-test response and processing response) (Hall et al., 2015; Bilby et al., 2022; Katsis et al., 2024) with their flight initiation distance in response to an approaching human in the field (Cooper and Frederick, 2007; Gotanda, 2020). We predicted a positive association between our two handling assays during short-term captivity and that birds with high handling scores would have shorter FIDs in the field. We also predicted that finches would be bolder (i.e. would have shorter flight initiation distances) at sites with greater human presence (Gotanda, 2020). We measured boldness in Darwin's finches between 2020 – 2025, a period that includes,

in 2023, a major ecological change on the island following implementation of a massive invasive predator removal initiative (Island Conservation and Galapagos National Park Directorate, 2020).

Methods

Study site and species

This study was conducted on Floreana Island in the Galápagos Archipelago between January and April in 2020, 2022, 2023, 2024, and 2025 and between June and July in 2023. The highlands of the island were sampled at two sites: Cerro Pajas (-1.293479, -90.452012; low human impact) and Asilo de la Paz (-1.314003, -90.455512; high human impact). Both sites are characterized by moist evergreen vegetation dominated by *Scalesia pedunculata* (family Asteraceae), with adjacent agricultural land. The lowlands were also sampled at two sites: the first was the community of Puerto Velasco Ibarra (hereafter referred to as Town; -1.274698, -90.487202; high human impact) and the second was the arid landscape surrounding Puerto Velasco Ibarra, which forms part of the Galápagos National Park and is dominated by *Opuntia echios* (family Cactaceae) and *Bursera graveolens* (family Burseraceae) (hereafter Scrubland; -1.277433, -90.478093; low human impact). We quantified boldness in the five finch species extant on the island: the small ground finch (SGF; *Geospiza fuliginosa*), medium ground finch (MGF; *G. fortis*), common cactus finch (CF; *G. scandens*), small tree finch (STF; *Camarhynchus parvulus*), and medium tree finch (MTF; *C. pauper*). The latter is an island endemic species restricted to the highlands of Floreana Island and categorized as Critically Endangered by the International Union for Conservation of Nature (Freile et al., 2019). All study sites are commonly used by Darwin's finches for foraging and nesting, although some species show distinct habitat preferences: the

cactus finch and medium ground finch occur primarily in the lowlands and the medium tree finch mostly occurs in the highlands (Kleindorfer et al., 2021, 2022).

Levels of human activity

To assess the influence of human activity on finch boldness, we followed the site categorizations used in previous studies on the archipelago (Hohl et al., 2025), which counted the number of vehicles and humans per hour at each site. In the lowlands, the Town site received 12.5 vehicles and 60 humans per hour, while the Scrubland site received only 0.12 vehicles and 0 humans per hour. In the highlands, Asilo de la Paz received 7 vehicles and 58 humans per hour, while Cerro Pajas received 0 vehicles and 0 humans per hour (Hohl et al., 2025). Based on those calculations, we considered Town (lowlands) and Asilo de la Paz (highlands) as sites of high human activity, and Scrubland (lowlands) and Cerro Pajas (highlands) as sites of low human activity.

Boldness of wild-caught birds: back test and processing test

During the 2020, 2022, and 2025 field seasons, we used mist-nets to capture Darwin's finches and banded them with a numbered aluminum band and a unique combination of between one to three colour-bands. Birds were sexed based on their plumage colouration and/or the presence of an active brood patch. In these Darwin's finch species, males become increasingly black-headed (in tree finches) or black-bodied (in ground and cactus finches) with each annual moult across their first six years (Price, 1984; Kleindorfer, 2007; Langton and Kleindorfer, 2019; Huge et al., 2024); hence, only yearling males can be confused with females. Because we collected data during the breeding season, we provisionally scored any bird with a brood patch as female and any grey-brown bird without a brood patch as a yearling male, with many individuals later verified in the field based on their singing or breeding behaviour. At

the time of capture, birds were placed in cotton bags and brought to the banding station. Once the bird was removed from the bag, we measured its boldness using two handling assays. First, the bird was held in the bander's grip and then reclined on its back, with its legs free and with the handler's thumb gently placed on its chest. Over the next 30 secs, we counted the number of times the bird struggled, defined as a continuous bout of wriggling or leg-kicking (*back-test response*) (Hall et al., 2015; Bilby et al., 2022; Katsis et al., 2024). The bird was then banded, after which we recorded its response to five standardized measurement procedures (*processing response*). 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. For each morphological measure, we noted whether or not the bird struggled, thereby generating a score between 0 (subject did not struggle during any measurement) to 5 (subject struggled during all five measurements) (Katsis et al., 2024). For each handling assay, we conducted 554 trials using 516 individuals across our five study species (trial per species: SGF = 218, MGF = 32, CF = 33, STF = 165, MTF = 106) (Tables 1, S1). Of these individuals, 7% (N = 41) were captured and assayed multiple times (range 2–4 trials). When birds were tested in the cage assay, they were released at their site of capture, typically within 60 minutes of capture.

Boldness in the wild: flight initiation distance (FID)

Flight initiation distance was opportunistically measured in wild birds that were observed foraging on the ground or up to 0.3 m high, using an approaching human observer as the potential predator stimulus. The bird could be alone or part of a foraging group; if the latter, we randomly selected a focal bird, usually at the periphery of the group. After selecting a focal bird, the observer began to approach the bird from

a starting distance of 10 m at a constant speed (~1 m/s). Once the focal bird moved away by hopping or flying, the observer estimated the distance (in m) between themselves and the location from which the bird began to flee. To standardize our estimates of flight initiation distance, all observers (nine people across the study period) had previously practiced distance estimation using laser pointers and tape measures and walking speed using headphones and a digital metronome. We conducted 606 human approach trials using 542 individuals from our five study species (trials per species: SGF = 420, MGF = 20, CF = 18, STF = 90, MTF = 58) across three years (2023 = 134, 2024 = 241, 2025 = 231) (Tables 1, S1). For FID, we have 461 observations for unbanded individuals and repeated measures are available for 25 individuals, each of which was scored two or more times (range: 2–11).

Rodent and feral cat eradication

In 2023, between October and December, an island-wide rodent and feral cat removal project was implemented in Floreana Island, led by the Galápagos National Park in collaboration with partner institutions (Island Conservation and Galapagos National Park Directorate, 2020). The poison (cereal-based bait containing brodifacoum for rodents; meat-based bait containing para-aminopropiophenone for cats) was deployed both by hand-baiting and aerial distribution using a helicopter (Floreana Vuelve a Florecer, https://floreanavuelveaflorecer.ec/index_en.php). As a mitigation measure against non-target poisoning, 65 short-eared owls were caught and kept in captivity on Santa Cruz Island (Rodríguez and Fessl, 2016; Tanty-Lamothe, 2024). This study compares among-individual consistency in boldness scores before and after these predator removals, providing a rare opportunity to assess personality stability during a period of major ecological change.

Statistical analysis

We performed statistical analyses using the software R version 4.3.1 (R Core Team, 2023). Trivariate generalized linear mixed models (GLMM) were implemented using the package 'MCMCglmm' version 2.35 (Hadfield, 2010) and results are reported as estimate ± SE with 95% credible intervals (CrI) (Bates et al., 2015). Figures were created using the package 'ggplot2' version 3.5.1 (Wickham, 2009).

Repeatability of boldness and correlation between behavioural traits

To estimate the adjusted repeatability of our three boldness variables and their among-individual correlations, we used a trivariate Bayesian GLMM with three response variables: back-test response, processing response, and FID. Analyzing all three traits simultaneously using a multivariate framework allowed us to account for shared variance amongst the three response variables (Houslay and Wilson, 2017). We modelled back-test response and processing response as Poisson-distributed count data and FID as a continuous Gaussian variable. Using a Poisson distribution for the handling response variables allowed direct modeling of skewed count data without requiring transformation, while a Gaussian distribution was appropriate for the continuous FID data after standardization (using the *scale* function in the package 'stats') to improve convergence and ensure comparability across traits, adding stability to the model. To account for repeated observations from the same individual, we included Bird ID (the bird's unique band number for banded birds or a unique alphanumeric code for unbanded birds) as a random effect in the model. As assays in different contexts were conducted on different days, we set within-individual covariances to zero (i.e. rcov = ~idh(trait):units, Scenario 4 in Table 2 of Dingemanse and Dochtermann (2013)). The model was run for 2.5×10^5 iterations, with a burn-in of 150,000 and thinning interval of 1,000. The prior followed a moderately informative

(nu = 2.003) inverse-Wishart distribution. Model fit was evaluated using the deviance information criterion (DIC) and fixed effects were summarized with posterior means, 95% credible intervals, and Bayesian p-values (pMCMC). We assessed MCMC convergence using a combination of visual and formal diagnostics. Trace plots of all parameters were visually inspected for stationarity and mixing. Autocorrelation was < 0.1 for each run, calculated using the function 'autocorr'. We used Geweke's diagnostic to compare early and late segments of the chain and ensure that the length of the burn-in period was sufficient. Heidelberger and Welch's stationarity and half-width tests were also applied, with all chains passing at a 0.05 significance level. The Gelman-Rubin statistic was approximately 1 for all models. Effective sample sizes (ESS) exceeded 2,000 for all parameters. Overdispersion and zero-inflation were not evident for the Poisson-modeled traits based on residual inspection and posterior variance structure.

We calculated the adjusted repeatability of each trait from the posterior distributions of the among-individual (Bird ID) and residual variance components of each trait (Houslay and Wilson, 2017). We assessed the statistical significance and uncertainty of repeatability estimates using 95% highest posterior density (HPD) intervals obtained using the *HPDinterval* function in the 'coda' package version 0.19.4.1 (Plummer et al., 2006). Individual-level repeatability was considered statistically significant when the 95% highest posterior density interval did not approach zero (i.e., > 0.01). We calculated among-individual correlations between behavioural traits for 77 color-banded birds for which we had back-test response, processing response, and FID data (SGF = 49, MGF = 3, CF = 4, STF = 12, MTF = 9), resulting in a total of 279 combined measurements (back test = 137, processing test = 137, FID = 142). We estimated among-individual correlations between traits by extracting posterior

covariances for each pair of traits and calculating the product of the square roots of their respective variances. This standardization scales covariances to the range of –1 to 1 and allows meaningful interpretation of the direction and strength of associations between traits (Houslay and Wilson, 2017). We computed posterior distributions of each correlation from the model's variance-covariance (VCV) matrix and 95% credible intervals using the *HPDinterval* function. Correlations were considered statistically supported when the credible intervals did not cross zero. We conducted post-hoc pairwise comparisons between species for each behavioural trait using posterior samples from the model. For each species pair and trait, we calculated the difference in posterior estimates and derived the mean difference, along with the 95% credible interval; statistical significance for each comparison was assessed using the Bayesian p-value (pMCMC), calculated as twice the smaller tail probability of the difference distribution crossing zero.

Effects of species and ecological variables on boldness

We included habitat type (lowlands, highlands), level of human activity (low, high), species (SGF, MGF, CF, STF, MTF), and predator removal status (pre-removal, post-removal) as fixed effects in the trivariate model. Fixed effects were summarized from the posterior distributions using posterior means and 95% credible intervals. Significance of fixed effects was inferred when the 95% credible intervals did not cross zero.

To assess whether the cross-context consistency of boldness differed in the short-term versus long-term, we also estimated among-individual correlations between traits in two separate subsets. The first subset included only individuals whose handling assays and human approach assay were conducted in the same year (2025, N = 25), while the

second subset included individuals whose handling assays and approach trials occurred in different years (2020 – 2025, N = 49). For each subset, we fitted a trivariate Bayesian GLMM, using the same variables and parameters as in the previously described model. However, the within-year subset model was simpler, including only human activity levels and species as fixed effects, because all observations were conducted in the highlands and therefore involved only three of the five species present on the island (SGF, STF, MTF).

Results

a) Repeatability of boldness over time

Individual differences in response to handling were significantly repeatable for both the back test (adjusted R = 0.89, 95% CrI = 0.78 – 0.97) and processing test (adjusted R = 0.81, 95% CrI = 0.70 – 0.90) (Figure 1). Boldness in the field, as measured by flight initiation distance, was also significantly repeatable (adjusted R = 0.49, 95% CrI = 0.35 – 0.63) (Figure 1).

b) Consistency of boldness across contexts

There were significant among-individual correlations between all three measures of boldness (Table 2; Figures 2, S1). First, there was a strong positive correlation between back-test response and processing response (R^2 = 0.81, 95% CrI = 0.71 – 0.90) (Figure S1), meaning that birds that struggled more during the 30-sec back test also struggled during more measurement procedures. There were moderate negative correlations between flight initiation distance and both back-test response (R^2 = -0.49, 95% CrI = -0.72 – -0.22; Figure 2) and processing response (R^2 = -0.46, 95% CrI = -0.71 – -0.19; Figure 2), indicating that individuals that tolerated closer human approaches in the

wild also struggled more during handling. When we analysed two subsets separately to disentangle short- and long-term associations, this significant negative correlation across contexts (handling assays vs FID) was maintained only when considering individuals whose handling responses and FID were measured in different years (N = 49; back test: R^2 = -0.65, 95% CrI = -0.90 – -0.37; processing test: R^2 = -0.59, 95% CrI = -0.86 – -0.25) (Figure S5), but not when considering individuals that undertook all three assays in 2025 (N = 29; back test: R^2 = -0.45, 95% CrI = -0.87 – 0.06; processing test: R^2 = -0.39, 95% CrI = -0.81 – 0.13) (Figure S4) .

c) Factors influencing boldness

Boldness during handling was not influenced by either habitat type or human activity level (Figures 3, 4). Flight initiation distance did not differ between habitat types, but was significantly predicted by human activity level (estimate = 0.42, 95% CrI = 0.24 – 0.59, *p*MCMC < 0.001), with bolder birds (i.e., those with shorter FID) found at sites with higher human activity level (Table 3; Figures 3, 4). We observed a shift in boldness levels following the beginning of the predator removal campaign on Floreana Island, with birds struggling more during handling during the pre-removal period (2020–2023) compared to the post-removal period (2024–2025) (back test: estimate = -2.29, 95% CrI = -2.77 – -1.82, *p*MCMC < 0.001; processing test: estimate = -0.42, 95% CrI = -0.62 – -0.20, *p*MCMC < 0.001). However, flight initiation distances did not differ between the pre- and post-removal periods (estimate = -0.03, 95% CrI = -0.23 – 0.18, *p*MCMC = 0.79) (Table 3; Figure 5). Post-hoc pairwise comparisons showed significant species differences in back-test response, processing response, and flight initiation distance (see Table S2, Figures S2, S3).

Discussion

In this study, we assessed the consistency of individual differences in boldness in five Darwin's finch species on Floreana Island, Galápagos. We quantified two measures of boldness during human handling (back-test response and processing response) and one measure in the field in response to an approaching human (flight initiation distance). Individual differences in boldness were consistent both over time and across contexts, with individuals that moved more during handling also tolerating closer human approaches in the field, even when trials were separated by one to five years. In addition, we compared boldness patterns at the landscape scale in relation to levels of human activity, finding that birds were bolder (i.e. had shorter FIDs) at sites with higher levels of human activity. Our results support the idea of boldness as a personality trait in Darwin's finches and suggest that human disturbance can influence individual behavioural responses on the Galápagos Islands.

