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EDITED BY
Alejandro Ariel Ríos-Chelén,
Autonomous University of Tlaxcala, Mexico

REVIEWED BY
J. Roberto Sosa-Lopez,
National Polytechnic Institute (IPN), Mexico
Beate Anna Apfelbeck,
Technical University of Munich, Germany

*CORRESPONDENCE
Sonia Kleindorfer
✉ Sonia.kleindorfer@univie.ac.at

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Darwin's finches in human-altered environments sing common song types and are more aggressive

Diane Colombelli-Négrel[1], Çağlar Akçay[2,3] and Sonia Kleindorfer[1,4]*

[1]College of Science and Engineering, Flinders University, Adelaide, SA, Australia, [2]Department of Psychology, Koç University, Istanbul, Türkiye, [3]School of Life Sciences, Anglia Ruskin University, Cambridge, United Kingdom, [4]Department of Behavioral and Cognitive Biology, Konrad Lorenz Research Center for Behavior and Cognition, University of Vienna, Vienna, Austria

Human-altered landscapes may act as an environmental filter benefiting species or individuals with specific sets of capacities or behaviors. Yet the effects of human activity on culturally transmitted traits in animals are still poorly understood. Combining song recordings and simulated territory intrusions, we investigated whether songs (a cultural trait) and aggressiveness (a personality trait) in small ground finches (*Geospiza fuliginosa*) differed along a gradient of human activity levels (high-low-high) spanning two habitats with contrasting levels of rainfall (arid lowlands, humid highlands). We found that more common syllable types were more prevalent in arid lowland sites and at sites with high human activity. The number of syllables per song, song duration, song tempo and song rhythmicity did not differ across habitats or levels of human activity. During simulated territorial intrusions, small ground finches living in areas with higher levels of human activity and in the arid lowlands (regardless of human activity) showed the strongest aggressive response compared to those living in areas with lower levels of human activity or in the humid highlands. Thus, prevalence of aggression and syllable commonness correlated with each other across sites. Our results support the idea that resource distribution and human-impacted environments may select jointly for specific behavioral phenotypes such as aggression as well as common cultural traits.

KEYWORDS

animal communication, cultural signals, territory defense, Darwin's finches, urbanization, urban ecology

1. Introduction

Environments are changing at unprecedented speed due to human activities, which imposes challenges for many species. Animal behavioral responses to such changes may influence evolutionary processes by determining which individuals survive and reproduce under altered conditions (Sih et al., 2011; Chapple et al., 2012), which in turn can have long-term consequences for biodiversity. Such responses may be driven by pressures within the environments or selection for individuals with traits that make them better suited to colonize changing environments (Marzluff and Neatherlin, 2006; Carrete and Tella, 2010; Cote et al., 2010; Hu and Cardoso, 2010; Holtmann et al., 2017). However, the ultimate and proximate mechanisms behind such responses, as well as the role of individual differences in behavior associated with population persistence in rapidly changing environments, remain poorly understood (Maspons et al., 2019).

Human activities and human-altered landscapes are now recognized as ecological filters benefiting certain species or individuals with specific sets of characteristics, capacities, or behaviors (e.g., Silva et al., 2016; Callaghan et al., 2019; Patankar et al., 2021). Compared with their more rural counterparts, individuals living near humans are generally more aggressive toward conspecifics (Coss et al., 2002; Scales et al., 2011; Baxter-Gilbert and Whiting, 2019), more prone to take risks when facing predators (Møller, 2010; Scales et al., 2011; Tryjanowski et al., 2016; Ducatez et al., 2017; Holtmann et al., 2017; Gotanda, 2020), more exploratory (Charmantier et al., 2017), and differ in their signaling (Hu and Cardoso, 2010; Luther and Derryberry, 2012; Kunc and Schmidt, 2021) and dispersal (Partecke and Gwinner, 2007) behaviors. Such behavioral differences can also correlate with greater innovativeness and cognitive performance that may lead to adaptive responses to challenging environments (see Sol et al., 2005; Lowry et al., 2013; Lee and Thornton, 2021).

Risk-taking behaviors such as territorial aggression are predicted to be particularly important to determine the survival or success of an individual when faced with environmental changes, such as human-altered landscapes (see Lapiedra et al., 2017). The higher levels of territorial aggression in urban habitats seen for instance in several songbird species (e.g., Evans et al., 2010; Scales et al., 2011; Foltz et al., 2015; Myers and Hyman, 2016; Hardman and Dalesman, 2018) is likely due to a combination of factors. In particular, anthropogenic noise (e.g., Phillips and Derryberry, 2018; Akçay et al., 2020), higher conspecific density (e.g., Fokidis et al., 2011) or variation in the availability of resources, such as food or nesting spaces (e.g., Fox et al., 1981; Scales et al., 2013) may lead to higher levels of boldness and aggressiveness in human-altered landscapes, which in turn may elevate the level of competition for territories.

Bird song is a culturally learned trait, which has a very important function in territory establishment and maintenance (Searcy and Beecher, 2009; Logue, 2021). Indeed, there is evidence from several species of songbirds that singing locally common song types (i.e., conformity in song types) correlates positively with components of individual fitness such as territory tenure and mating success (Payne, 1982; O'Loghlen and Rothstein, 1995; Beecher et al., 2000; Demko et al., 2016). Such correlations may come about because common songs (i) may better transmit in the local habitat than uncommon songs (Morton, 1975), (ii) be indicators of genotypes better suited to the local habitat and thus be preferred by mates (Baker, 1975; Stewart and MacDougall-Shackleton, 2008), (iii) serve as honest signals of song learning ability (Rothstein and Fleischer, 1987) or (iv) facilitate cooperative behaviors between territory owners and serve as signals of alliances toward third parties (Beecher et al., 2020). Therefore, individuals singing common song types may be favored during territory establishment and maintenance, particularly when competition for territories is higher, as expected in human-altered landscapes. For instance, in a study by Laiolo and Tella (2005), song sharing between neighboring male Dupont's larks (*Chersophilus duponti*) increased with anthropogenic habitat fragmentation, suggesting that heightened competition for the limited suitable territories may select for high cultural conformity in song. This study remains one of only a handful of studies investigating differences in discrete cultural elements in human-altered landscapes (but see Deoniziak and Osiejuk, 2019; Brewer and Fudickar, 2022).

