Darwin's small and medium ground finches might have taste preferences, but not for human foods

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Abstract

Urbanization is rapidly changing ecological niches. On the inhabited Galapagos Islands, Darwin's finches consume human-introduced foods preferentially; however, it remains unclear why. Here we presented pastry with flavour profiles typical of human foods (oily, salty, sweet) to small and medium ground finches to test if latent taste preferences might drive selection of human foods. If human-food flavours were consumed more than a neutral or bitter control only at sites with human foods, then we predicted tastes were acquired after urbanisation; however, if no site-differences were found then this would indicate latent taste preferences. Contrary to both predictions, we found no evidence that human-food flavours were preferred compared to control flavours. Instead, medium ground finches consumed the bitter control pastry most and wiped their beaks more frequently after feeding on oily and sweet pastry (post-ingestion beak-wiping can indicate aversions). Small ground finches showed no differences in consumption but wiped their beaks most after feeding on sweet pastry. We found no evidence that medium and small ground finches found bitter-tasting food aversive. Furthermore, we found no evidence that taste preferences could have played a major role in Darwin's finches responding to the presence of human foods during increased urbanization.

Key words: *Geospiza fortis*, *Geospiza fuliginosis*, foraging, human influences, urbanization, Galapagos

Introduction

Human behaviour is now recognised to be a strong driver of local adaptation and differences among populations of animals [1,2]. Urbanization [3–5], for example, can have profound effects on foraging because humans often introduce novel foods to the surrounding environment either intentionally (e.g. via garden bird feeding [6–8]) or unintentionally (e.g. by planting ornamental, invasive plants [9,10] or food waste [11,12]). This changes the diversity and availability of food items, and generates different foraging landscapes from those in which most animals evolved [13–15]. However, organisms' responses to these altered niches vary, with some birds, for example, not only adapting more readily to incorporate human-foods into their diet, but even preferentially consuming them over native food sources [14,16–19]. These differences in whether, and how, populations and species utilise human foods can then have consequences for local adaptation [7,20] and potentially affect species divergence [21]. Taste preferences can also have implications in conservation, mediating the potential for invasive species to establish [22,23], for example, or making native species vulnerable to accidental poisoning [24]. Furthermore, the gut microbiome, which is increasingly recognised to affect a suite of physiological, immune, and cognitive functions in wild non-human animals [25,26], can also vary with consumption of human foods [27–29]. Nevertheless, understanding why some species in urban areas shift their diets to preferentially forage on human foods remains unclear.

Taste plays an important role in foraging as it allows individuals to detect nutritious versus unprofitable substances in food items [30,31]. Although taste was long assumed to be of little importance for birds, they have sophisticated sensory adaptations with taste receptors identified for bitter [30,32,33], sweet [30], and salt [34] flavours. Furthermore, experiments have

demonstrated that birds can use bitter tastes to avoid toxic foods [32,34,35], use sweet tastes to detect sugars [30,34,36–39] indicating high caloric content [40], and use salty tastes to detect salts [39,41,42] indicative of necessary minerals and proteins [43]. Preferences for certain tastes can therefore evolve when flavours are linked to food quality and nutrient content [30]. For example, omnivorous and frugivorous birds are able to detect sugars at low levels and prefer sweet tastes compared to birds that forage on other types of food [34], potentially because this facilitates optimal foraging for caloric content of nectar and ripe fruit.

Taste preferences can also be maladaptive, however, if they lead to the preferential consumption of human foods. The introduction of human foods in urban areas causes changes in resource availability, including calories and nutrient concentration [44,45] as much of the human foods accessible to birds consists of discarded ‘junk food’ and snacks that are high in fat, sugar, and salt. The availability of these foods can alter natural nutritional landscapes with detrimental effects [24,46]. For example, hibernation in mammals is perturbed when human foods are consumed [47,48], and racoons feeding on human foods in urbanised areas show greater weight and blood sugar content [49]. In birds, American crow (*Corvus brachyrhynchos*) chicks are smaller [50] and Canadian geese (*Branta canadensis maxima*) have higher rates of angel wing disorder in urbanised areas, likely as a result of nutrient deficiency [51], and Australian magpies (*Gymnorhina tibicen*) show alterations to blood chemistry following backyard provisioning [52]. If animals are adapted to detect and prefer foods based on taste profiles that are coincidentally elevated in human foods, then they could assess these foods erroneously as high quality and favour consumption [24,45]. On the other hand, if their taste receptors are adapted to prefer flavours characteristic of human foods, then they might be better able to take advantage of this

newly available resource if native foods decline (i.e. poor condition is preferable to starvation). Therefore, preferential consumption of different foods due to taste preferences, especially in the context of urbanization, could be either adaptive or maladaptive. However, it remains largely unknown whether taste preferences actually underlie the preferential consumption of human foods in urban areas.