The high adjusted repeatability estimates for all three boldness variables, along with significant among-individual correlations between these variables, support the classification of boldness as a personality trait in Darwin's finches (Réale et al., 2007; David et al., 2012; Kerman et al., 2016). Boldness has previously been measured in wild (Dammhahn and Almeling, 2012; Romero-Vidal et al., 2023) and captive contexts (Dammhahn et al., 2022; Eccard et al., 2022; Stiegler et al., 2022); however, few studies have validated behavioural measures across both captive and field settings (Petelle et al., 2013; West et al., 2019). Our study integrates short-term captivity tests with field-based behavioural assays, making a valuable contribution towards validating personality axes across contexts. Our previous work on Darwin's finches has shown comparable patterns for other behavioural traits: individuals that spent more time near their mirror-image during a mirror stimulation test also reacted more

strongly towards conspecific playback in their territory (García-Loor et al., 2024) and more exploratory individuals during a novel environment test were also quicker to approach a novel object in the field (García-Loor et al., 2025). In each of these cases, traits measured during short-term captivity were significantly correlated with corresponding behaviours in the wild.

The consistency of individuals' responses across contexts was maintained even with multi-year intervals (up to five years) between individuals' handling and approach assays, supporting the long-term stability of this relationship. Surprisingly, however, this correlation was not significant when considering only individuals tested within the same year, with the credible intervals narrowly overlapping zero. This inconsistency may be related to the fact that this same-year subset only included individuals tested in 2025, after a major predation removal campaign on the island. In 2023, the Galápagos National Park Directorate conducted an island-wide removal of invasive mammals via aerial rodenticide application. To mitigate secondary poisoning risk, 65 Galápagos short-eared owls were captured and held in captivity from 2023, further reducing predation pressure on Darwin's finches during 2024–2025 (Island Conservation and Galapagos National Park Directorate, 2020). Darwin's finches can live 17–18 years (Langton and Kleindorfer, 2019; Common et al., in review), so many individuals in our dataset experienced both pre- and post-predator removal conditions. Following the predator removal, we observed a marked shift in finches' mean back-test and processing responses, without a corresponding change in mean FID (see also Common et al., 2025). This suggests that the large-scale ecological intervention may have weakened the relationship between handling response and flight initiation distance. This is consistent with the 'adaptive' hypothesis for behavioural syndromes, which proposes that correlated behavioural traits are

independently plastic to environmental factors, such as predation pressure (Bell and Stamps, 2004; Dhellemmes et al., 2020; Dingemanse et al., 2007), and may only correlate when favoured by ecological conditions (Sih et al., 2004; Smith and Blumstein, 2012). Handling tests may capture a different component of the boldness axis than FID—perhaps akin to tonic immobility—whereby a reduced handling response reflects a freeze reaction in individuals without regular predator experience. Alternatively, mist-net captures during the years after predator removal may have sampled a different subset of the population, potentially including a greater proportion of low-response individuals, even if the full range of boldness phenotypes persisted in the population.

Finches that hatched in 2024 and 2025, after island-wide predator removal, developed in a predator-reduced environment. Some studies in other taxa have found that younger individuals can be bolder than older ones (Patrick et al., 2013; Starling et al., 2013), although the more common pattern is increased boldness with age (Møller, 2014; Holtmann et al., 2017; Bubac et al., 2018), which could arise if bolder individuals have a survival advantage. Future research should aim to understand why finches had reduced responses to handling after predator removal compared with before predator removal, and interrogate how birds perceive and respond to risk in relation to changes in their "landscape of fear" (Dammhahn et al., 2022). Further research is needed to determine whether finches can differentiate between types and levels of risk, and to explore the ecological and evolutionary implications of such perception as a selective force shaping behavioural phenotypes.

Boldness in Darwin's finches varies across species and ecological contexts, reflecting patterns found in other taxa and linked to differences in foraging risk (Dammhahn and

Almeling, 2012; Dammhahn et al., 2022). Across species, ground finches (cactus finch, small ground finch, medium ground finch) were consistently bolder than tree finches (small tree finch, medium tree finch) in both handling assays (back test and processing test; Table S2). These species differences between the two main Darwin's finch genera (ground finches and tree finches), suggests that boldness may be shaped by ecological factors such as foraging risk—the different risk perception of birds that forage on the ground versus those that forage in trees, where increased predation risk in the open may select for greater risk tolerance (Dammhahn and Almeling, 2012; Lu et al., 2012). Future research could test whether boldness in Darwin's finches is associated with increased ground-foraging now that rodents and other invasive mammals have been significantly reduced on Floreana Island. The availability of safer foraging habitats may alter species coexistence and/or shift the distribution of boldness within species, potentially selecting for different personality types under predator-reduced conditions (Common et al., in review).

These interspecific patterns may partly reflect body size differences: cactus finches (~20.3 g), among the largest finch species on Floreana, also showed the shortest FIDs and were significantly bolder than other finches (Table S2). Small ground finches (~14.4 g) were also significantly bolder and slightly larger than small tree finches (~12.7 g) (Table S2). However, our results do not reveal a consistent relationship between species-level body size and FID. Among tree finches, larger-bodied medium tree finches had shorter FIDs than small tree finches, whereas among ground finches, the smaller-bodied small ground finches had shorter FIDs than medium ground finches. Future research could test for within-species associations between body size and boldness, but our current data do not support this as the primary explanation for individual or habitat-level differences. Instead, ecological factors may be important:

cactus and ground finches tend to forage in more open and exposed areas and may, therefore, take greater risks during foraging (Lu et al., 2012; Kleindorfer et al., 2022).

Several studies have shown that urban birds, or birds exposed to higher levels of human impact, tend to be bolder (i.e. have shorter FIDs) than their counterparts in rural areas or areas with lower human impact (Blumstein and Fernández-Juricic, 2004; Merrall and Evans, 2020; Abou-Zeid et al., 2024). Similarly, we found that finches had shorter FIDs at the two sites with higher levels of human activity, in both the highlands and lowlands, consistent with findings in dark-eyed juncos (Atwell et al., 2012), white-rumped shamas (Teo et al., 2024), greylag geese (Katsis et al., 2025) and Darwin's small ground finches (Gotanda, 2020). Conversely, our two measures of boldness scored during handling (back-test response and processing response) did not vary with levels of human activity – again suggesting that handling assays may measure a different component of the overall boldness response compared with FID. Importantly, no individuals in our study were tested in both high- and low-human activity areas, which precludes us from assessing whether differences between sites are due to behavioural plasticity, habitat choice, or differential selection for boldness phenotypes. Across 13 breeding seasons between 2004 and 2025, our long-term research program on Floreana Island captured 1917 individual Darwin's finches. Of 167 recaptured birds, only one individual (a medium tree finch) was captured at multiple sites—at Asilo de la Paz in 2020 and Cerro Pajas in 2022—suggesting strong site fidelity in these species.

Conclusion

Our study demonstrates, first, that boldness represents a personality trait in Darwin's finches, with individual differences consistent both over time and across contexts, validating flight initiation distance estimation as a reliable proxy for boldness when handling assays are not feasible (e.g. when animals are large or dangerous, or when capturing individuals is difficult). Second, our findings highlight the role of anthropogenic environments in shaping behavioural traits: birds in areas of higher human activity exhibited bolder behaviours, as indicated by shorter FIDs, suggesting that variation in individually consistent behavioural traits may influence species' ecological interactions and adaptive responses to environmental change, including urbanization. Third, following an island-wide predator removal campaign, we observed significantly lower handling scores in Darwin's finches at the time of mist-netting, but did not measure a change in FID at the population level. This shift in population-level boldness may be due to demographic differences arising from the predator removal: during the predator-reduced 2025 season, we mist-netted a larger proportion of yearling males with limited predator experience (Common et al., in review), a factor which may have contributed to the lower handling response scores. Further research is needed to explore ontogenic mechanisms underlying individual behavioural differences in boldness, interrogate the role of plasticity versus personality-matching habitat in choice, measure risk perception across behavioural assays, and examine the potential evolutionary implications of these patterns within and across species.

Table 1. Annual sample sizes for boldness variables recorded during handling (back-test response and processing response; in 2020, 2022, and 2025) and in response to a human approach (flight initiation distance; in 2023, 2024, and 2025). Species abbreviations: small ground finch (SGF), medium ground finch (MGF), cactus finch (CF), small tree finch (STF), and medium tree finch (MTF).

Assay type	Year	Species				
		SGF	MGF	CF	STF	MTF
Handling assays*	2020	152	25	8	66	24
	2022	15	2	0	23	23
	2025	51	5	25	76	59
FID	2023	97	20	8	5	4
	2024	193	0	10	25	13
	2025	130	0	0	60	41

** The two handling assays (back test and processing test) had identical sample sizes*

Table 2. Output from a trivariate GLMM showing among-individual variances (diagonals, in bold), correlations between traits at the individual level (above diagonals), and covariances between traits at the individual level (below diagonals) for three boldness traits (back-test response, processing response, and FID) measured in five Darwin's finch species (small ground finch, medium ground finch, cactus finch, small tree finch and medium tree finch). Lower and upper bounds of 95% credible intervals are shown in parentheses.

	Back test	**Processing test**	**FID**
Back test	**2.01 (1.41, 2.74)**	0.81 (0.65, 0.91)	−0.49 (−0.76, −0.18)
Processing test	0.67 (0.46, 0.89)	**0.34 (0.22, 0.47)**	−0.47 (−0.69, −0.29)
FID	−0.49 (−0.76, −0.18)	−0.19 (−0.30, −0.06)	**0.48 (0.33, 0.65)**

Table 3. Output from a trivariate GLMM testing the effects of habitat (highlands as reference category), level of human activity (high as reference category), species, and predator removal status (pre as reference category) on our three measured boldness variables (back-test response, processing response, and flight initiation distance). Species abbreviations: cactus finch (CF as reference category), small ground finch (SGF), medium ground finch (MGF), small tree finch (STF) and medium tree finch (MTF).

	Estimate	**SE**	**Test statistic***	***P***
a) Back test				
Intercept	0.96	0.58	1.66	0.107
Habitat [lowlands]	−0.57	0.33	−1.74	0.079
Human Activity Level [low]	−0.13	0.21	−0.63	0.532
Species [SGF]	−1.49	0.52	−2.87	**0.006**
Species [MGF]	−0.78	0.54	−1.44	0.153
Species [SGF]	−1.38	0.55	−2.52	**0.009**
Species [MTF]	−0.79	0.57	−1.38	0.159
Predator Removal Status [post]	−2.29	0.24	−9.54	**< 0.001**
b) Processing test				
Intercept	1.2	0.27	4.46	**< 0.001**
Habitat [lowlands]	−0.19	0.18	−1.06	0.240
Human Activity Level [low]	0.01	0.1	0.1	0.923
Species [SGF]	−0.75	0.23	−3.26	**0.002**
Species [MGF]	−0.46	0.26	−1.79	0.065
Species [SGF]	−1.34	0.25	−5.36	**< 0.001**
Species [MTF]	−1.10	0.27	−4.07	**< 0.001**
Predator Removal Status [post]	−0.42	0.11	−3.82	**< 0.001**
c) Flight initiation distance				
Intercept	−0.84	0.27	−3.11	**0.002**

	Estimate	SE	Test statistic*	*P*
Habitat [lowlands]	−0.02	0.11	−0.15	0.900
Human Activity Level [low]	0.42	0.09	4.67	**< 0.001**
Species [SGF]	0.65	0.25	2.6	**0.009**
Species [MGF]	0.82	0.33	2.48	**0.014**
Species [SGF]	0.91	0.28	3.25	**0.003**
Species [MTF]	0.88	0.29	3.03	**0.004**
Predator Removal Status [post]	−0.03	0.1	−0.30	0.791

** Test statistic: either z-value for Poisson distributions or t-value for Gaussian distributions.*

Figure 1. Adjusted repeatability (estimate ± 95% CrIs) for three boldness traits (back-test response, processing response, and FID (flight initiation distance) measured in Darwin's finches on Floreana Island. Traits are significantly repeatable when 95% credible intervals do not approach zero.

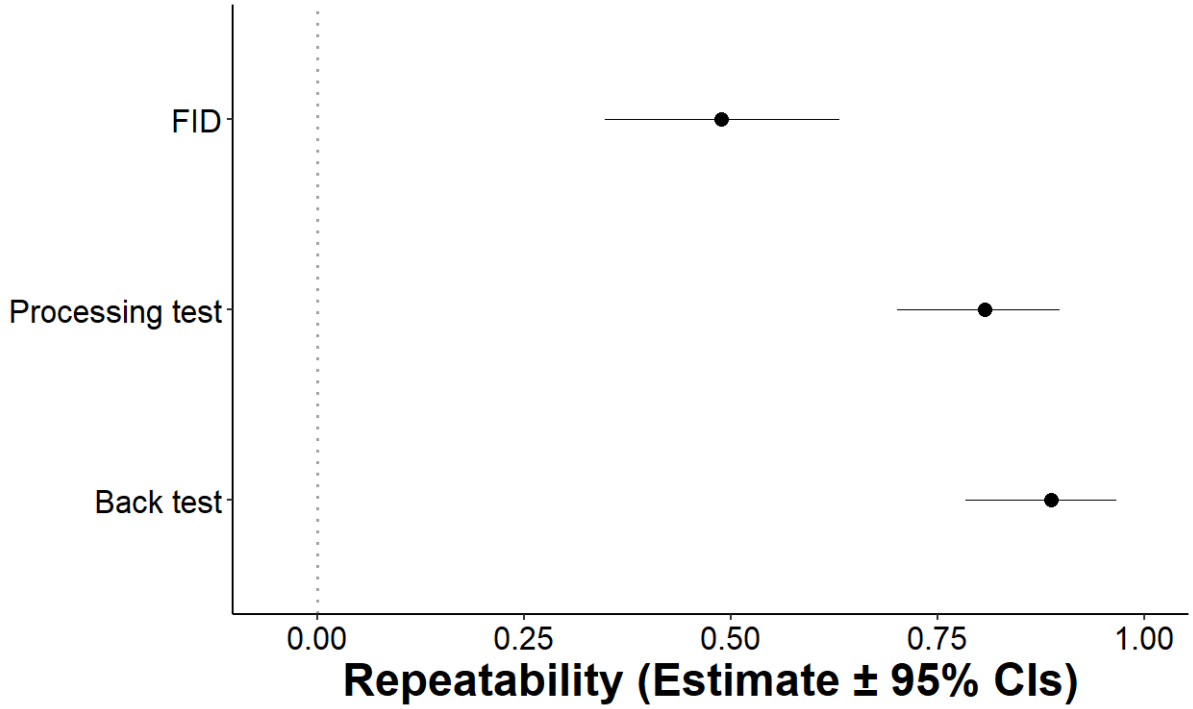


Figure 2. The among-individual correlation between individuals' response to handling (boldness scored during short-term captivity) and flight initiation distance (FID, boldness scored in free-flying birds). a) Individuals that struggled more during the back test tolerated closer human approaches in the field, and b) Individuals that struggled during more processing procedures also tolerated closer human approaches in the field. Species abbreviations: small ground finch (SGF), medium ground finch (MGF), cactus finch (CF), small tree finch (STF) and medium tree finch (MTF).