The islands of the Galapagos archipelago represent an excellent opportunity to investigate the effects of human-induced environmental changes on cultural and behavioral traits. Human settlement in the Galapagos islands is recent, having occurred over the past 200 years and especially since the 1950s (see Watson et al., 2010), and most islands have small and localized urban centers. The endemic Darwin's finches are one of the best examples of adaptive radiation, where a single species evolved into 17 known species that exploit different ecological niches (Grant and Grant, 2002, 2008, 2014a; Kleindorfer et al., 2022). Darwin's finches are opportunistic breeders that strongly depend on rainfall for breeding (Grant and Boag, 1980; Gibbs and Grant, 1987; Hau et al., 2004; Kleindorfer, 2007a; Camacho et al., 2019), and studies have shown differences in diet (De León et al., 2019), microbiota (Knutie et al., 2019), morphology (Hendry et al., 2006; De Leon et al., 2011), breeding success (Harvey et al., 2021) and tolerance toward humans (Gotanda, 2020) between Darwin's finches living near or away from humans. Specifically, a previous study showed that overall, small ground finches (*Geospiza fuliginosa*) living near humans were more tolerant toward humans (i.e., took longer to initiate flight in response to a human approaching) than finches in areas less exposed to humans. Interestingly, the study also found that among the populations studied, the finches in the town of Puerto Velasco Ibarra on Floreana Island (one of the sites in the present study) were the least tolerant toward humans (Gotanda, 2020). The author suggested that Puerto Velasco Ibarra (a town of about ~140 permanent residents) may simply be too small to be considered an "urban" site to investigate the impacts of urbanization on the finches' behavioral adaptations (Gotanda, 2020).

In this study, we investigated whether song syllable type (a culturally learned trait) and aggressiveness (territorial response to simulated conspecific intruders) in small ground finches differed along a gradient of human activity levels (high-low-high) spanning 20 km and two habitats with contrasting levels of rainfall (and thus resources; arid lowlands and humid highlands) on Floreana Island. The only road on the island passes from the lowlands to the highlands, and the areas differ in resource availability (food and availability of nest sites). The majority of lowland human activity occurs in the town, Puerto Velasco Ibarra, where 90% of the houses are found, and near the highland farms, where 90% of the food-growing agricultural land is managed, which is adjacent to Asilo de la Paz, the main tourist site on the island for day-trip visitors. The two main areas rich in food for birds are the town in the lowlands and the agricultural zone (near Asilo de la Paz) in the highlands. The agricultural zone has the most fruit-bearing trees, but some can also be found in town near individual family homes. In addition, inhabitants in town often dry their crops collected from the agricultural zone in open areas, and captive tortoises near Asilo de la Paz produce dung that attracts many insects. Human impacts in the town and Asilo de la Paz, however, differ in scope as the habitat structure of the town is highly modified (with different types of trees, more open spaces, fewer shrubs, additional noise from human activities, traffic, etc.), while the Asilo de la Paz tourist site (where many finches co-occur near the tortoise holding pens) is exposed to humans walking along trails and noise from the adjacent agricultural lands.

We predicted that small ground finches living in areas with higher levels of human activity would have the strongest territorial response if human environments or human-provided food select for more aggressive behavioral phenotypes (in line with Evans et al., 2010; Scales et al., 2011; Foltz et al., 2015; Myers and Hyman, 2016; Hardman and Dalesman, 2018). Additionally, we predicted that birds living in

TABLE 1 Summary of the differences in habitats, levels of human activity, food, and small ground finch nesting densities (average number of active nests within 20m) across our four study sites.

Study site	Habitat type	Human activity	Food	Nesting density
Puerto Velasco Ibarra (Lowlands 1)	Arid lowlands rainfall 100–700 mm per year	High	High	Moderate
		12.5 vehicles per hour; 60–95 tourists/locals per day	Rich in food	1.60 ± 0.50
Arid zone outside the town (Lowlands 2)	Arid lowlands rainfall 100–700 mm per year	Low	Low	Low
		0.12 vehicles per hour; 0 tourists/locals per day	Low in food	1.41 ± 0.33
Cerro Pajas Volcano (Highlands 1)	Humid highlands	Low	Moderate	High
	rainfall 600–2,300 mm per year	0 vehicles per hour; 0 tourists/locals per day	Moderate in food	1.94 ± 0.39
Asilo de la Paz (Highlands 2)	Humid highlands	High	High	High
	rainfall 600–2,300 mm per year	7 vehicles per hour; 30–58 tourists/locals per day	Rich in food	1.78 ± 0.32

the lowlands, with lower rainfall and more patchy natural resources (food and availability of nest sites), would have the strongest territorial response if natural resource limitation selects for more aggressive behavioral phenotypes (see Foltz et al., 2015). In a previous study, we found that singing common song syllable types was associated with aggressiveness in three species of Darwin's finches including small ground finches (Colombelli-Négrel et al., unpublished data). We therefore also predicted a greater prevalence of song with the common syllable type in areas with higher levels of human activity and in the lowlands, and song with rare or uncommon syllable types in areas with lower levels of human activity and in the highlands.