Here, we investigate if Darwin's finches, which on human-inhabited islands are known to vary in their preferential consumption of human foods [14], have taste preferences for flavours associated with human foods. Darwin's finches are a model system for demonstrating how foraging ecology shapes adaptation into different ecological niches and results in an adaptive radiation [53,54]. Contemporary work has shown that the presence of humans is affecting traits such as beak morphology [55] and this has been linked to the consumption of human foods [21]. Indeed, we know that Darwin's finches on human-inhabited islands can preferentially consume human foods including crisps (potato chips), biscuit (hard cookies), and rice at sites where these foods are abundant such as at tourist beaches and in urban areas [14]. Indeed, urban finches can have higher nesting success than non-urban finches [56], suggesting that at least some species of Darwin's finches can become locally adapted to urban environments. Thus, the Darwin's finches on the Galapagos represent an excellent opportunity to test whether taste preferences might underpin consumption of human foods where these are available and abundant, such as in urban or tourist areas.

We assessed taste preferences in Darwin's finches in separate populations with little to no movement of finches among sites [57] that varied in the availability of human foods previously

shown to be attractive to finches [14]. We presented flavours in the absence of visual cues typical to human foods to exclude the role of learned associations with packaging (e.g. crisp packets [14]). If taste preferences arise because of the consumption of human foods, we predicted finches at sites with human foods would only prefer flavours associated with human foods (e.g. sweet, salty, and oily) at sites where human foods are abundant. If taste preferences are innate (i.e. latent), we predicted preferences would occur for such flavours across sites, regardless of the presence or absence of human foods. Potential taste preferences can be quantified as variation in feeding rate, or as variation in post-feeding beak-wiping rate [30,58–60]. Although beak-wiping can clean the beak of debris [61], vigorous beak-wiping commonly occurs after feeding on something unpalatable [30,60]. Therefore, we measured taste preferences in terms of consumption and beak-wiping behaviour compared to two controls, neutral pastry that had no flavour added and bitter-flavoured pastry as a negative control. Bitter substances are aversive to many bird species, so we expected finches to consume less bitter-flavoured pastry compared to neutral or other flavoured pastry across all sites as well as to elicit more beak-wiping behaviour [30,60] .

Materials and Methods

Study species and location

We focused on Darwin's finches, an endemic group of passerines on the Galapagos Islands, at three sites on Santa Cruz Island that varied in their exposure to human foods (Supplemental Figure 1). The remote site was a non-urban site 12 km from the main urban town with no presence of human foods (El Garrapatero proper) [27], the beach site was El Garrapatero beach, a tourist, non-urban site 12 km from Puerta Ayora where visitors often bring picnics so human

food is present and abundant (de León et al. 2018, Knutie et al. 2019), and the town site was Puerto Ayora, a fully urbanized town where humans and their food are ubiquitous throughout the entire town [14]. The two focal species were small ground finches (*Geospiza fuliginosa*) and medium ground finches (*Geospiza fortis*). Galápagos mockingbirds (*Mimus parvulus*) and two other finch species (the cactus finch, *Geospiza scandens* and the small tree finch, *Camarhynchus parvulus*) were also present occasionally, but rarely interacted with our experiments.

Experimental protocol and video recording

We conducted trials at each of the three sites (remote = 16 trials, beach = 15 trials, and town = 18 trials; Supplemental Table 1) using a 'cafeteria' tray experiment [14]. Five plastic cups with the diameter of a chicken egg were randomly positioned in the periphery of a 3x3 egg carton and placed on the ground on a white plastic dinner plate that was visible below the egg carton (e.g. the carton did not hang over the sides of the plate; Supplemental Figure 2). The central dimple of the egg carton was weighted with a small rock, and the unused dimples were left empty. The trial began when the first bird approached the tray and fed, and then continued for 10 minutes [14]. If no finches fed, the trial was aborted after 20 minutes. All trials were performed during the rainy season from February 20th to March 25th, 2018, between 6am and 11am, or 3pm and 6pm and were filmed using a video camera (Sony HDR-CX625 Full HD Compact Camcorder or Canon 7D Mark II with 100-400mm lens) positioned 10 metres from the cafeteria tray. The majority of individuals were not uniquely identifiable (fewer than 4%), so we cannot be sure that birds participating in different trials were independent. However, to reduce the potential for pseudo-replication between trials, we conducted each trial at least 100 m apart within the study locations.