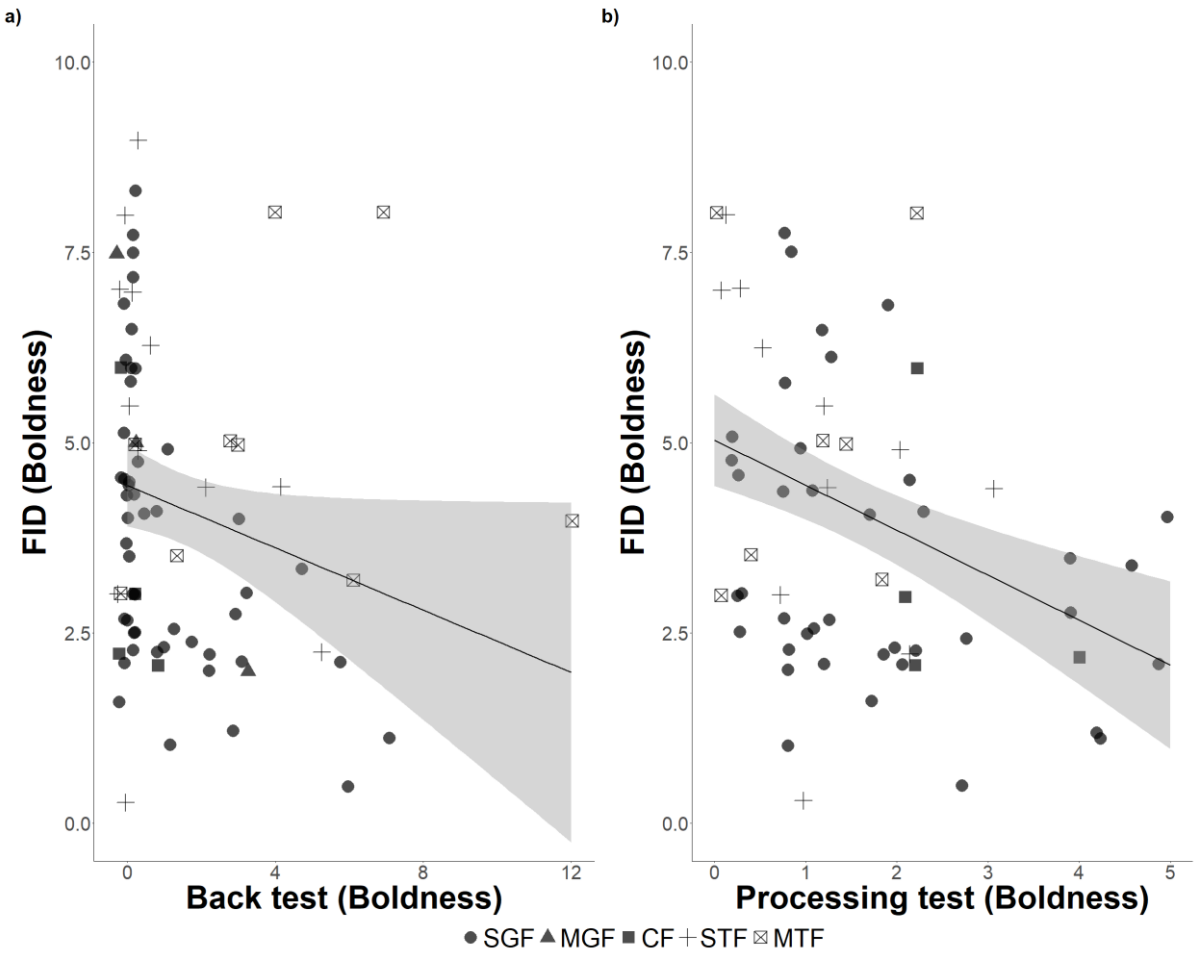


Figure 3. Differences in boldness among birds from the highland (dark grey) and lowland (light grey) habitats. Violin plots show mean ± SE values for each variable. Panels a) and b) present responses to handling assays during short-term captivity, while panel c) presents flight initiation distance in response to a human approach in the field. Individuals were interpreted as being bolder if they moved more during the back test and processing test and had shorter flight initiation distance (FID).

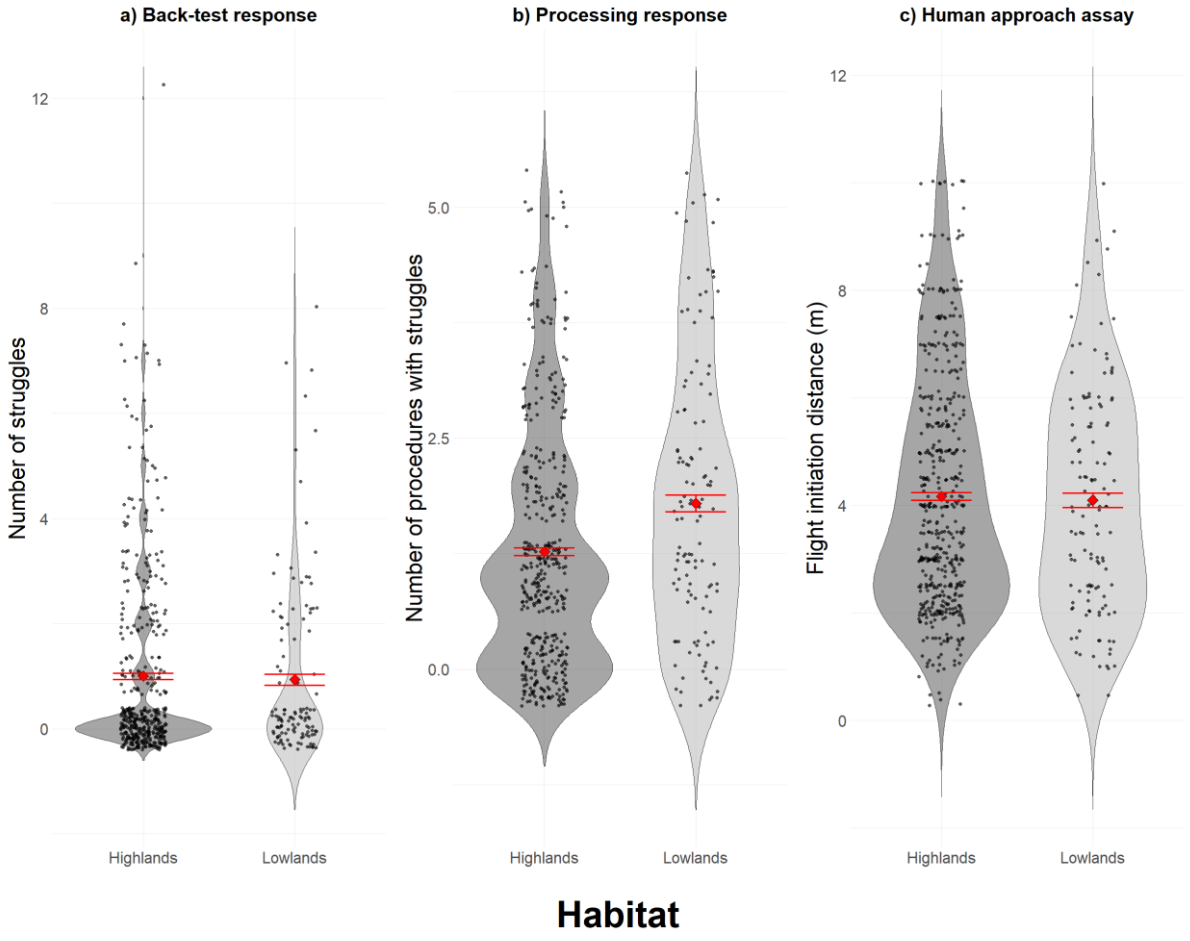


Figure 4. Differences in boldness between individuals at sites with low (dark grey) and high (light grey) human activity. Panels a) and b) present responses to handling assays during short-term captivity, while panel c) presents flight initiation distance in response to a human approach in the field. Violin plots show mean ± SE values for each behavioural variable. Individuals were interpreted as being bolder if they moved more during the back test and processing test and had shorter flight initiation distance (FID). An asterisk indicates the significant difference in boldness between areas with high and low human impact.

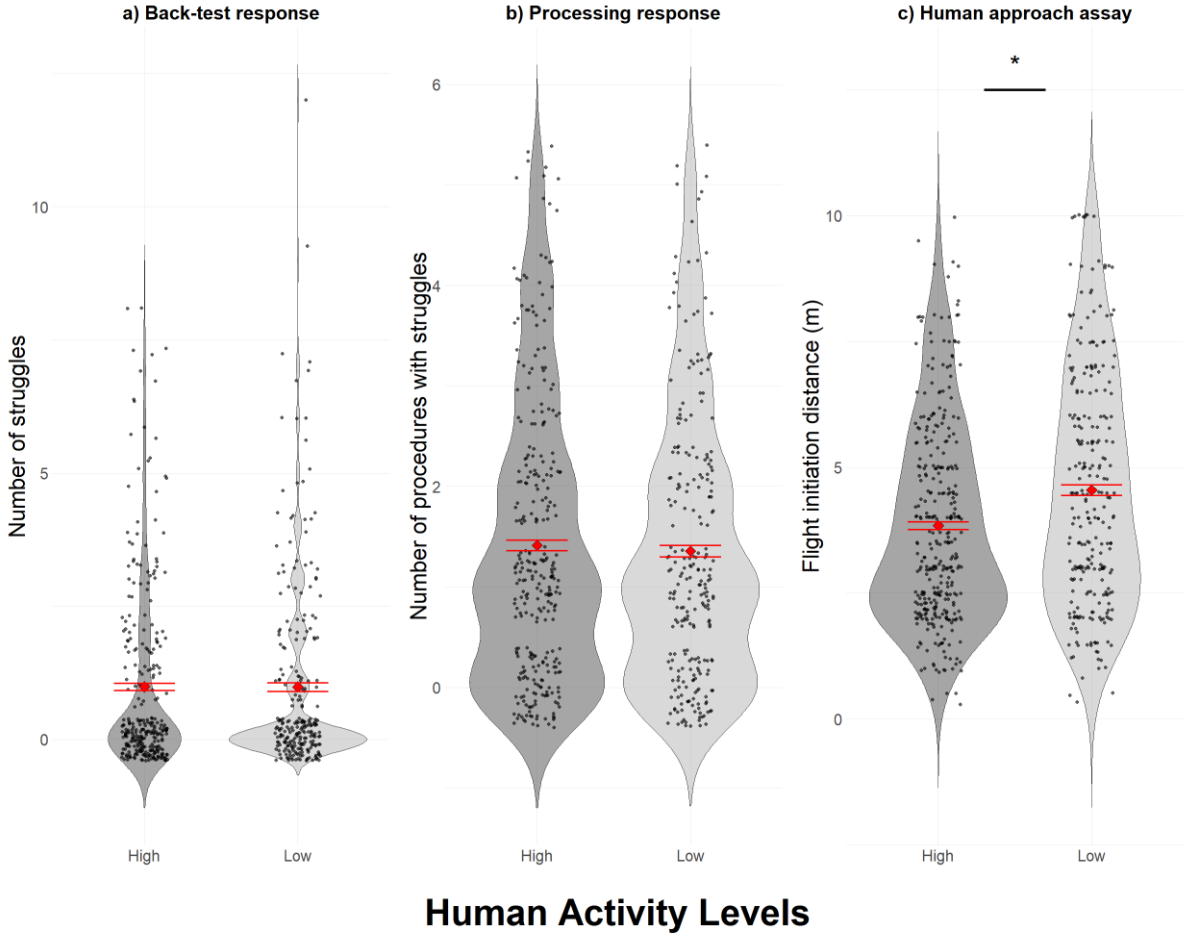
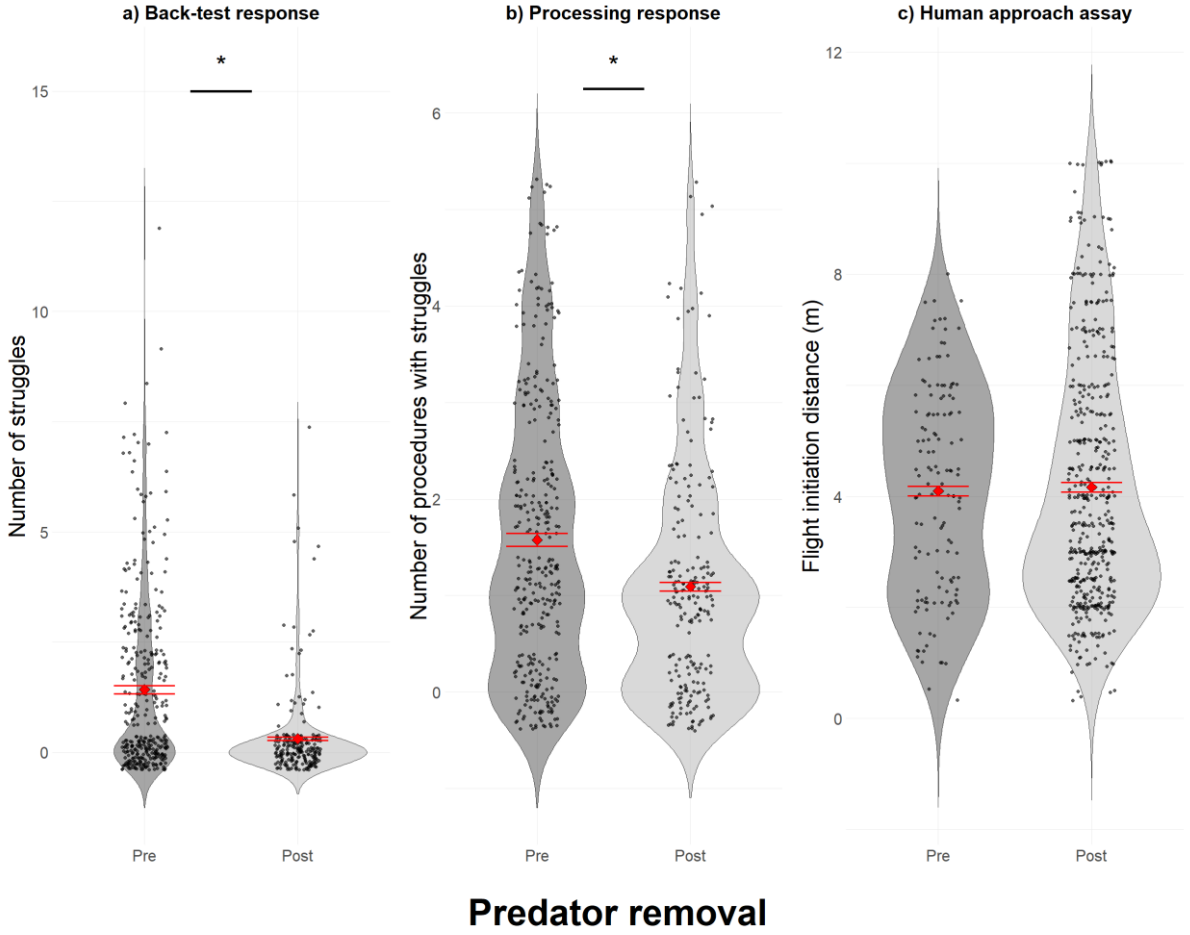


Figure 5. Boldness scores in Darwin's finches measured before (dark grey) and after (light grey) an island-wide mammal removal program. Boldness was measured in response to human handling (back-test response and processing response) and an approaching human (flight initiation distance). Panels a) and b) present responses to handling during short-term captivity, while panel c) presents flight initiation distance in response to a human approach in the field. Violin plots show mean ± SE values for each variable. Asterisks indicate a significant difference in boldness between the pre- and post-predator removal periods.