2. Materials and methods

2.1. Study site and species

We conducted all recordings and simulated territorial intrusions at the start of the breeding season (January–February) in 2020 and 2022 on Floreana Island (Galapagos archipelago). Floreana island has the longest record of human settlement in the Galapagos archipelago and currently has ~140 permanent inhabitants (Lack, 1947a; Sulloway, 1982; Steadman, 1986). The highland is characterized by agricultural areas with *Cedrela* trees and a humid *Scalesia* forest (rich in nesting resources as many finches prefer to nest in *Scalesia* trees) located at the base of the Cerro Pajas volcano (01°17′S, 90°27′W) ~ 300–400 m above sea level and adjacent to the agricultural zone and the main tourist area, Asilo de la Paz (01°18′S, 90°27′W). Rainfall in the highland varies between 600 and 2,300 mm per year (Ben-Yosef et al., 2017; Conservancy, 2022; see also Common et al., 2022). The lowlands are adjacent to the town of Puerto Velasco Ibarra (01°16′S, 90°29′W) ~0–150 m above sea level and the vegetation is dominated by Palo Santo (*Bursera graveolens*) and Acacia (*Parkinsonia aculeata and Scutia spicata*; Dvorak et al., 2017). Rainfall in the lowlands varies between 100 and 700 mm per year (Common et al., 2022; Conservancy, 2022). Vegetation surveys across eight 100 m-transects in February 2020 in the highlands and lowlands showed that the two habitats differed in tree density and hence in the number of available nest sites: we found 12 trees in the lowlands (none of them *Scalesia*) during our transects vs. 240 trees (including 167 *Scalesia*) in the highlands.

To assess differences in levels of human activity across our study sites, we counted the number of vehicles per hour at each site in February 2022 between 6 am and 10 am on two different days. We counted on average 12.5 vehicles per hour in Puerto Velasco Ibarra (hereafter referred to Lowlands 1), 0.12 vehicles per hour in the arid zone outside the town (hereafter referred to Lowlands 2), 0 vehicles per hour in Cerro Pajas Volcano (hereafter referred to Highlands 1), and 7 vehicles per hour in Asilo de la Paz (hereafter referred to Highlands 2). Each vehicle had 4 to 10 passengers. On the same days, we also counted the number of tourists and locals seen during the day. We counted 60 tourists/locals per day and 95 tourists/locals at night in Lowlands 1, 0 local/tourist per day in Lowlands 2, 0 local/tourist per day in Highlands 1, and 58 tourists/locals per day and 30 locals per night in Highlands 2 (Table 1).

We conducted all our field work along a gradient of human activity levels (high-low-high) spanning two rainfall-influenced habitats (arid lowlands and humid highlands). Our gradient started in the lowland town of Puerto Velasco Ibarra (lower rainfall, higher level of human activity, rich in food; Lowlands 1), extended from the town edge through the lowland arid zone (lower rainfall, lower level of human activity, low in food and nesting sites; Lowlands 2), along the road to the highland forest trail to Cerro Pajas Volcano (higher rainfall, lower level of human activity, rich in nesting sites; Highlands 1) and finished at the highland tourist destination of Asilo de la Paz (higher rainfall, higher level of human activity, rich in food and nesting sites; Highlands 2; Figure 1; Table 1).

We recorded and tested territorial small ground finch males occurring in both the lowlands and highlands (Petren et al., 2005; Grant and Grant, 2008; Grant and Grant, 2014b; Lamichhaney et al., 2015; Kleindorfer et al., 2019). Ground finches typically feed on seeds but are often described as "imperfect generalists" because they also feed on a wide variety of foods, such as invertebrates and plant material (Tebbich et al., 2004; De León et al., 2014; Loo et al., 2019; Kleindorfer et al., 2022). Male age in Darwin's finches can be estimated by the proportion of black body plumage, which increases with each annual molt: yearling males have no black (black 0) while fully black