Each cup was filled with 2.5 g of pastry made from flour, unsalted butter, and water, following methods from Speed and colleagues (2000). The pastry (335 g flour, 135 g unsalted butter, and 30 g water) was flavoured according to commonly available human-foods in the environment [14] and each cup was coloured (blue, green, pink, purple, and yellow) to facilitate recognition of the contents: (i) blue indicated high in fat (6g vegetable oil/pastry batch), (ii) green indicated bitter (0.1g quinine/pastry batch), (iii) purple indicated sweet (23g sugar/pastry batch), (iv) yellow indicated salty (1.333g salt/pastry batch), and (v) pink indicated neutral or unflavoured pastry. To habituate the birds to the experimental set-up, we first conducted trials at each site with only unflavoured pastry (remote = 17 trials, beach = 17 trials, town = 19 trials; Supplemental Materials, Supplemental Table 1). Birds can have latent colour preferences, either from experience or evolutionary history [e.g., 62]. However, we detected no strong biases within finch species towards, or against, any of the coloured cups based on these trials (Supplemental Materials; Supplemental Table 2; Supplemental Figures 3 & 4). Therefore, any preferences detected using flavoured pastry were most likely due to taste and not visual preferences.

Video analysis

Videos were analysed using BORIS (Behavioral Observation Research Interactive Software) (Friard and Gamba, 2016) and each 10-minute trial was analysed by one observer (DL). Species identification was done based on bill and body size in comparison to the size of the cafeteria tray. The observer was trained by KMG to first identify still images of birds (taken from videos collected during trials), and then by using the videos. We counted the number of feeding events at the level of the trial and assigned these to each species of finch based on their body size and beak morphology. We defined a feeding event as when a bird's beak was submerged into a cup,

lifted, and then food was consumed (Supplemental Figure 2). If at least one cup was visited during a trial, any cups not visited received a score of 0. Following each feeding event, we then recorded the number of times the finch wiped its beak on a surface within 20 seconds in accordance with published methods on beak-wiping [60,61].

Statistical analyses

Statistical analyses were undertaken using the R environment version 4.0.2 (R Core team, 2020; analyses code and data are available as Supplemental Materials). To analyse differences in taste preferences, we used generalised linear mixed-effect models (GLMMs) with a negative binomial error distribution (using the glmer.nb() function in the lme4 package; Bates et al. 2015) to account for overdispersion in the number of feeding events (response variable). Trial number was included as a random effect to account for non-independence of feeding events within trials and the fixed effects were site, pastry flavour, and their interaction. If the interaction did not contribute significantly to model fit (using a likelihood ratio test to compare with a simpler model containing only additive fixed effects) it was removed, but site and pastry flavour were retained in all models. We then used z-tests to assess the significance of differences in consumption among pastry flavour and site using ‘neutral flavour (pink)’ and ‘town’ as the reference level (i.e. intercept). We report estimates and standard errors and provide incidence rate or odds ratios to compare effects.

The number of beak wipes following a feeding event were low (5 or fewer) and highly right-skewed (medium ground finch = 3.69, small ground finch = 3.44; calculated using the ‘moments’ package; Komsta and Novomestky 2015) so we therefore we modelled the occurrences of beak wipes using a binomial distribution, where the denominator in the response

variable was the number of feeding events when no beak wipes occurred. Assumptions of homogeneity of variance and uniformity of the residuals for all models were checked using Kolmogorov-Smirnov tests for uniformity, simulation tests for dispersion, and a binomial test for outliers (implemented using the 'DHARMa' package [65]). The cactus finch and small tree finch rarely came to the experimental trays so only medium and small ground finches were included in the data set. Furthermore, attendance of medium ground finches at beach trials was very low and they did not feed from all cups within any trial. Therefore, data from this location were excluded for medium ground finches and the two species were analysed separately.