General Discussion

In this dissertation, I first aimed to validate three behavioral traits across contexts, comparing assays conducted in short-term captivity with those performed on free-flying individuals in the wild. In Chapter 1, I did not calculate repeatability within the same context, as I lacked repeated tests over time, which prevented me from calculating the temporal consistency of exploration and aggressiveness. Instead, I validated traits via cross-context correlations (e.g., mirror vs. playback) and found a positive correlation between individuals' responses to a mirror test in captivity and their responses to a conspecific intruder simulation. In Chapter 2, exploration scores were correlated between a novel arena test and a novel object test, and repeatability analyses further confirmed that exploration behavior was temporally consistent across years ($R = 0.37–0.80$). In Chapter 3, boldness showed high individual-level repeatability in both handling and field assays (back test $R = 0.89$, processing test $R = 0.81$, flight initiation distance $R = 0.49$), with significant correlations between handling responses and human approach distance maintained across multiple years, confirming that boldness is a temporally stable and cross-contextually consistent personality trait in Darwin's finches. In a follow-up field season in 2024, Katsis et al. (2025) conducted multiple playback experiments to test for aggressiveness and found high repeatability ($R = 0.60$) within and across breeding stages. The results overall support the hypothesis that the behavioral traits I measured in chapters 1-3 can be considered personality traits, given their repeatability, contextual consistency, and influence on evolutionary and adaptive processes that are central to the natural history of individuals and species. These processes include territorial defense, resource acquisition, risk-taking, and tolerance to habitat degradation or human disturbance.

In Chapter 1, I analyzed how animal movement dynamics and territory defense are influenced by individual differences in aggressiveness and exploration in two species of Darwin's finches: the generalist and widespread small ground finch (*G. fuliginosa*, SGF) and the medium tree finch (*C. pauper*, MTF), a dietary specialist with a restricted range. Birds that spent more time close to the mirror or attacked the mirror more frequently were also those that showed a stronger response toward a simulated conspecific intrusion stimulus (see also Katsis et al. 2025), and they occupied smaller home ranges. These findings are consistent with previous research showing that more aggressive individuals occupy smaller home ranges, as reported in meadow voles (*Microtus pennsylvanicus*) by Spritzer et al. (2005) and in great tits (*Parus major*) by Naguib et al. (2022).

This analysis also revealed a significant negative association between exploratory behavior and home range size in SGF, where more exploratory individuals occupied smaller home ranges. In contrast, and possibly reflecting differences in foraging ecology, MTF showed a non-significant trend toward a positive association between exploration and home range size. From a foraging and habitat-use perspective, generalist species are known to occupy larger home ranges and tend to be more resilient to ecological changes such as habitat loss, whereas specialist species are typically more vulnerable and often restricted to smaller areas (Owens & Bennett, 2000; Slatyer et al., 2013; Castañeda et al., 2019; Guerrero-Sanchez et al., 2022). The association between both behavioral traits and home range size also varied with breeding status: paired males occupied smaller home ranges, suggesting a potential reduction in movement area after pairing. This may reflect a trade-off with territory quality, as higher-quality territories can be defended or guarded more vigorously for the mating partner (García-Loor et al., 2024). Together, these results highlight how

individual behavioral variation interacts with species ecology to shape space use and territorial defense strategies in Darwin's finches.

In Chapter 2, I examined the exploratory behavioral responses of six landbird species, including four species of Darwin's finches, and their association with foraging behavior. Exploration measured during a novel arena test was repeatable over time and consistent across contexts, as assessed in a novel object test in the field. This significant positive correlation, observed even with intervals of up to two years between assays, adds to the growing body of evidence supporting and validating exploration as a personality trait.

These findings further indicate that species that were more exploratory during the novel object test exhibited a higher foraging diversity index. This pattern aligns with previous research on Darwin's finches (Tebbich et al., 2009) and supports the neophobia threshold hypothesis, which predicts that species with greater dietary specialization tend to be less exploratory (Greenberg, 1990; Greenberg & Mettke-Hofmann, 2001). Such individual-level diversity in foraging behavior may contribute to evolutionary change and facilitate adaptive radiation (Gavrilets & Losos, 2009; Araújo et al., 2011). Recent evidence from the adaptive radiation of cichlid fishes demonstrates that individual behavioral differences, specifically exploration behavior, play a key role in ecological diversification (Sommer-Trembo et al., 2024). In that system, genetic variation associated with ecological specialization among closely related species was linked to niche-specific behavioral tendencies, particularly those related to foraging and exploration. These findings suggest that heritable behavioral variation can facilitate the occupation of distinct trophic niches and promote diversification within adaptive radiations.

Innovative behavior had been linked with exploratory behaviour, usually as a proxy for problem/task solving, in some cases including foraging tasks (Greenberg, 2003; Biondi et al., 2010; Forss et al., 2017). Small ground finches and medium tree finches exhibited the highest foraging diversity, the former is a diet-generalist, recently evolved, and widely distributed across the archipelago (Petren et al., 1999), while the critically endangered MTF feeds on invertebrates, fruits, seeds, and flowers (Tebbich et al., 2009; Kleindorfer et al., 2022). Colonization history may explain their exploratory behavior and broad foraging niches: SGF recently expanded into the highlands of Floreana and Santa Cruz Islands (Galligan & Kleindorfer, 2009; O'Connor et al., 2010), and MTF may have originated from colonist large tree finches from Isabela Island (Grant & Grant, 2014; Peters & Kleindorfer, 2018). These patterns support the idea that exploratory individuals facilitate dispersal, colonization, and establishment of new ecological niches (Cote et al., 2010; Liebl & Martin, 2012).

In this chapter, I present comparable evidence from island songbirds, showing that exploratory behavior is consistent and correlated with foraging strategies (García-Loor et al., 2025). Together, these findings highlight that personality-linked foraging behaviors can act both as a product and a driver of adaptive diversification, bridging ecological opportunity, behavioral specialization, and evolutionary diversification.

In Chapter 3, I showed that individual differences in boldness among five species of Darwin's finches were consistent both over time and across contexts, even across intervals of one to five years. Individuals that struggled more during handling also tolerated closer human approaches in the field, supporting the classification of

boldness as a personality trait in Darwin's finches (Réale et al., 2007; David et al., 2012; Kerman et al., 2016).

Boldness patterns also varied across the landscape: birds were bolder (i.e., had shorter flight initiation distances) at sites with higher levels of human activity. This result is consistent with several studies showing that urban birds tend to be bolder than those in rural or less disturbed areas (Blumstein & Fernández-Juricic, 2004; Gotanda, 2020; Merrall & Evans, 2020; Abou-Zeid et al., 2024; Katsis, Common, Lesigang, et al., 2025). Furthermore, I observed a decrease in the number of struggles during handling after island-wide predator removal (Island Conservation and Galapagos National Park Directorate, 2020), indicating a shift in boldness responses likely related to reduced predation risk. Finches hatched in 2024 and 2025 may have developed in a predator-reduced environment, which could explain this behavioral change.

It is well established that younger individuals tend to be bolder (Patrick et al., 2013; Starling et al., 2013), although natural ontogenetic patterns often show increasing boldness with age (Møller, 2014; Holtmann et al., 2017; Bubac et al., 2018). In addition, I found evidence for interspecific variation in boldness among Darwin's finches, that could be associated with ecological differences in risk perception during foraging (Dammhahn & Almeling, 2012; Dammhahn et al., 2022). During handling, ground finches (*Geospiza* spp.) were consistently bolder than tree finches (*Camarhynchus* spp.), suggesting possible selection for greater risk-taking behavior in ground-foraging species, where predation risk is typically higher than in arboreal habitats (Dammhahn & Almeling, 2012; Lu et al., 2012). Moreover, the availability of safer foraging habitats may influence species coexistence and shift the distribution of boldness within species, potentially selecting for different personality types under

predator-reduced conditions (Common et al., in review). Overall, this chapter demonstrated that boldness is a consistent personality trait in Darwin's finches and suggests that both human disturbance and predator removal can influence individual behavioral responses.

Limitations of the study

While each chapter provided key insights into the behavioral ecology of Darwin's finches, they also presented specific methodological and conceptual challenges that highlight directions for future research. For example, in Chapter 1, the main limitation was the lack of repeated testing of behavioral traits over time, which did not allow us to estimate the temporal consistency of exploration and aggressiveness (Niemelä & Dingemanse, 2018). Consequently, we could not distinguish between phenotypic correlations occurring within individuals and those occurring between individuals. Nevertheless, this chapter provided some evidence of cross-context consistency in between-individual behavioral differences for both analyzed traits. Moreover, in a subsequent study in a later field season, aggressiveness measured as response to conspecific song playback (similar to the approach I used in Chapter 1) was validated as a personality trait, showing temporal repeatability (Katsis et al., 2025). In Chapter 2, the main limitation was that we were not able to obtain exploration responses, neither from the novel arena test nor from the novel object test, for the same individuals from which foraging observations were collected. This limitation prevented us from analyzing between-individual differences and/or individual consistency in foraging behavior. Future studies should aim to address this gap and also compare foraging variation between habitats (e.g., highlands vs. lowlands), as interspecific differences in foraging diversity may partly reflect habitat differences among species. In Chapter 3, there remains a gap in our understanding of the

"landscape of fear" (Dammhahn et al., 2022) in Darwin's finches, particularly regarding their capacity to discriminate among and perceive different levels of risk across ecological and life-history contexts, such as age, reproductive status (e.g., pairing success), and predator type. Addressing these limitations will help clarify how ecological, developmental, and environmental factors shape the emergence and maintenance of consistent behavioral differences in island birds.

General Conclusion

In this dissertation, it has been shown that exploration and boldness represent personality traits in Darwin's finches, where individual behavioral differences were consistent over time and across contexts, confirming their stability at the individual level. Although aggressiveness could not be assessed for within-context repeatability due to limited data in my study, the assays developed here laid the groundwork for its later validation as a personality trait in Darwin's finches (Katsis et al. 2025). Overall, my thesis contributes methodological approaches for estimating repeatability when assessing personality traits and validates field assays, such as the simulated conspecific intrusion, novel object test (neophilia), and human approach assay (flight initiation distance, FID), as reliable proxies for measuring personality in the wild, especially when capturing individuals is difficult or not feasible. These results also help to refine our understanding of the ecological validity of behavioral phenotypes, emphasizing the importance of a broader framework that can provide relevant information for developing effective conservation management strategies.

Moreover, understanding a population's behavioral heterogeneity may help predict its resilience, limitations, and adaptive capacity following major disturbances such as drought, habitat loss, or predator removal, particularly in island populations where birds live under constant ecological and evolutionary pressure. With the large-scale ecological restoration currently taking place on Floreana Island, through the implementation of a large-scale predator reduction program followed by the reintroduction of 12 locally extinct species, this scenario offers a once-in-a-lifetime opportunity to measure changes in the distribution of behavioral phenotypes at both population and community levels. It will also allow us to observe how these distributions fluctuate depending on different ecological contexts, such as competition

arising from the presence of new species in the community or from the absence or presence of predators.

Finally, this work underscores the value of long-term studies, which allow behavioral and ecological changes to be tracked against established baselines. Further research is needed to explore the ontogenetic mechanisms underlying individual behavioral differences in Darwin's finches. Such work will help build a framework that disentangles the role of plasticity versus personality–habitat matching and examine the potential evolutionary implications of these patterns within and across species. Future studies should also investigate possible trade-offs between behavioral syndromes and ecological variables such as movement patterns, breeding success, predator removal, foraging behavior, and risk perception across behavioral assays, as well as tolerance to urbanization and other anthropogenic pressures.

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Appendix I

Supplementary material Chapter 1

Aggressive behavior as a predictor of home range size: findings from both range-restricted and widespread Darwin's finch species

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Table S1. Sample sizes for each behavioral assay (data type) in the study are shown for both focal species as medium tree finch / small ground finch. The diagonals indicate the total number of individuals for each of the assays whereas the cells above indicate sample sizes of individuals tested for both of the respective assays.

	Radiotracking	*Exploration Cage*	*Exploration Wild*	*Aggressiveness Cage*	*Aggressiveness Wild*
Radiotracking	20/15	19/15	5/3	19/14	8/12
Exploration Cage		44/59	8/7	44/59	15/20
Exploration Wild			8/7	8/7	2/2
Aggressiveness Cage				42/59	15/20
Aggressiveness Wild					15/23

Table S2. Summary of Darwin's finch personality variables per species (medium tree finch = MTF, small ground finch = SGF) in paired and unpaired males per year. Data are shown with sample size (n), mean, standard error (SE) and range classified by species, year and pairing status. *Unique sector visits* and *total sector visits* are measures of exploration (novel environment test), while *time near mirror* is a measure of aggressiveness (mirror stimulation test). All monitored finches remained unpaired during the 2022 field season.

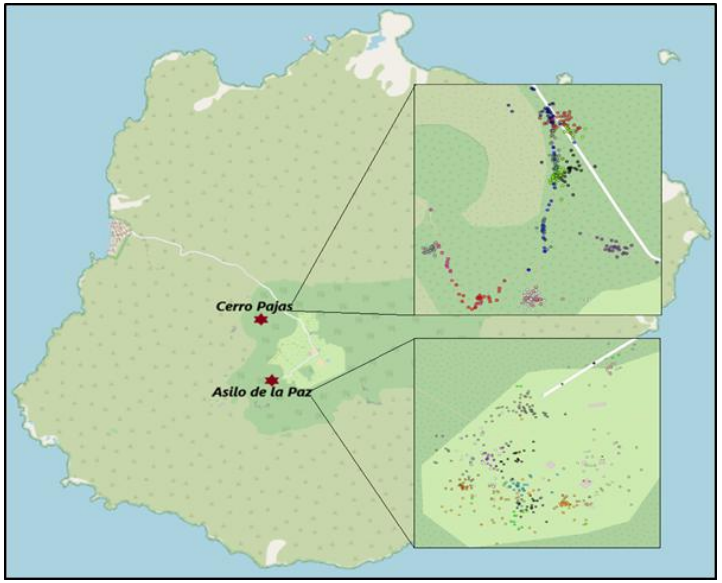
		2020 Paired			***2020 Unpaired***			***2022 Unpaired***		
MTF		**n**	**Mean ± SE**	**Range**	**n**	**Mean ± SE**	**Range**	**n**	**Mean ± SE**	**Range**
	Unique Sector Visits	5	2.8 ± 1.11	(1–7)	5	3.6 ± 0.4	(2–4)	9	5.1 ± 0.96	(2–10)
	Total Sector Visits	5	23.6 ± 14.2	(1–70)	5	21.4 ± 11.9	(2–65)	9	33.9 ± 15.5	(2–113)
	Time Near Mirror	5	14.8 ± 12.7	(0–65.5)	5	54.9 ± 27.9	(0–139.5)	9	3.4 ± 2.4	(0–21.2)
SGF		**n**	**Mean ± SE**	**Range**	**n**	**Mean ± SE**	**Range**	**n**	**Mean ± SE**	**Range**
	Unique Sector Visits	7	6.6 ± 0.65	(4–10)	3	3.3 ± 0.67	(2–4)	5	3 ± 0.6	(2–5)
	Total Sector Visits	7	70.3 ± 16.5	(16–50)	3	9.7 ± 6.23	(2–22)	5	3.4 ± 0.9	(2–6)
	Time Near Mirror	7	60.4 ± 16.1	(0–106.5)	3	0	(0)	4	0	(0)

Table S3. Output from linear models testing whether exploration (unique sector visits) or aggressiveness (time near mirror) predicts home range size in medium tree finches (MTF) and small ground finches (SGF). Species (MTF, SGF) and pairing status (paired, unpaired) were included as fixed effects.