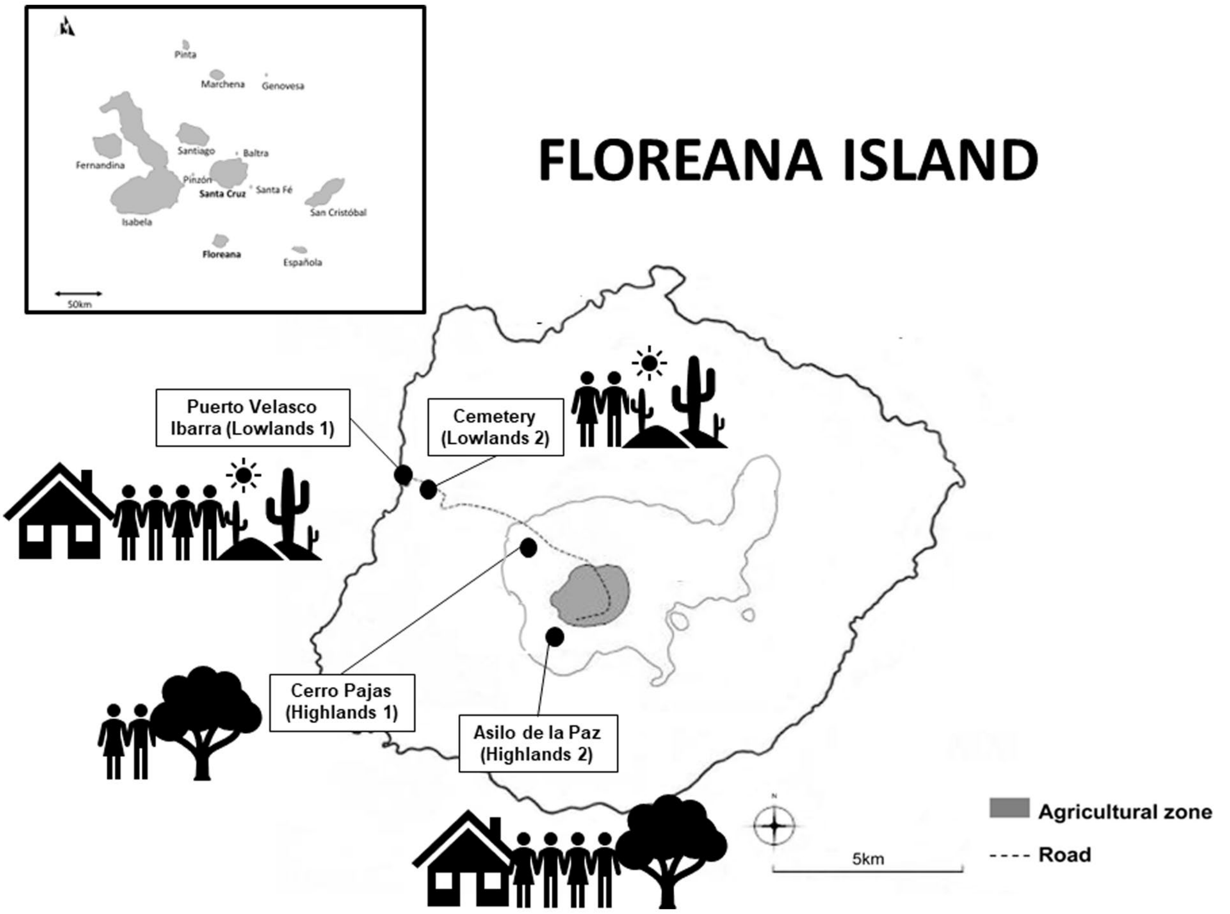

FIGURE 1
Map illustrating the urban gradient used in this study. The gradient started in the lowland town of Puerto Velasco Ibarra (lower rainfall, higher level of human activity; referred to as Lowlands 1), extended from the town edge through the lowland arid zone (lower rainfall, lower level of human activity; referred to as Lowlands 2), along the road to the highland forest trail to Cerro Pajas Volcano (higher rainfall, lower level of human activity; referred to as Highlands 1), and finished at the highland tourist destination of Asilo de la Paz (higher rainfall, higher level of human activity; referred to as Highlands 2).

males (black 5) are at least 5 years old (Grant, 1990; Kleindorfer, 2007b; Langton and Kleindorfer, 2019). At the start of the breeding season, which occurs after high rainfall (Kleindorfer and Dudaniec, 2020), males build a display nest and sing to attract prospective mates (Lack, 1947b; Christensen et al., 2006; Kleindorfer, 2007b). We located all nests by systematic searches in the study area—using cues such as singing males, nest building behavior or pair activity—and recorded the location of each nest using a Garmin GPS 64 (Garmin Ltd., Australia).

2.2. Song recordings and analyses

In 2020, we recorded 70 singing males (14 males at Lowlands 1, 22 males at Lowlands 2, 20 males at Highlands 1, and 14 males at Highlands 2) at their nest between 0600 and 1,100 (peak of song activity) as wave files using either (1) a Zoom H6 recorder (Zoom North America, United States) and a Sennheiser ME67 directional microphone (Sennheiser electronic GmbH & Co., United States) or (2) a Marantz PMD 661 Solid State recorder (Sound United, LLC, United States) and a Sennheiser ME66/K6 directional microphone (24 kHz sampling rate, 16-bit depth). We visualized all recordings with Raven Pro 1.6 Sound Analysis Software (Cornell Lab of Ornithology Bioacoustics Research Program, Ithaca, New York) using the Hann algorithm (DFT = 512 samples; frequency resolution = 124 Hz; time resolution = 11.6 ms; frame overlap = 50%). We categorized syllable types as previously described in Darwin's finches (Bowman, 1983; Ratcliffe and Grant, 1985; Gibbs, 1990; Colombelli-Négrel and Kleindorfer, 2021). Each individual small ground finch sings a trilled song that consists of several repetitions of a single syllable type (Bowman, 1979, 1983; Grant, 1984; Millington and Price, 1985; Grant and Grant, 1996; Figure 2). A male only sings one syllable type throughout its life. This syllable is learned early in life and does not change subsequently (Grant and Grant, 1996). We recorded nine different syllable types in our population of small ground finches (Colombelli-Négrel et al., unpublished data using 578 songs from 70 males; Figure 2). Previous analyses showed that the complete repertoire of syllable types was recorded for the species within our sample size (Colombelli-Négrel et al., unpublished data). Syllable types recorded from the individuals in the present study were defined as being "common" (types IV, V, and VI) or "uncommon" (types I, II, III, VII, VIII, IX) in the population based on a previous study in which uncommon syllable types were sung by less than 20% of the recorded males (Colombelli-Négrel et al., unpublished data). From the