Results

A total of 53 taste preference trials were conducted across three sites. Both medium and small ground finches varied in their propensity to participate in experimental trials at different locations. Medium ground finches participated at 16 of the 16 trials conducted at remote sites, 0 of the 15 trials conducted at beach sites, and in 10 of the 18 trials conducted at town sites. Small ground finches participated at 10 of the 16 trials conducted at remote sites, 15 of the 15 trials conducted at beach sites, and 14 of the 18 trials conducted at town sites (Supplemental Table 1).

Medium ground finches

Medium ground finches engaged in significantly more feeding events at the remote site than the town site (Table 1, Figure 1C, Supplemental Table 1b), but we found no evidence that taste preferences differed according to location (location*flavour-type: $\chi^2 = 4.687$, d.f. = 4, p = 0.321). Medium ground finches did, however, differ in their feeding events with respect to flavour-type (flavour-type: $\chi^2 = 11.810$, d.f. = 4, p = 0.019), with significantly more feeds

occurring on the bitter (green) pastry than the neutral flavoured pastry (Table 1; Figure 1A & 1C). No other flavour-types were consumed more frequently than the neutral pastry (Table 1; Figure 1A & 1C). We next assessed behavioural wiping responses to each flavour-type (Figure 1B &1D). However, as there were fewer than 10 trials at town sites where each flavour was consumed (neutral (pink): N = 5, oily (blue): N = 5, bitter (green): N = 8, sweet (purple): N = 3, salty (yellow): N = 6); we could not test whether responses to specific flavour-types differed among the locations. Overall, medium ground finches were more likely to wipe their beaks after consuming oily (blue; 14.7% of feeding events) or sweet (purple; 15.5% of feeding events) flavours than after consuming neutral flavoured pastry (pink; Table 1; Figure 1B & 1D) and wiped their beaks the least after consuming bitter (green; 5% less than after consuming neutral pastry (Figure 1D)). Beak-wiping also tended to occur more often after feeding events at town sites compared to remote sites, although this was not significant (Table 1, Figure 1B & 1D). Together, these results suggest that medium ground finches consumed bitter-flavoured pastry the most (at both town and remote sites) yet wiped their beaks the least after feeding on this flavour.

Small ground finches

Small ground finches, on the other hand, showed no significant differences in their feeding preferences (Figure 2), either among flavour-types ($\chi^2 = 1.160$, d.f. = 4, p = 0.885, Table 1; Figure 2A & 2C), among the three sites ($\chi^2 = 2.866$, d.f. = 2, p = 0.239; town vs. beach estimate = 0.424 ± 0.319, z = 1.329, p = 0.184; town vs. remote estimate = -0.112 ± 0.357, z = -0.315, p = 0.753; Table 1; Figure 2A & 2C), or in interaction ($\chi^2 = 4.728$, d.f. = 8, p = 0.786; Table 1; Figure 2A &2C). Overall, while there were no differences among locations in the proportion of feeding events that led to beak-wiping ($\chi^2 = 2.298$, d.f. = 2, p = 0.317; Table 1; Figure 2B & 2D),

small ground finches were 63% more likely to wipe their beaks after consuming sweet-flavoured (purple) rather than neutral pastry (pink; Figure 2D). There were no significant differences between other flavours and neutral-flavoured pastry (Table 1; Figure 2B & 2D). The number of feeding trials where each flavour was consumed were too few to statistically test for location-specific differences in beak-wiping responses to flavours. Nevertheless, together the feeding events and beak-wiping data suggest that small ground finches show little discrimination of foods based on human-food flavours, regardless of location.

Discussion

Taste preferences have often been overlooked in understanding animals' foraging decisions, yet in human-modified environments, latent taste preferences could explain why some species are able to readily adapt to novel foods while others do not. Here we investigated if taste preferences can explain preferential consumption of human foods by Darwin's finches [14]. We predicted that if finches at sites with more exposure to human foods (i.e. at the tourist beach or in town) showed greater consumption and reduced aversive behavioural responses to flavours typical of these foods (salty, oily, sweet), then taste preferences could have developed from experience with the changed foraging landscape. However, if finches across sites preferred these 'human-food flavours' then latent taste preferences could have facilitated rapid adoption of human foods into the diet. Against both predictions, the only evidence we detected for a taste preference was that medium ground finches favoured the bitter-flavoured control. Medium ground finches fed most often on the bitter-flavoured pastry and wiped their beaks the least following its ingestion. This was surprising, given that bitter-tasting foods often elicit increased beak-wiping in birds [30,60]. It is possible that our sample sizes were too small to detect preferences for human-food

flavours, or that we did not add sufficient flavour to the pastry to be detectable. However, previous work detecting taste preferences had smaller sample sizes than our study (e.g., n = 6 per group [36]; n = 11 [37]; n = 6 and 10 [38], and the amount of flavour we added to the pastry emulated human foods as closely as possible. It therefore seems unlikely that our results can only be explained by methodological issues. Since Darwin's finches consume human foods preferentially when available, why did we not find preferences for flavours associated with commonly available human foods?