	Estimate	***Std. Error***	***t***	***p***
(Intercept)	-0.425	0.481	-0.884	0.384
Unique Sector	0.085	0.074	1.147	0.261
Time Near Mirror	-0.013	0.005	-2.858	**0.008**
Species (SGF)	0.249	0.351	0.710	0.484
Status (Unpaired)	0.572	0.375	1.526	0.138

Figure S1. Sightings, or so-called 'tracking fixes', of medium tree finches (MTF) and small ground finches (SGF) on Floreana Island. To project and plot the fixes, we used the packages 'moveVis' version 0.10.9 (Schwalb-Willmann et al. 2020), 'move' version 4.2.4 (Kranstauber et al. 2023), and 'RgoogleMaps' version 1.4.5.3 (Loecher and Ropkins 2015). a) Tracking fixes plotted on a map of Floreana Island, with each color representing a tracked individual. *N* = 822 fixes from 35 males (21 medium tree finches, 14 small ground finches). b) The polygons of the occupancy area of the tracked individuals at both study sites.

a) Image of tracking 'fixes'



b) Image of home range polygons

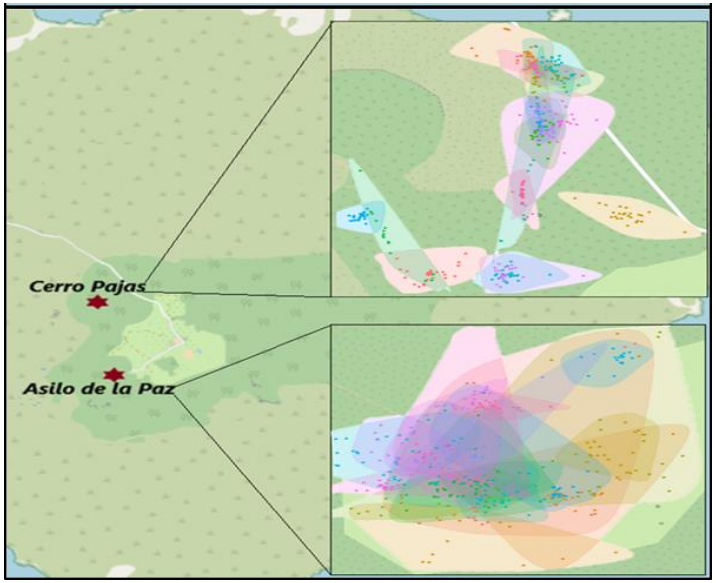


Figure S2. Picture of the metal flight cage (75 × 44 × 42 cm) with three perches (one at 6 cm height and the other two at 20 cm height) where the novel environment test and the mirror simulation test was performed. Photo take by Andrew Katsis.

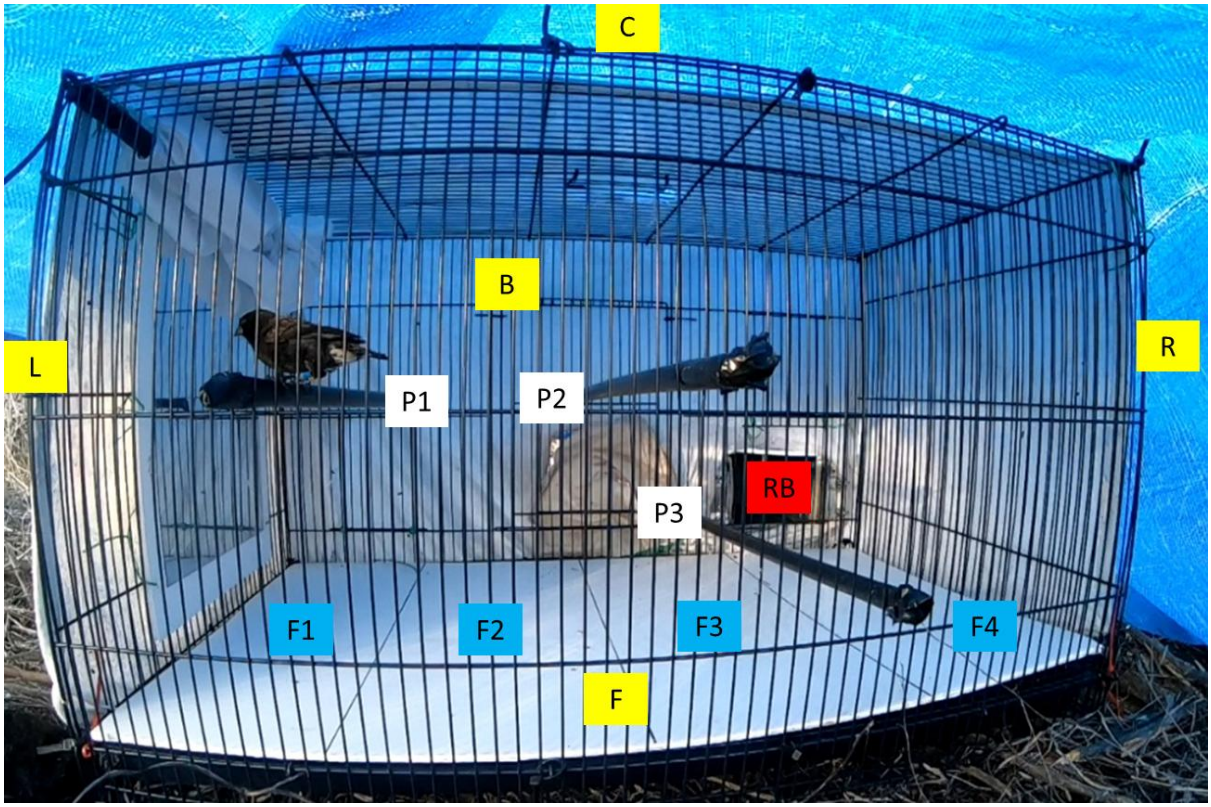


Figure S3. Consistency within contexts for exploration variables scored during a novel environment test (*unique sectors* and *total sectors*). The two exploration variables were positively correlated, both when species were analyzed together or separately for medium tree finches (open circles) and small ground finches (filled triangles).

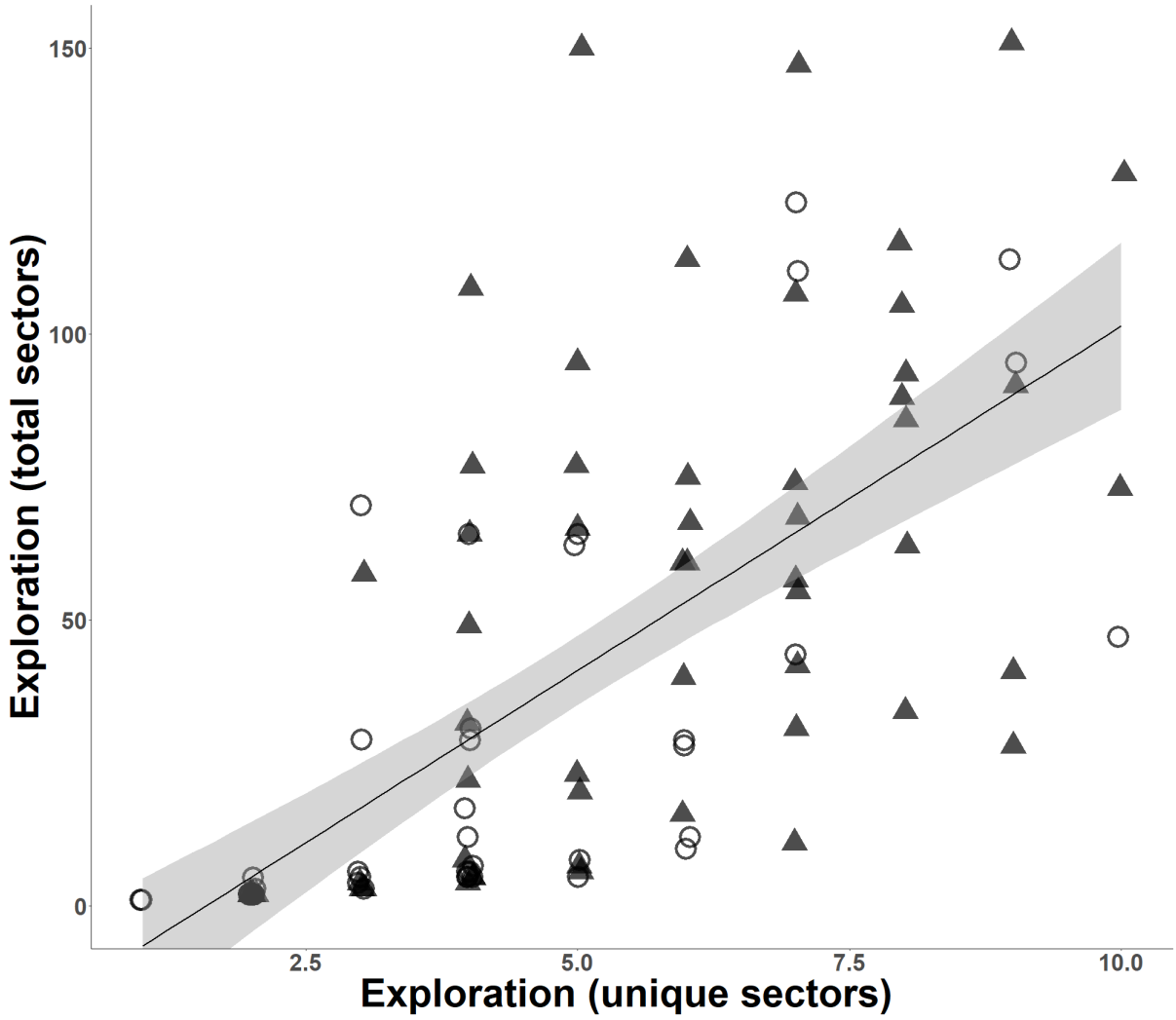


Figure S4. Consistency within contexts for aggressiveness variables scored using a mirror stimulation test (*time near mirror* and *mirror contact*) in medium tree finches (open circles) and small ground finches (SGF). Males that contacted the mirror (*mirror contact*) also spent significantly longer near the mirror (*time near mirror*, secs).

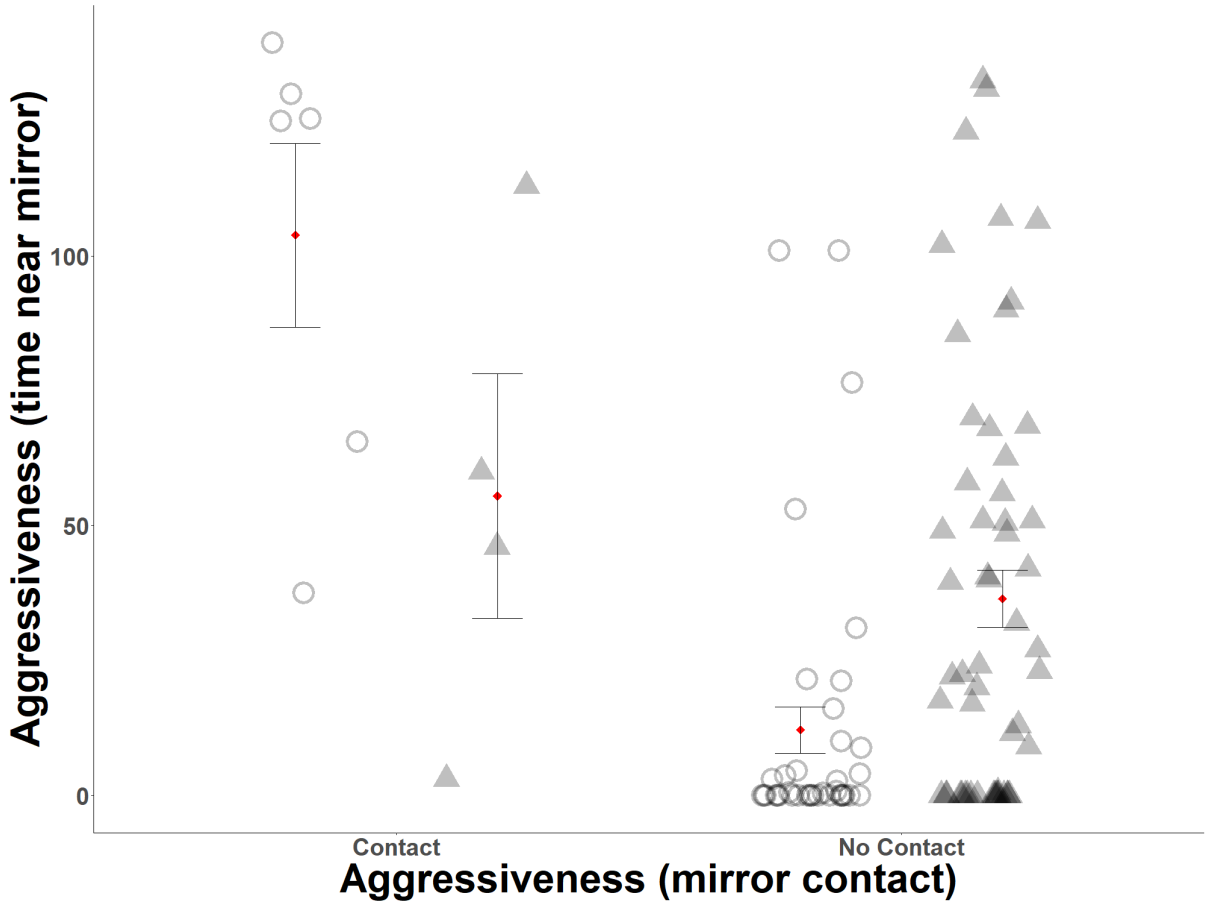


Figure S5. The relationship between exploration (*total sectors visited*) and log transformed home range size was not significantly associated with home range size (ha) in medium tree finches (open circles) and small ground finches (filled triangles), albeit with a negative trend (r = -0.4, N = 20, p = 0.10). The standard error level is at 95% confidence (gray shadow).