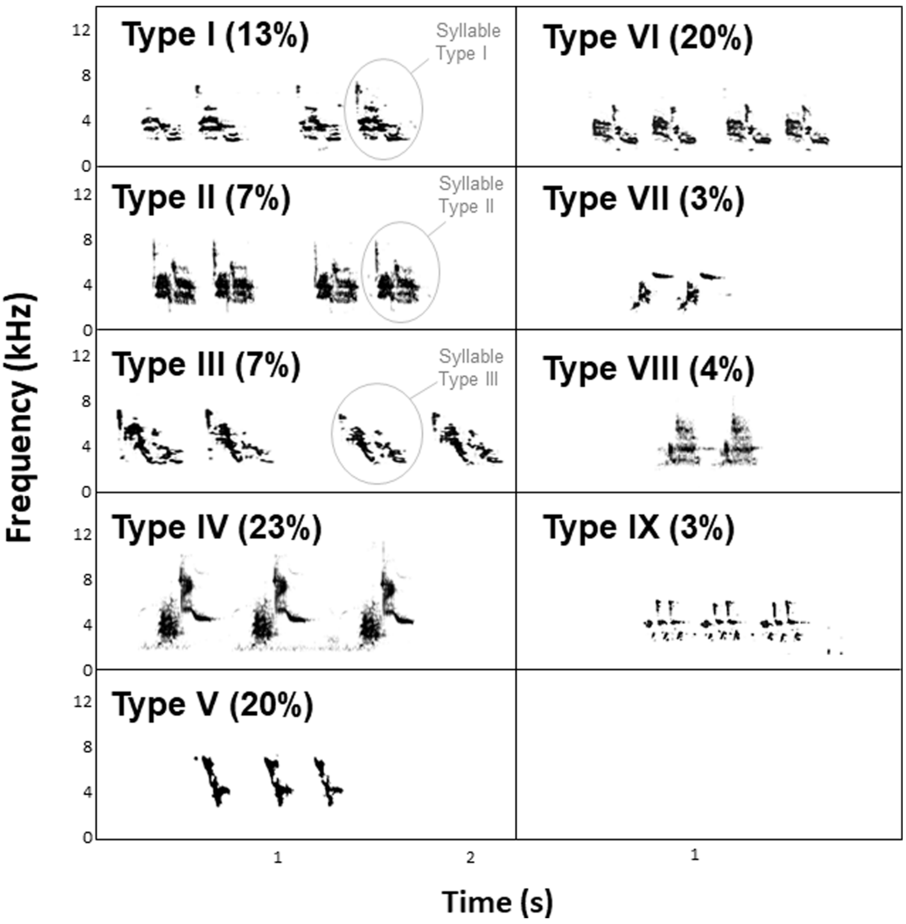

FIGURE 2
Spectrograms and percentages of the different syllable types recorded in small ground finches on Floreana Island in 2020.

recordings, we also noted for each male: (1) the average number of syllables per song, (2) the average song duration (s), (3) the average song tempo (sometimes referred to as the "pace" of the song or trill rate in trilled songs; the average number of syllables per second), and (4) the average song rhythmicity, calculated as the average duration of silence between two syllables divided by the average syllable duration (Sasahara et al., 2015).

2.3. Simulated territorial intrusions

We prepared all song playback tracks for the simulated intrusions using previously recorded conspecific songs with a good signal-to-noise ratio. All songs used for the playback were recorded on Floreana Island in 2020 as described above; all individuals used for the intrusions differed from those used in the song analyses. We used a high pass filter to remove sounds < 1.5 kHz and saved the tracks as uncompressed 16-bit broadcast wave files (.wav). We prepared a total of 18 different playback tracks using songs from 18 different birds. Each playback track was played on average 1.8 ± 0.4 times; range 1–8 times. Each track consisted of 3 min: 1 min of playback (six evenly spaced songs from the same individual) followed by 1 min of silence, and then a repeat of 1 min of songs. We then transferred these playback tracks onto an Apple iPod (Apple Inc., United States). We did not use a control (heterospecific) treatment in this study as previous experiments using Darwin's finches on Floreana showed very little response to our control treatment (yellow warbler, *Setophaga petechia aureola*, songs; Colombelli-Négrel and Kleindorfer, 2021), with birds rarely responding within the 3 min of playback (average latency 146 s out of 180 s) and remaining on average 9.32 m from the speaker.

In 2020 and 2022, we tested the response of 82 territorial males (47 in 2020 and 35 in 2022: 14 at Lowlands 1, 16 at Lowlands 2, 22 at Highlands 1, and 30 at Highlands 2) to the simulated intruder (via song playback) of the same species and the same location (i.e., we played Lowlands 1 songs to males tested at Lowlands 1, Lowland 2 songs to males from Lowland 2 and so on) but located at least three territories away. Out of the 82 males, we tested 30 males with an uncommon syllable type (a syllable defined as uncommon in the population as described above) and 52 males with a common syllable type (a syllable defined as common in the population as described above). We did all simulated intrusions via playback of songs between 0600 and 1,100, which corresponds to the peak of song activity. We never started playback until the male was observed within a 20 m radius of its nest prior to the experiment. All birds were tested once. Once we located a singing male and its nest, we placed the playback 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 started 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 posted within the focal male's territory (~10 m from the speaker) narrated the trial using a Marantz PMD 661 Solid State recorder (Sound United, LLC, United States) and a Sennheiser ME66/K6 directional microphone (Sennheiser electronic GmbH & Co., United States) or a Zoom H6 recorder (Zoom North America, United States) and a Sennheiser ME67 directional microphone. During the 3 min of playback, we recorded: (1) the latency (s; latency of first approach or song within 20 m); (2) the minimum distance (m; minimum distance between the focal bird and the speaker); (3) the time at 1 m (total time (s) spent within 1 m of the speaker during the 3 min of playback); (4) the number of flights over the speaker (crosses); as well as (5) the total number of songs produced by the male during the 3 min of playback.

2.4. Statistical analysis

We used SPSS version 25.0 for Windows (SPSS Inc., Chicago, IL, United States) for all statistical analyses. Data are shown as means ± S.E.

2.4.1. Songs, human activity, and habitat

We analyzed difference in the prevalence of syllable types (common, uncommon) across the four study sites using a Chi-squared test. We quantified differences in song characteristics (number of syllables per song, song duration, song tempo and song rhythmicity) in relation to "habitat" (lowlands, highlands), "human activity" (low, high) and the interaction "habitat × human activity" using MANOVAs and Bonferroni *post hoc* pairwise comparisons.