It could be that Darwin's finches have not evolved a preference for tastes associated with human foods because these species are generalist feeders, especially during periods of non-drought [13]. We conducted our trials during the traditional rainy season when the finches would be more generalist. Taste preferences evolve when they allow animals to identify food items that offer important nutrients (e.g., high in lipids, salts, or sugars)[30,31,34,46]. Yet for generalists, it might not be adaptive to have latent taste preferences if these limit individuals from consuming a wide variety of dietary items [13] or they might not need to discern specific foods that are high in lipids, salts, or sugars. Indeed, many studies that have found taste preferences in birds have been conducted with specialists [37,38]. Another possibility is that Darwin's finches have not yet acquired preferences for flavours associated with human foods. Tourism has grown exponentially only relatively recently [66]. At the tourist beach site, easy access to the public only became available around 2010 [J. Podos, personal communication], and the town of Puerto Ayora was established in 1926 [67; E. Hennessey, personal communication], so perhaps not enough generations have passed from when finches gained access to human foods for finches to acquire taste preferences.

For the medium ground finch, we found that the bitter taste is preferred across sites (Figure 1; Table 1), suggesting a latent taste preference for bitter, and the presence or absence of human foods did not correlate with different taste preferences as predicted. We also found no evidence for a lack of aversion to bitter pastry in both species with finches not wiping their bills more after consuming bitter pastry. This was unexpected because we know birds possess TAS2R bitter taste receptors [33], and often discriminate against toxic prey via bitterness. In fact, of the species studied by Wang and Zhao [33], medium ground finches had the second most TAS2R genes. So why would medium ground finches prefer bitter tastes as opposed to being averse? If the natural foods found at remote sites are bitter in taste, that might explain why medium ground finches have a latent preference for bitter tastes. Bitter tastes are often associated with aposematic prey, and the relative lack of aposematic prey on the Galapagos [68] suggests finches do not need to develop an aversion to bitter tastes as shown by the preferential consumption of bitter tastes and not wiping their bills after consuming bitter pastry. Another possibility is zoopharmacognosy, where animals eat medicinally advantageous foods, despite possible aversive qualities. This is common in birds; great bustards (*Otis tarda*) ingest toxic blister beetles to control digestive tract parasites [69] , and house sparrows (*Passer domesticus*) ingest leaves containing quinine (our bittering agent) during malaria outbreaks [70], alleviating symptoms. Quinine is an invasive plant found on the Galapagos. However, no finch has ever been observed consuming quinine (Heinke Jäger, personal communication), so this possibility is unlikely.

The Galapagos Islands are experiencing an exponential increase in urbanization and tourism, including permanent human residents [66], and we know Darwin's finches

preferentially consume human foods over natural food sources when readily available [14]. However, here we found no evidence for taste preferences for flavours associated with human foods during the traditional rainy season. It therefore seems likely that finches do not have latent preferences for these flavours, nor acquired a preference through repeated exposure to human foods. Why then have Darwin's finches adapted rapidly to changing food availability and incorporated human foods into their diet when human foods are readily available? One possibility is that they could be attracted to other sensory cues such as aural or visual cues associated with human foods. For example, in town and on the beach (but not in remote areas), finches respond to brightly coloured visual cues of human food packaging and are attracted to the 'crinkle' sound associated with foil and plastic food packaging [Supplemental Figure 4; 11]. Alternatively, it could be driven by availability itself at the beach and town sites. While the food sources Darwin's finches normally feed upon are available within town and at the beach [14] (though we did not control for this), the abundance of human foods at these sites simply make these more accessible to finches, and therefore, finches did not need to discriminate between different flavours typically associated with human foods and aversive flavours to expand their diet diversity [14]. Further work is required to understand the mechanisms underlying how Darwin's finches developed a preference for consuming human foods at sites where human foods are readily available.