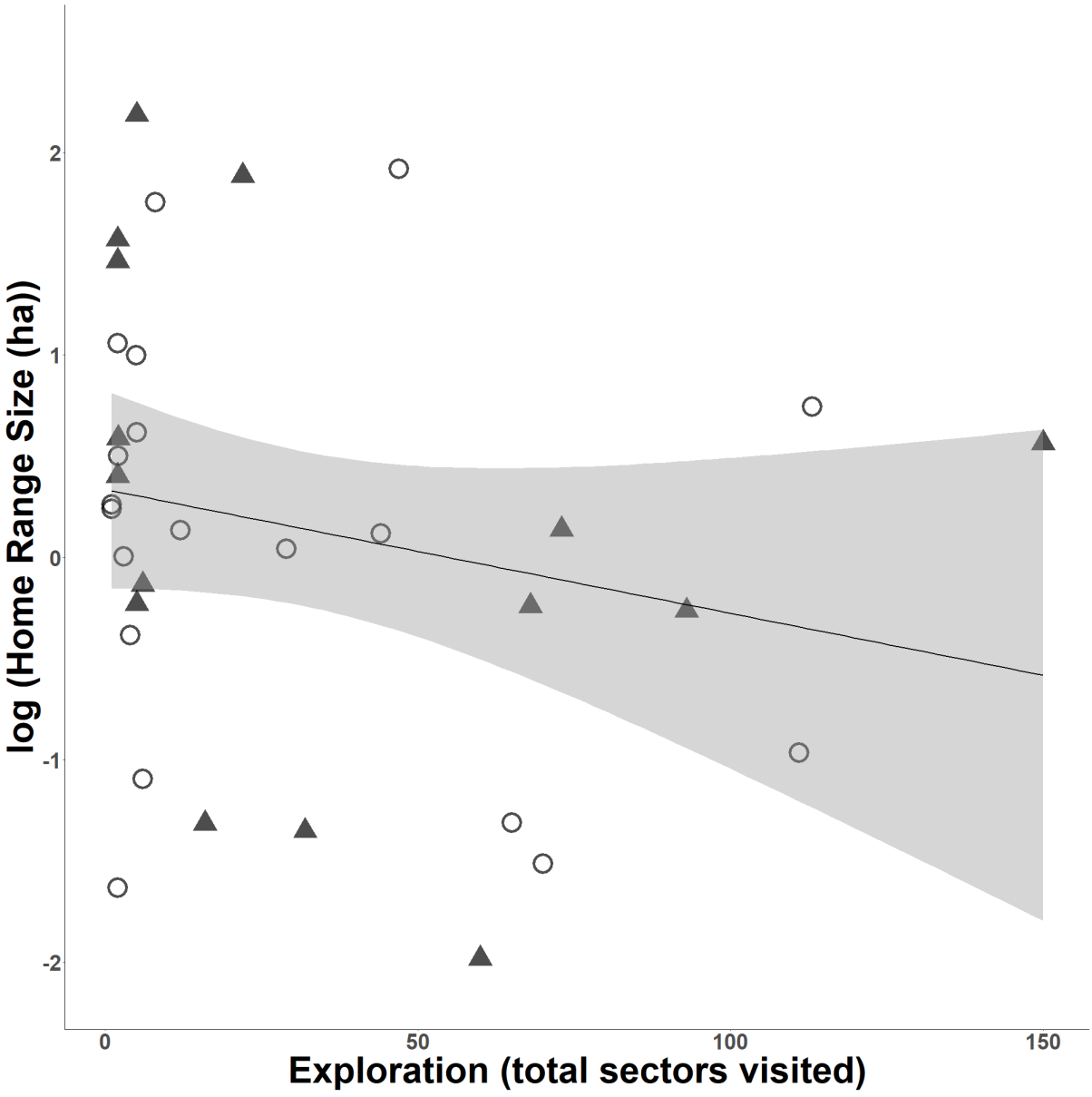
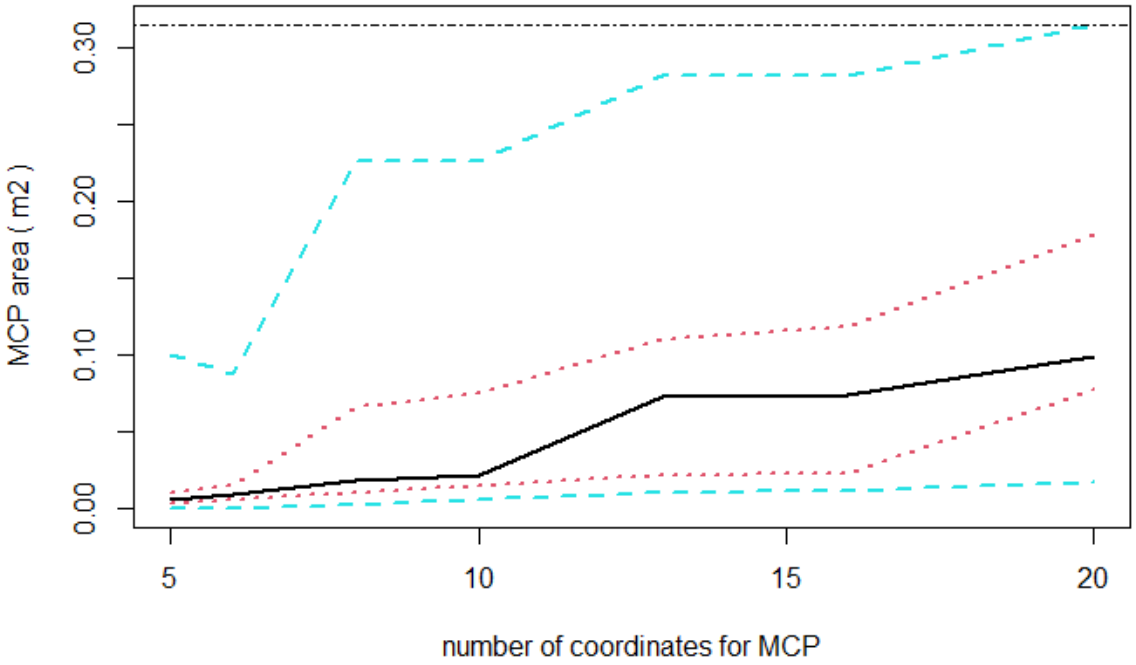


Figure S7. Bootstrap used to estimate the number of fixes needed, we observed how the trend starts to flattened after 13–14 fixes, which suggests that enough fixes were taken for the individuals



Appendix II

Supplementary material Chapter 2

Exploration behavior is consistent and associated with foraging behavior in island songbirds

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Table S1. Output from linear mixed models testing which factors influence exploration during a novel environment test in six Galápagos passerine species, with (a) unique sector visits or (b) total sector visits (log-transformed) as the response variable. Each model included year, species, and sex as fixed effects and individual ID as a random effect. Species abbreviations: small ground finch (SGF), medium ground finch (MGF), small tree finch (STF), medium tree finch (MTF), Galápagos flycatcher (GFC), and yellow warbler (YW). Individual ID explained (a) 1.66 ± 1.29 and (b) 0.16 ± 0.40 of the variance. Statistically significant ($P < 0.05$) values are shown in bold.

	Estimate	SE	df	t-value	χ^2	P-value
a) Unique sector visits						
Intercept	4.70	1.66	235.89	2.83		
Year	-0.44	0.33	194.22	-1.32	1.74	0.187
Species [MGF]	2.21	1.69	235.73	1.31		
Species [MTF]	0.31	1.63	235.70	-0.19		
Species [SGF]	1.83	1.64	235.66	1.12		
Species [STF]	-0.45	0.65	235.58	-0.27	63.02	**< 0.001**
Species [YW]	2.33	1.70	235.95	1.37		
Sex [Male]	-0.74	0.35	236.94	-2.13	4.64	0.098
Sex [Unknown]	-0.94	1.14	236.18	-0.82		
b) Total sector visits						
Intercept	1.26	0.41	231.40	3.05		
Year	-0.34	0.08	97.16	-4.27	18.21	**< 0.001**
Species [MGF]	0.32	0.42	230.60	0.77		
Species [MTF]	0.02	0.41	230.53	0.04		
Species [SGF]	0.34	0.41	230.43	0.82	93.47	**< 0.001**
Species [STF]	-0.12	0.41	230.22	-0.29		
Species [YW]	1.05	0.42	231.86	2.47		
Sex [Male]	-0.06	0.09	236.96	-0.72	0.62	0.733
Sex [Unknown]	0.04	0.28	233.32	0.14		

Table S2. Output from bivariate LMMs showing variances (diagonals, shown in bold), covariances (below diagonals) and correlations (above diagonals) between two measures of exploration measured in different contexts: exploration during a novel environment test (PC_Exploration) and exploration during a novel object test (inverse latency to 10 m) in (a) yellow warblers and (b) Darwin's finches (small ground finch, small tree finch and medium tree finch, pooled). Lower and upper bounds of 95% credible intervals are shown in parentheses. For both response variables, high scores indicate more exploratory behavior.

a) Yellow warblers		
	PC_Exploration	Inverse latency
PC_Exploration	**0.72 (0.12, 1.25)**	0.54 (0.13, 0.98)
Inverse latency	1.30 (0.08, 2.38)	**8.74 (6.89, 10.84)**
b) Darwin's finches		
	PC_Exploration	Inverse latency
PC_Exploration	**0.43 (< 0.01, 0.84)**	0.47 (-0.03, 0.99)
Inverse latency	0.86 (-0.21, 1.81)	**8.68 (6.79, 10.81)**

Table S3. Summary data per species from novel object tests conducted in the wild: *Response 10 m*, the number of individuals per species to approach to 10 m divided by the total number of individuals from all species that approached to 10 m; *Response 3 m*, the number of individuals per species to approach to 3 m divided by the total number of conspecifics that approached to 10 m; *Latency to 10 m*, the time (secs) to approach to 10 m from the start of the trial (mean ± SE); and *Latency to 3 m*, the time (secs) to approach from 10 m to 3 m (mean ± SE), among individuals than entered the 3-m zone. N = 259 birds approached to 10 m and 46 birds approached to 3 m. Species abbreviations: small ground finch (SGF), medium ground finch (MGF), small tree finch (STF), medium tree finch (MTF), Galápagos flycatcher (GFC), and yellow warbler (YW).

Species	***N***	***Response 10 m***	***Response 3 m***	***Latency 10 m***	***Latency 3 m***
SGF	98	0.38	0.17	4.08 ± 0.41	0.59 ± 0.14
MGF	6	0.02	0.00	5.17 ± 2.11	3.60*
STF	37	0.14	0.14	4.95 ± 0.81	1.60 ± 0.72
MTF	33	0.13	0.27	5.18 ± 0.90	0.67 ± 0.22
GFC	21	0.08	0.19	4.67 ± 1.02	0.75 ± 0.38
YW	64	0.25	0.16	4.28 ± 0.54	2.60 ± 0.82

** In medium ground finches, no individuals approached to within 3 m and, hence, in this species we allocated the highest latency value plus one, indicating the longest latency to approach among the six species.*

Table S4. Foraging diversity scores for six Galápagos passerine species, calculated as the Shannon diversity indices for foraging technique and foraging substrate per species. Species abbreviations: small ground finch (SGF), medium ground finch (MGF), small tree finch (STF), medium tree finch (MTF), Galápagos flycatcher (GFC), and yellow warbler (YW).

Species (sample size)	***Foraging Technique***	***Foraging Substrate***
SGF (n = 166)	1.66	1.54
MGF (n = 25)	0.86	0.86
STF (n = 67)	1.26	0.96
MTF (n = 30)	1.54	1.67
GFC (n = 6)	1.01	1.01
YW (n = 26)	1.22	1.28

Figure S1. Among-individual correlation estimates (mean ± 95% CrI) between PC_Exploration (the number of total and unique sectors visited during the novel environment test) and exploration during a novel object test (inverse latency to 10 m) in (a) yellow warblers and (b) all species of Darwin's finches (small ground finch, small tree finch and medium tree finch). Higher scores for both PC_Exploration and inverse latency to 10 m indicate higher exploration. In (a), the correlation estimates do not overlap with 0, indicating exploration during the novel environment test and the novel object test are significantly correlated in yellow warblers.

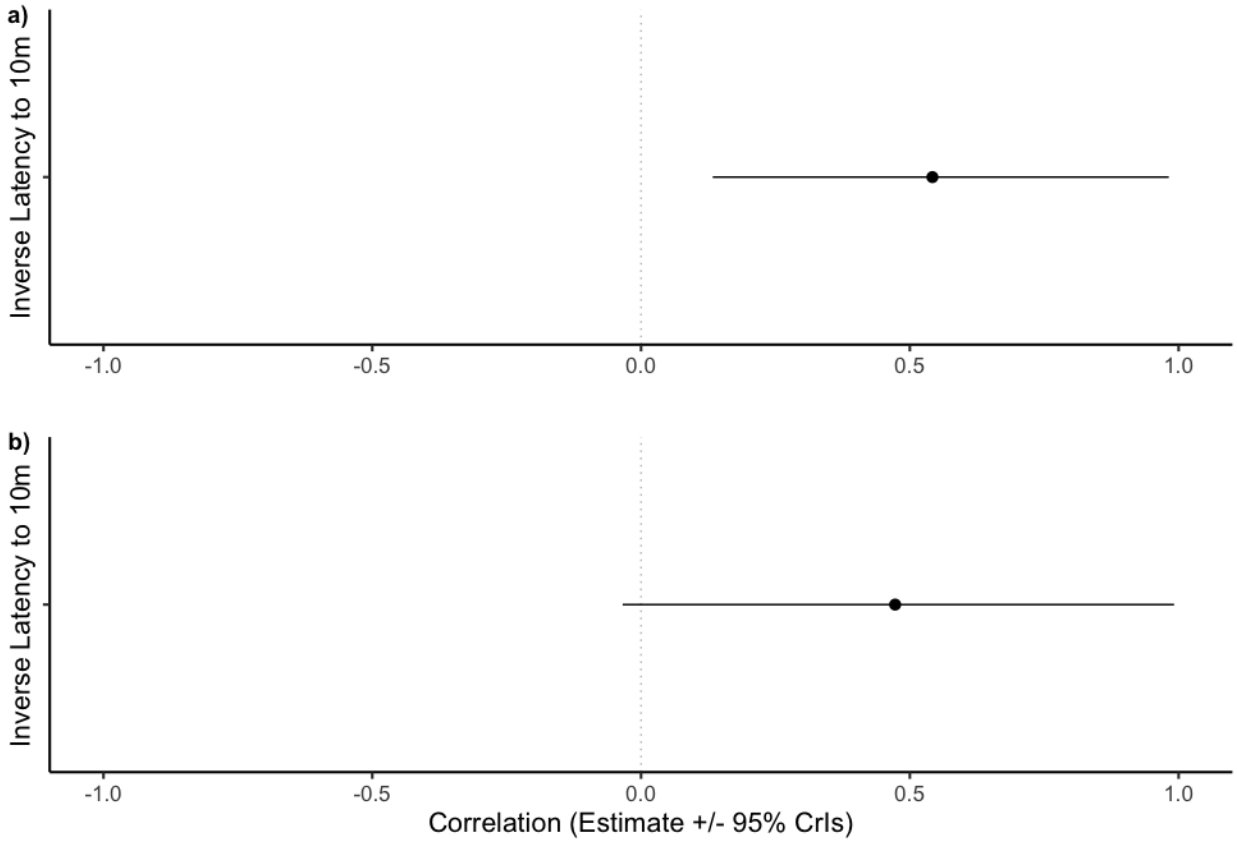


Figure S2. Mean values and error bars (standard error) per species for unique sector visits during the novel environment test. Species abbreviations: small ground finch (SGF), medium ground finch (MGF), small tree finch (STF), medium tree finch (MTF), Galápagos flycatcher (GFC), and yellow warbler (YW).