2.4.2. Responses to simulated territorial intrusions, human activity, and habitat

We used principal component analysis (PCA, correlation matrix) with Varimax rotation to reduce playback responses (minimum distance, latency, time within 1 m, number of flights over the speaker, and number of songs produced during the playback period), which produced two principal components with eigenvalues > 1 (Kaiser-Meyer-Olkin = 0.73; Bartlett's test: $\chi 2(10) = 91.96$, $p < 0.0001$): PC1 (which we label PCA Physical Behaviors) with an eigenvalue of 2.40 and accounting for 48% of variance and PC2 (which we label PCA Vocal Behaviors, as it primarily depends on number of songs) with an eigenvalue of 1.12 and accounting for 22% of variance (Table 2). High PCA scores indicated a strong response to playback (a shorter latency to respond, a shorter minimum distance, more time spent close the speaker, many flights over the speaker, many songs produced). We analyzed playback response with a generalized linear mixed model (GLMM; PCA Physical Behaviors) and a general linear model (GLM; PCA Vocal Behaviors). Both models had normal distributions (identity link) and included "year" (2020, 2022), "habitat" (lowlands, highlands), "human activity" (low, high), the interaction effect "habitat × human activity," playback syllable (common vs. uncommon), and "male black" (as an indication of male age; categorized between 0 and 5 as mentioned above) as fixed factors. We included "stimulus ID" as a random effect when analyzing PCA Physical Behaviors (GLMM) but not PCA Vocal Behaviors (GLM) due to the lack of a positive definite covariance matrix of the random effect when "stimulus ID" was added to the model.

TABLE 2 Factor loadings from principal component analysis (PCA) of the small ground finches' responses to playback (*n*=82 individuals).

Playback response	PCA physical behaviors	PCA vocal behaviors
	(2.40; 48%)	(1.12; 22%)
Latency (s)	−0.43	−0.66
Min distance (m)	−0.76	−0.32
Time within 1 m	0.84	−0.26
Crosses	0.84	0.06
Number of songs	−0.09	0.89

High PCA scores indicated a strong response to playback (a shorter latency to respond, a shorter minimum distance, more time spent close the speaker, many flights over the speaker, many songs produced). The eigenvalues and the percentage of variance explained by each factor are presented in brackets.

3. Results

3.1. Songs, human activity, and habitat

The prevalence of common syllable types differed across study sites [$\chi 2(3) = 7.90$, $p = 0.048$; Figure 3], with common syllable types being more prevalent at Lowlands 1, Lowlands 2, and Highlands 2 compared to Highlands 1 site. The number of syllables per song, song duration, song tempo and song rhythmicity did not differ across habitats or levels of human activity (all $p > 0.06$).

3.2. Responses to simulated territorial intrusions, human activity, and habitat

During our simulated territorial intrusions, 75 males (91%) approached the speaker within less than 10 m. We found significant main effects of habitat, year, and levels of human activity but no interaction effect of habitat × human activity on behavioral response to playback (PCA Physical Behaviors; GLMM: Figure 4; Table 3). Specifically, finches living in the lowlands were more aggressive than finches living in the highlands, irrespective of human activity (Figure 4; Table 3). Within each habitat (lowland and highland), birds were more aggressive in areas with more human activity (Lowlands 1 and Highlands 2) compared to areas with less human activity (Lowlands 2 and Highlands 1; Figure 4; Table 3). Behavioral responses were stronger in 2020 compared to 2022 (Table 3). Behavioral responses did not differ in relation to playback syllable or male black (Table 3). The random effect stimulus ID did not significantly account for any variance within PCA Physical Behaviors (Wald Z = 0.81; $p = 0.42$).

During simulated territorial intrusions, 61 males (74%) sang at least one song. Vocal response to playback (PCA Vocal Behaviors) did not differ across years, levels of human activity, habitat or in relation to playback syllable (GLM: Table 3). Males categorized as 1 year old and 3 year old responded with significantly more vocalizations than older males (Table 3).

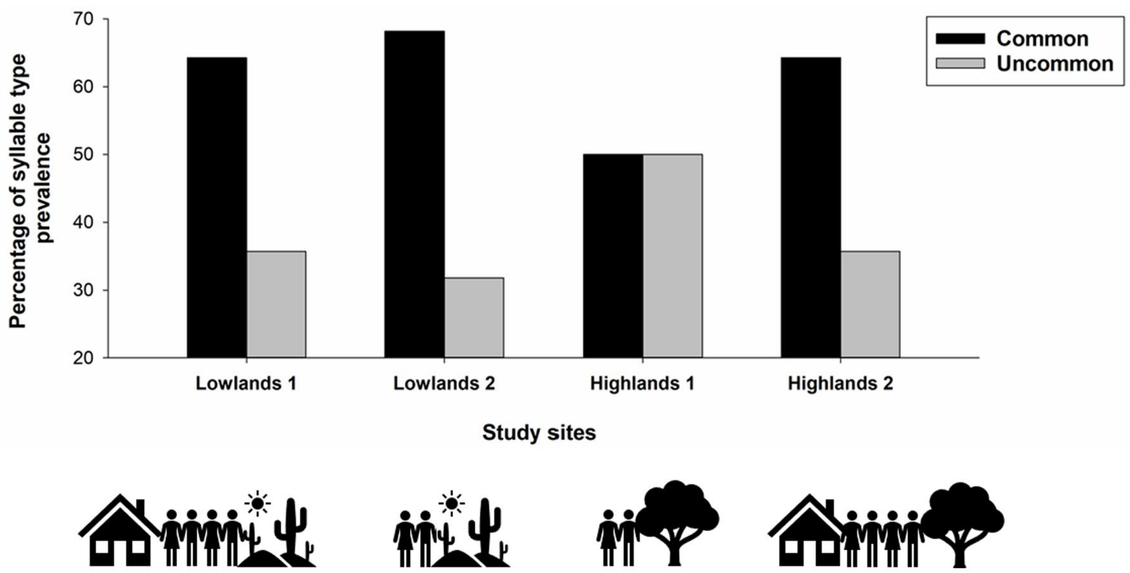

FIGURE 3
Prevalence of syllable types (common, uncommon) across study sites (Lowlands1, Lowlands 2, Highlands 1, Highlands 2). Small ground finches in our study sang IX different syllable types and syllable type was defined as "common" (types IV, V, and VI) or "uncommon" (types I, II, III, VII, IIX, IX) based on a previous study in which uncommon syllable types were sung by fewer than 20% of the recorded males (Colombelli-Négrel et al., unpublished data).