Humans, through processes such as urbanization, can have a major impact on foraging ecology by introducing novel foods that can become preferentially consumed by birds [16,17]. However, the mechanisms leading to changes in foraging ecology remain largely unknown. Although we cannot yet explain *why* Darwin's finches prefer human foods, our results help to rule out the

possibility that taste preferences play an important role in incorporating human foods into their diets. Similarly, our finding that ground finches do not find bitter tastes aversive expands the increasing knowledge on variation in response to tastes among species. As the adoption of human foods into animals' diets can have cascading effects on health, reproduction, and fitness [6,15,20,47,49], it remains of paramount importance to elucidate why some species integrate these foods while others do not.

Author contributions

KMG and RT designed the study, KMG and LVR collected the field data, DL analyzed the videos, RT, DL, and KMG analyzed the data, and all authors wrote and edited the manuscript.

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Tables

Table 1. Mean differences (± S.E.) in the (I) number of feeding events and (II) proportion of feeding events followed by beak-wiping by (a) medium ground finches (I: N = 130 observations from 26 trials, II: N = 95 observations from 26 trials) and (b) small ground finches (I: N = 195 observations from 39 trials, II: N = 114 observations from 39 trials) from coloured cups containing pastry flavoured to be salty (yellow), sweet (purple), bitter (green), or oily (blue) at sites in town (intercept), remote locations, or at a beach (small ground finches only). Differences in (I) were estimated using generalised linear mixed effects models with a negative binomial error distribution and where trial and site were included as random effects. Differences in (II) were estimated using a similar model but with a binomial error distribution to account for proportional response data. 'Neutral', unflavoured pastry consumed at town sites was set as the intercept (in parentheses) in all models.

	I. Feeding events			II. Beak-wiping		
	Mean difference ± S.E.	Z	p	Mean difference ± S.E.	Z	p
(a) Medium ground finches:						
(neutral)	0.689 ± 0.367	1.879	0.060	-2.696 ± 0.345	-7.489	<0.001
Oily (blue)	-0.442 ± 0.367	-1.206	0.228	**0.905 ± 0.433**	**2.090**	**0.037**
Bitter (green)	**0.751 ± 0.355**	**2.118**	**0.034**	-0.053 ± 0.403	-0.131	0.896
Sweet (purple)	0.427 ± 0.353	1.207	0.227	**0.936 ± 0.368**	**2.541**	**0.011**
Salty (yellow)	0.207 ± 0.355	0.584	0.559	0.593 ± 0.399	1.486	0.137
Site - remote	**1.075 ± 0.359**	**2.993**	**0.003**	0.565 ± 0.320	1.765	0.078
(b) Small ground finches:						
(neutral)	1.827 ± 0.348	5.258	<0.001	-1.815 ± 0.257	-7.050	<0.001
Oily (blue)	-0.326 ± 0.428	-0.762	0.446	0.060 ± 0.276	0.217	0.828
Bitter (green)	-0.152 ± 0.427	-0.356	0.722	-0.024 ± 0.274	-0.087	0.931
Sweet (purple)	-0.092 ± 0.425	-0.215	0.830	**0.489 ± 0.242**	**2.017**	**0.044**

Salty (yellow)	-0.396 ± 0.427	-0.929	0.353	0.121 ± 0.271	0.448	0.654
Site – beach	0.424 ± 0.319	1.329	0.184	0.144 ± 0.255	0.563	0.573
Site – remote	-0.112 ± 0.357	-0.315	0.753	0.438 ± 0.291	1.508	0.132

Figure Legend

Figure 1. Differences in the (A,C) number of feeding events and (B,D) proportion of feeding events that were followed by beak-wiping by Medium ground finches presented with pastry in coloured cups with neutral (pink), oily (blue), bitter (green), sweet (purple), or salty (yellow) flavours common to human-foods in either town (●, N = 10 trials) or remote (▲, N = 16 trials) locations. A and B present the raw data, C and D present the effect sizes of the differences between each flavour and the neutral pastry, or between town and remote locations, computed from generalised linear mixed effects models (see Methods for more details). Effects that were significantly different from zero (dashed pink vertical line) are indicated by asterisks (* $0.01 < p < 0.05$, ** $0.001 < p < 0.01$).