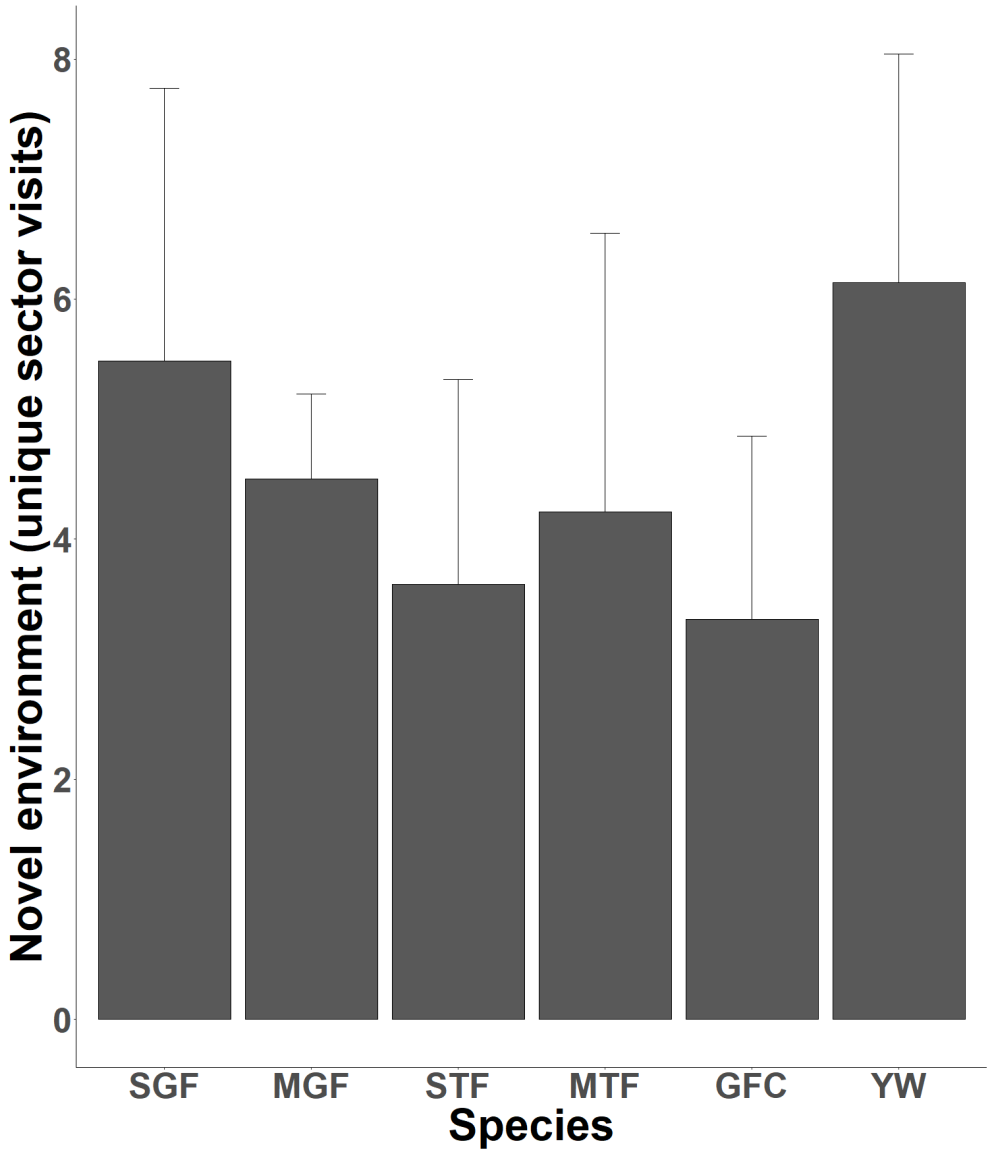
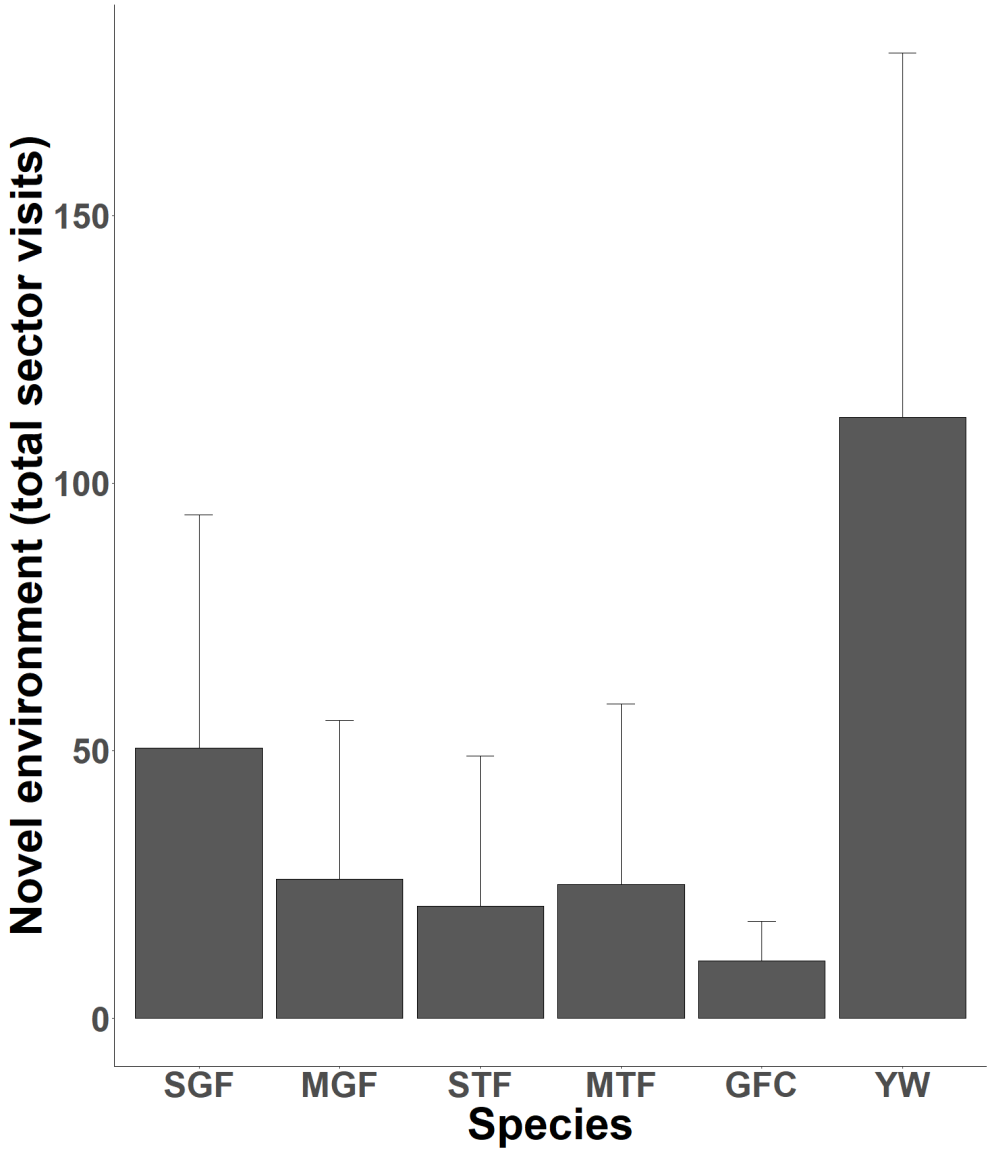


Figure S3. Mean values and error bars (standard error) per species for total sector visits during the novel environment test. Species abbreviations: small ground finch (SGF), medium ground finch (MGF), small tree finch (STF), medium tree finch (MTF), Galápagos flycatcher (GFC), and yellow warbler (YW).



Appendix III

Supplementary material Chapter 3

Boldness is consistent over time and across contexts in five Darwin's finch species.

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Table S1. Summary data (mean, SE, and range) for boldness measurements during human handling (back test and processing test) and in response to a human approach (flight initiation distance). Species abbreviations: small ground finch (SGF), medium ground finch (MGF), cactus finch (CF), small tree finch (STF), and medium tree finch (MTF).

	Back test			***Processing test***			***FID***		
	n	**Mean ± SE**	**Range**	**n**	**Mean ± SE**	**Range**	**n**	**Mean ± SE**	**Range**
SGF	218	0.9 ± 0.1	0–8	218	1.7 ± 0.1	0–5	425	4.1 ± 0.1	0.3–10.0
MGF	32	1.4 ± 0.4	0–7	32	2.0 ± 0.3	0–5	20	4.5 ± 0.3	2.0–7.5
CF	33	0.7 ± 0.3	0–7	33	2.3 ± 0.3	0–5	18	2.9 ± 0.4	1.0–6.8
STF	165	0.8 ± 0.1	0–8	165	0.9 ± 0.1	0–4	90	4.6 ± 0.3	0.3–10.0
MTF	106	1.3 ± 0.2	0–12	106	1.1 ± 0.1	0–5	58	4.2 ± 0.3	1.5–8.5

Table S2. Bayesian post-hoc pairwise comparisons between species for each boldness variable. Values presented are the posterior estimates of differences between species, 95% credible intervals, and p-values (pMCMC), with statistically significant differences (P < 0.05) indicated in bold. Species abbreviations: small ground finch (SGF), medium ground finch (MGF), cactus finch (CF), small tree finch (STF), and medium tree finch (MTF).

	Estimate	**95% CrI**	***P***
a) Back-test response			
CF vs SGF	1.49	0.45 – 2.49	**0.006**
CF vs MGF	0.78	-0.29 – 1.84	0.153
CF vs STF	1.38	0.30 – 2.47	**0.009**
CF vs MTF	0.79	-0.34 – 1.89	0.159
SGF vs STF	-0.11	-0.60 – 0.38	0.648
MGF vs SGF	0.71	-0.14 – 1.61	0.100
MGF vs STF	0.60	-0.31 – 1.55	0.203
MGF vs MTF	0.01	-1.00 – 1.02	0.997
MTF vs SGF	0.70	0.18 – 1.25	**0.012**
MTF vs STF	0.60	0.001 – 1.15	0.050
b) Processing response			
CF vs SGF	0.75	0.29 – 1.23	**0.002**
CF vs MGF	0.46	-0.03 – 0.98	0.065
CF vs MTF	1.34	0.85 – 1.81	**< 0.001**
CF vs STF	1.10	0.58 – 1.64	**< 0.001**
SGF vs STF	0.59	0.35 – 0.83	**< 0.001**
MGF vs SGF	0.29	-0.14 – 0.71	0.180
MGF vs STF	0.88	0.41 – 1.34	**< 0.001**
MGF vs MTF	0.64	0.14 – 1.15	**0.010**
MTF vs SGF	-0.35	-0.64 – -0.07	**0.013**
MTF vs STF	0.24	-0.07 – 0.54	0.140

	Estimate	95% CrI	*P*
c) Flight initiation distance			
CF vs SGF	-0.65	-1.14 – -0.14	**0.009**
CF vs MGF	-0.82	-1.48 – -0.17	**0.015**
CF vs STF	-0.91	-1.46 – -0.35	**0.003**
CF vs MTF	-0.88	-1.49 – -0.30	**0.004**
SGF vs STF	-0.26	-0.49 – -0.04	**0.022**
MGF vs SGF	0.18	-0.29 – 0.63	0.436
MGF vs STF	-0.09	-0.60 – 0.41	0.765
MGF vs MTF	-0.06	-0.60 – 0.49	0.820
MTF vs SGF	0.24	-0.05 – 0.53	0.102
MTF vs STF	-0.03	-0.36 – 0.31	0.866

Figure S1. Correlation between boldness measurements during handling (back test and processing response). During the back test, we measured boldness as the number of struggles over a 30-sec period; during processing, we measured boldness as the number of measurement procedures (0–5) during which the bird struggled. Birds that struggled more during the back test also struggled during more processing procedures. Species abbreviations: small ground finch (SGF), medium ground finch (MGF), cactus finch (CF), small tree finch (STF), and medium tree finch (MTF).

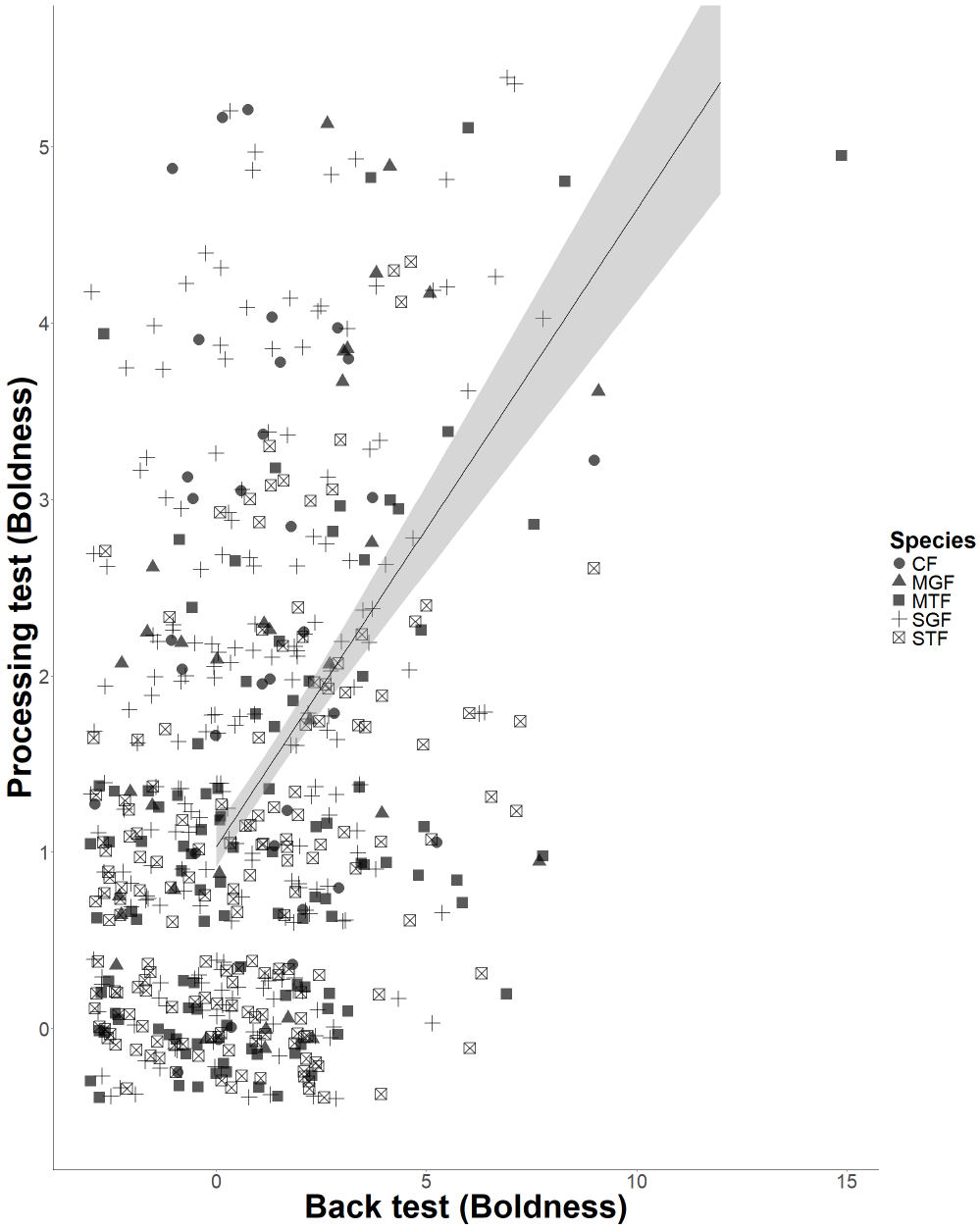


Figure S2. Species differences in boldness for each of three behavioral traits measured (back-test response, processing response, and flight initiation distance). Panels a) and b) present responses to handling assays during short-term captivity, while panel c) presents flight initiation distance in response to a human approach in the field. Species abbreviations: small ground finch (SGF), medium ground finch (MGF), cactus finch (CF), small tree finch (STF) and medium tree finch (MTF).