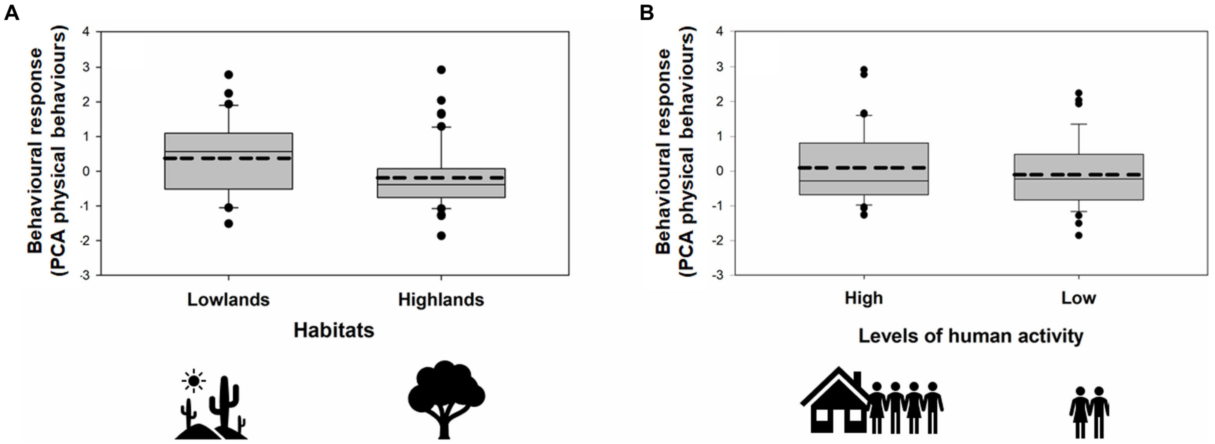

FIGURE 4
Behavioral playback responses of 82 resident males to the playback of conspecific intruder songs in relation to **(A)** habitat (lowlands, highlands) and **(B)** levels of human activity (high, low). The responses are shown as PCA scores (PCA Physical Behaviors) whereby higher scores indicate a stronger response to playback (a shorter latency to respond, a shorter minimum distance, more time spent close the speaker, many flights over the speaker). Horizontal lines within the boxes represent the means (hashed lines) and medians (straight lines). The upper and lower limits of the boxes show the 75th and 25th percentiles, respectively. Black circles indicate outliers.

4. Discussion

While human activities can have negative consequences for biodiversity (Shochat et al., 2010), some species can thrive in human-altered ecosystems. In this study, we provide the first evidence that a culturally learned signal (syllable type) that correlates with a behavioral trait (aggressiveness; Colombelli-Négrel et al., unpublished data) may be favored in human-affected environments. Specifically, we found that small ground finches living in human impacted areas and in the arid lowlands had the strongest behavioral response to stimulated territory intrusions. We also found that at sites with a higher percentage of males singing one of the three common syllables, males also had the strongest aggressiveness responses during playback. Our results add to the growing number of studies showing the importance of resource distribution and human-altered environments as potential selective forces in the evolution of differences between birds living near or away from humans (e.g., Evans et al., 2010; Scales et al., 2013; Foltz et al., 2015; Hardman and Dalesman, 2018; Gotanda, 2020).

Similar to previous studies showing that birds living near humans were more aggressive than those living away from

TABLE 3 Output from the GLMM and GLM testing whether year, habitat, human activity, habitat × human activity correlated with playback response in small ground finches.

Fixed effects	Estimate	Std. error	*t*	*P*
(1) PCA physical behaviors (GLMM)				
Intercept	0.33	0.30	1.09	0.28
Year	0.77	0.24	3.17	**0.002**
Habitat	−0.99	0.34	−2.87	**0.005**
Human activity	−0.97	0.38	−2.53	**0.014**
Habitat × human activity	0.73	0.43	1.71	0.09
Playback syllable	0.17	0.28	0.61	0.54
Male Black (0–1)	−1.19	0.94	−1.27	0.21
Male Black (1–2)	0.04	0.47	0.08	0.94
Male Black (2–3)	−0.11	0.43	−0.25	0.80
Male Black (3–4)	0.43	0.37	1.15	0.25
Male Black (4–5)	0.24	0.31	0.77	0.44
(2) PCA vocal behaviors (GLM)				
Intercept	−0.28	0.29	−1.00	0.33
Year	0.32	0.26	1.21	0.23
Habitat	0.05	0.32	0.17	0.87
Human activity	0.42	0.38	1.10	0.28
Habitat × human activity	−0.69	0.44	−1.57	0.12
Playback syllable	−0.10	0.23	−0.44	0.66
Male Black (0–1)	0.51	0.97	0.53	0.60
Male Black (1–2)	1.16	0.51	2.29	**0.02**
Male Black (2–3)	−0.16	0.46	−0.34	0.73
Male Black (3–4)	0.85	0.39	2.17	**0.03**
Male Black (4–5)	−0.24	0.32	−0.73	0.47

Our models included "year" (2020, 2022), "habitat" (lowlands, highlands), "human activity" (low, high), the interaction effect "habitat × human activity," playback syllable (common vs. uncommon), and "male black" (an indication of male age; categorized between 0 and 5) as fixed factors. Statistically significant (<0.05) values are marked in bold (*n* = 82 individuals).