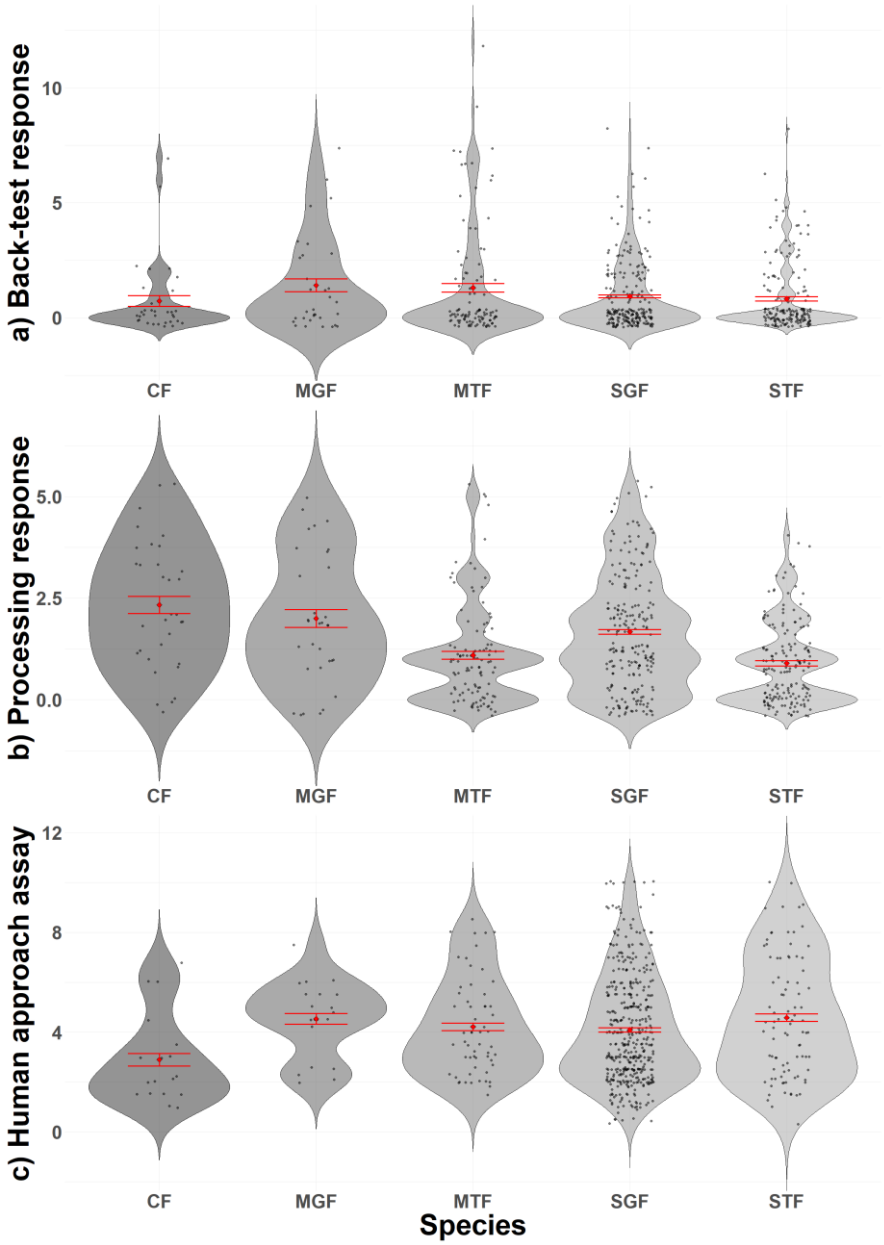


Figure S3. Post-hoc pairwise comparisons showing species differences in boldness with 95% credible intervals, for each of three variables measured (back-test response, processing response, and flight initiation distance). Significant differences are shown in black and non-significant comparisons in grey. Species abbreviations: small ground finch (SGF), medium ground finch (MGF), cactus finch (CF), small tree finch (STF), and medium tree finch (MTF).

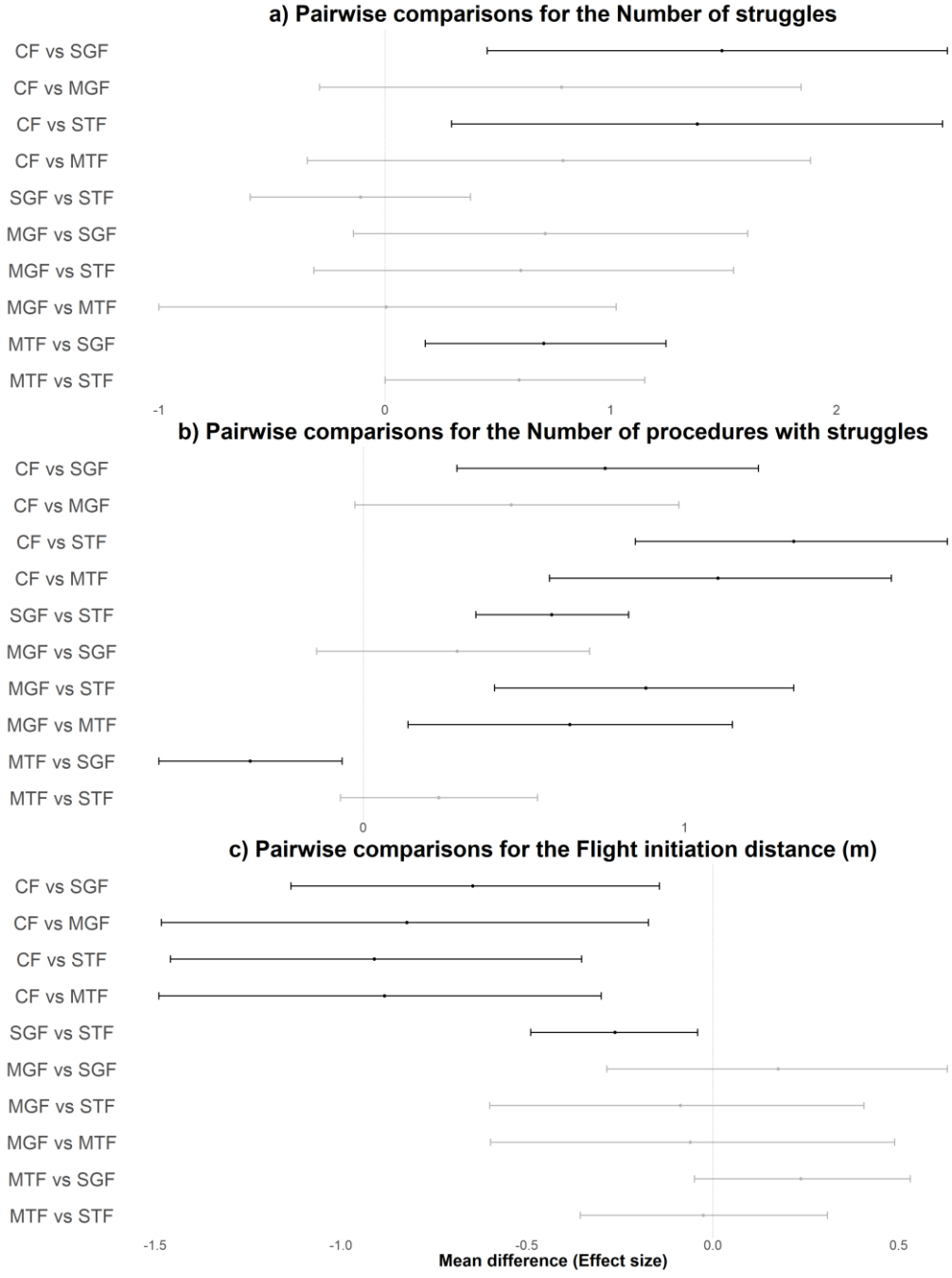


Figure S4. Scatterplots showing non-significant correlations between handling responses (back-test response and processing response) and flight initiation distance, for individuals that undertook both assay types within the same year (N = 29, all in 2025). a) Comparison of back-test response (number of struggles during a 30-sec back test) and flight initiation distance; and b) comparison of processing response (number of processing procedures in which the bird struggled, 0–5) and flight initiation distance. Species abbreviations: small ground finch (SGF), medium ground finch (MGF), small tree finch (STF).

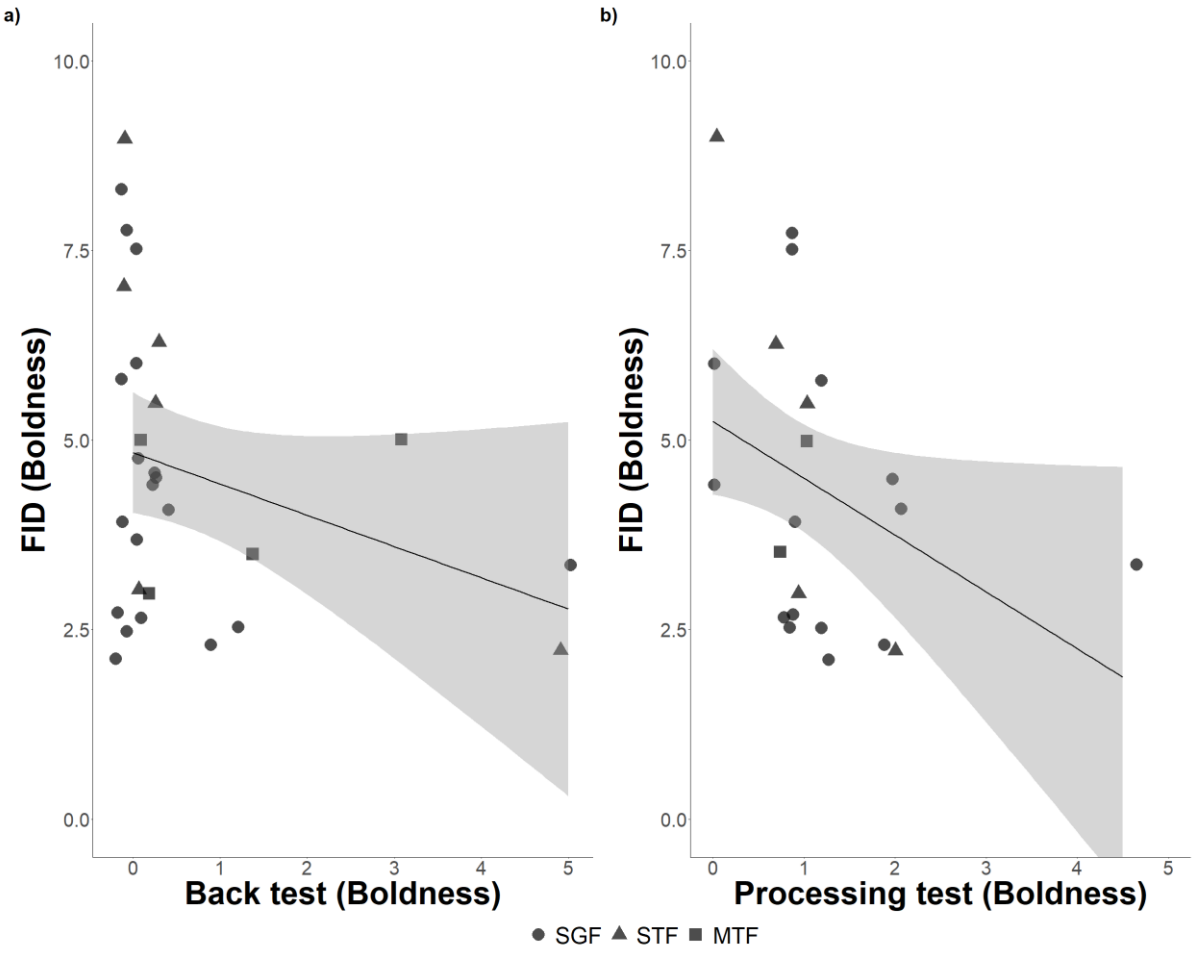
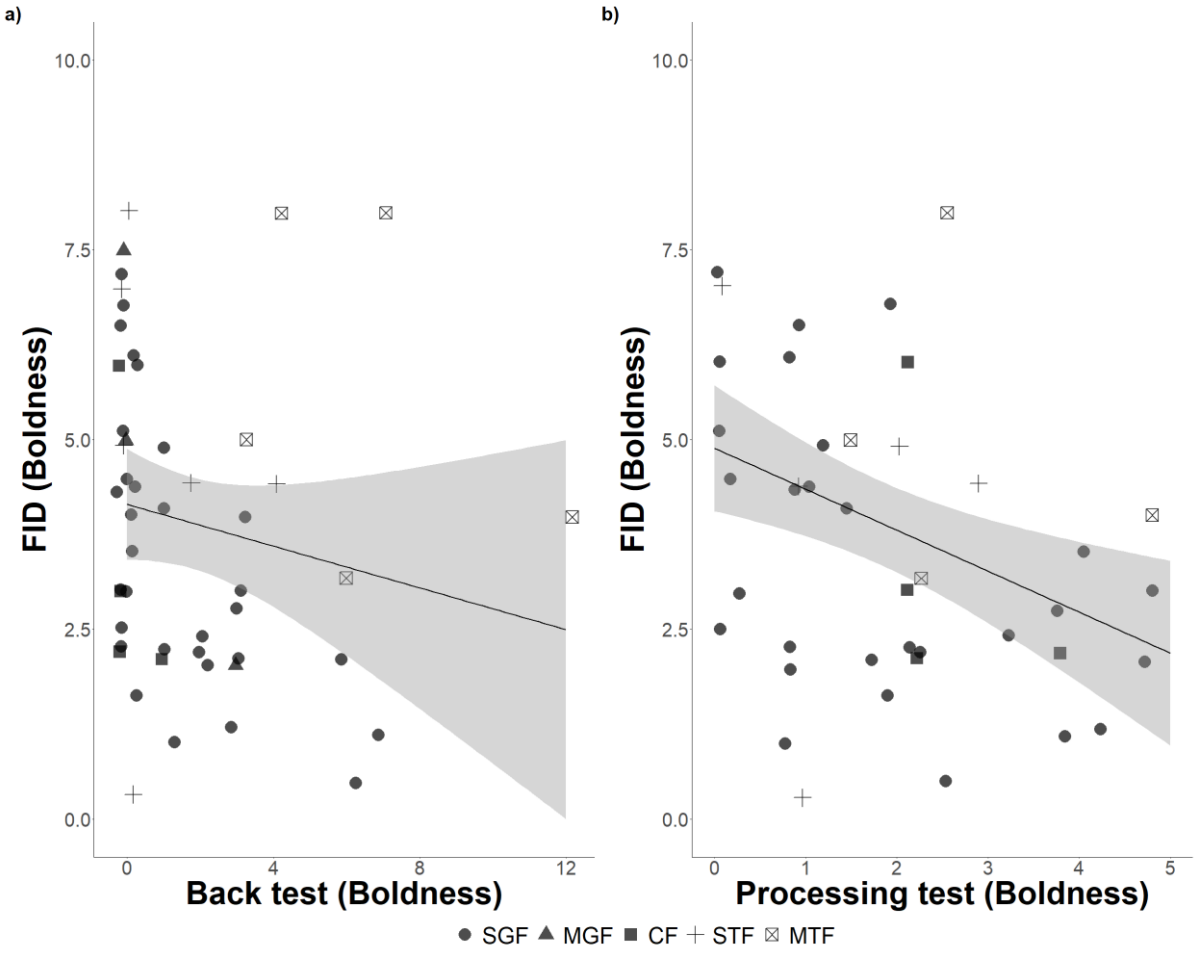


Figure S5. Scatterplots showing significant correlations between handling responses (back-test response and processing response) and flight initiation distance, for individuals that undertook each assay type in different years (N = 49). a) Comparison of back-test response (number of struggles during a 30-sec back test) and flight initiation distance; and b) comparison of processing response (number of processing procedures in which the bird struggled, 0–5) and flight initiation distance. In both comparisons, birds that struggled more during the handling also tolerated closer human approaches in the wild. Species abbreviations: small ground finch (SGF), medium ground finch (MGF), cactus finch (CF), small tree finch (STF) and medium tree finch (MTF).



Floreana Island

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