humans (e.g., Evans et al., 2010; Scales et al., 2011; Foltz et al., 2015; Myers and Hyman, 2016; Hardman and Dalesman, 2018), we found that small ground finches living in areas with more human activity (Lowlands 1, Highlands 2) showed stronger behavioral response to playback compared to those living in areas with less human activity (Lowlands 2, Highlands 1). This may be due to the fact that human impacted areas have more resources like food and water (e.g., Fox et al., 1981; Scales et al., 2013), which is the case on Floreana island (Lowlands 1) where the lowland town has water and many human food sources (inhabitants often dry their crops collected from the agricultural zone in the open) while the highland agricultural areas and the tortoise breeding center near Asilo de la Paz (Highlands 2) have large reservoirs of water and many tortoises that produce dung and attract insects. In addition, the town and agricultural areas are more likely to be impacted by noise from vehicles, or even generators, than the more rural areas (e.g., Phillips and Derryberry, 2018; Akçay et al., 2020). While both ideas remain to be tested to explain the observed differences in aggressiveness between our populations, our results support the idea that even small urban centers or the mere occurrence of human activity can influence birds and their behavior (see also Gutzwiller and Anderson, 1999; Fernández-Juricic, 2002).

Regardless of human activity, we found that ground finches living in the arid lowlands had the strongest behavioral response to a simulated intruder, suggesting that natural resource distribution or human-provided food may also select for more aggressive behavioral phenotypes (see Foltz et al., 2015). Non-random distribution of resources across the landscape can result in heterogeneity in territory or individual quality, which in turn may correlate with aggressive response in territory owners (Scales et al., 2013; Foltz et al., 2015). Higher quality territories may be subject to higher levels of intrusions by conspecifics (Piper et al., 2000; Ferrer et al., 2015), thereby resulting in higher levels of aggressive defense (Piper et al., 2022). High aggressiveness may also be driven by the supplementation of more human-related food, which could increase body condition and thus aggressiveness (see Foltz et al., 2015). In support of this idea, color banded lowland birds nesting outside of the town center in the arid Lowlands 2 site were often seen foraging in town near human dwellings.

Differences in song frequencies (kHz) in relation to human activities have been more commonly investigated than differences in cultural distribution of signals, such as learned syllable types (e.g., Seger-Fullam et al., 2011; Slabbekoorn, 2013; Moiron et al., 2015). Still, one study reports that birds living near humans were more complex singers (i.e., had larger syllable repertoires; Deoniziak and Osiejuk, 2019), while another study reports that they sang songs with fewer elements than forest birds (Nemeth and Brumm, 2009). Considering the importance of song and element or syllable type for territory defense and mate attraction (Catchpole and Slater, 2008), understanding how cultural aspects of bird songs may vary with the level of human activity could help predict which individuals may survive in human-altered environments.

There are several potential explanations for why the cultural distribution of signals may be different in human-impacted habitats. First, habitat fragmentation resulting from human activities may restrict connectivity between populations, and thus cultural transmission (Laiolo and Tella, 2005; Laiolo and Tella, 2007). Second, individuals may be surrounded by different conspecific densities (Fokidis et al., 2011), which would influence whom they learn their cultural traits from Grant and Grant (1997). Finally, differences in cultural traits may simply be a side effect of selection for other behavioral traits, such as higher aggressiveness (Coss et al., 2002; Scales et al., 2011; Baxter-Gilbert and Whiting, 2019), which may be a favorable trait in modified environments. For instance, social enforcement of conformity may be stronger in populations with higher aggressiveness levels (Lachlan et al., 2004). In this study, we found that more common syllable types were produced in areas where birds were also most aggressive, which aligns with previous research showing that males singing common syllable types had the strongest aggressive response to simulated territory intrusions (Colombelli-Négrel et al., unpublished data). Syllable types in Darwin's finches do not seem to influence breeding success, but could have important fitness consequences for individuals if, for example, common syllable types elicit stronger aggressive responses from conspecifics than uncommon syllable types

(Colombelli-Négrel et al., unpublished data). Despite the fact that our current study did not use the same birds for our song and playback analyses, it suggests that variation in song syllable types may be the result of selection for particular behavioral phenotypes, an idea that warrants further investigation.

While we found differences in the prevalence of common syllable types across our study sites, we found no differences in the number of syllables per song, song duration, song tempo or song rhythmicity between habitats or levels of human activity. One study suggested that acoustic signals may better transmit in human-altered (i.e., noisy) environments if produced at a faster rate (Redondo et al., 2013). Yet studies investigating temporal variation in relation to levels of human activities have found mixed results. For example, Potvin et al. (2011) and Hill et al. (2018) found that birds living near humans sang songs with slower syllable rate or longer inter-syllable rate compared to rural birds, while Nemeth and Brumm (2009) found that birds living near humans sang shorter songs than forest birds, and Brewer and Fudickar (2022) found no temporal differences. Further investigation into how human-altered environments may affect temporal aspects of bird songs is needed.

In conclusion, this study provides the first evidence that human-altered environments and resource distribution may select for behavioral phenotypes that carry a cultural tag. Interestingly, it should be noted that the small ground finches are expanding into highlands previously occupied by sharp-beaked ground finch (*Geospiza difficilis*; see Galligan and Kleindorfer, 2010), a species now extinct on Floreana island (Grant et al., 2005). The distribution of the new small ground finch populations on Floreana island—with persistence of (source) lowland small ground finch populations having different traits compared with (purported colonist) highland populations—suggests selective factors shaping behaviors and culture.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The animal study was reviewed and approved by Flinders University Animal Welfare Committee (E480-19).

Author contributions

DC-N, ÇA, and SK conceived the idea, designed the study, and collected the data. DC-N analyzed the data and wrote the first draft of the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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