Figure 2. Differences in the (A,C) number of feeding events and (B,D) proportion of feeding events that were followed by beak-wiping by small ground finches presented with pastry in coloured cups with neutral (pink), oil (blue), bitter (green), sweet (purple), or salty (yellow) flavours common to human-foods in either town (●, N = 14 trials), beach (■, N = 15 trials), or remote (▲, N = 10 trials) locations. A and B present the raw data, C and D present the effect sizes of the differences between each flavour and the neutral pastry, or between town, beach, and remote locations, computed from generalised linear mixed effects models (see Methods for more details). Effects that were significantly different from zero (dashed pink vertical line) are indicated by asterisks (* $0.01 < p < 0.05$, ** $0.001 < p < 0.01$).

Figures

Figure 1.

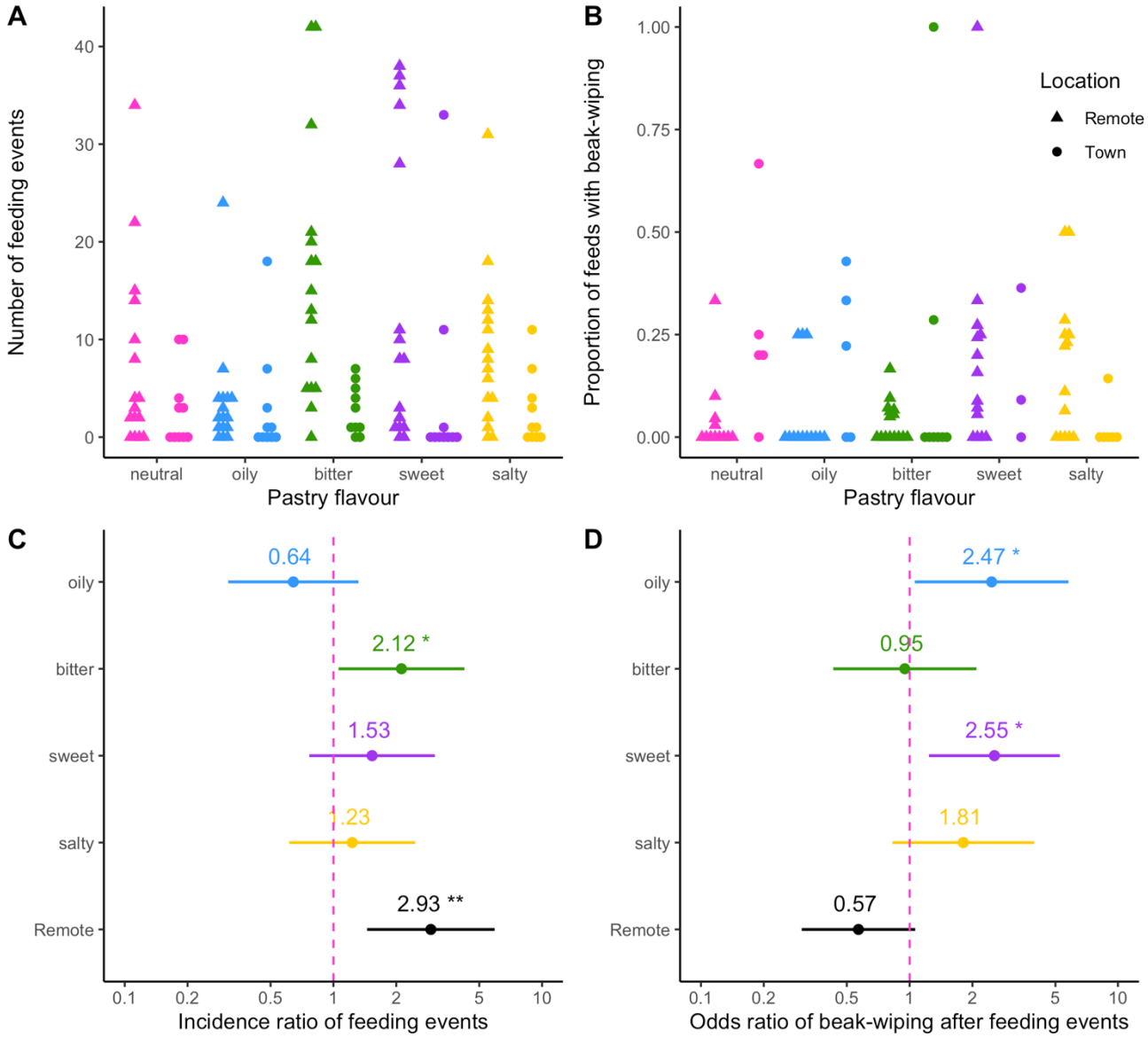
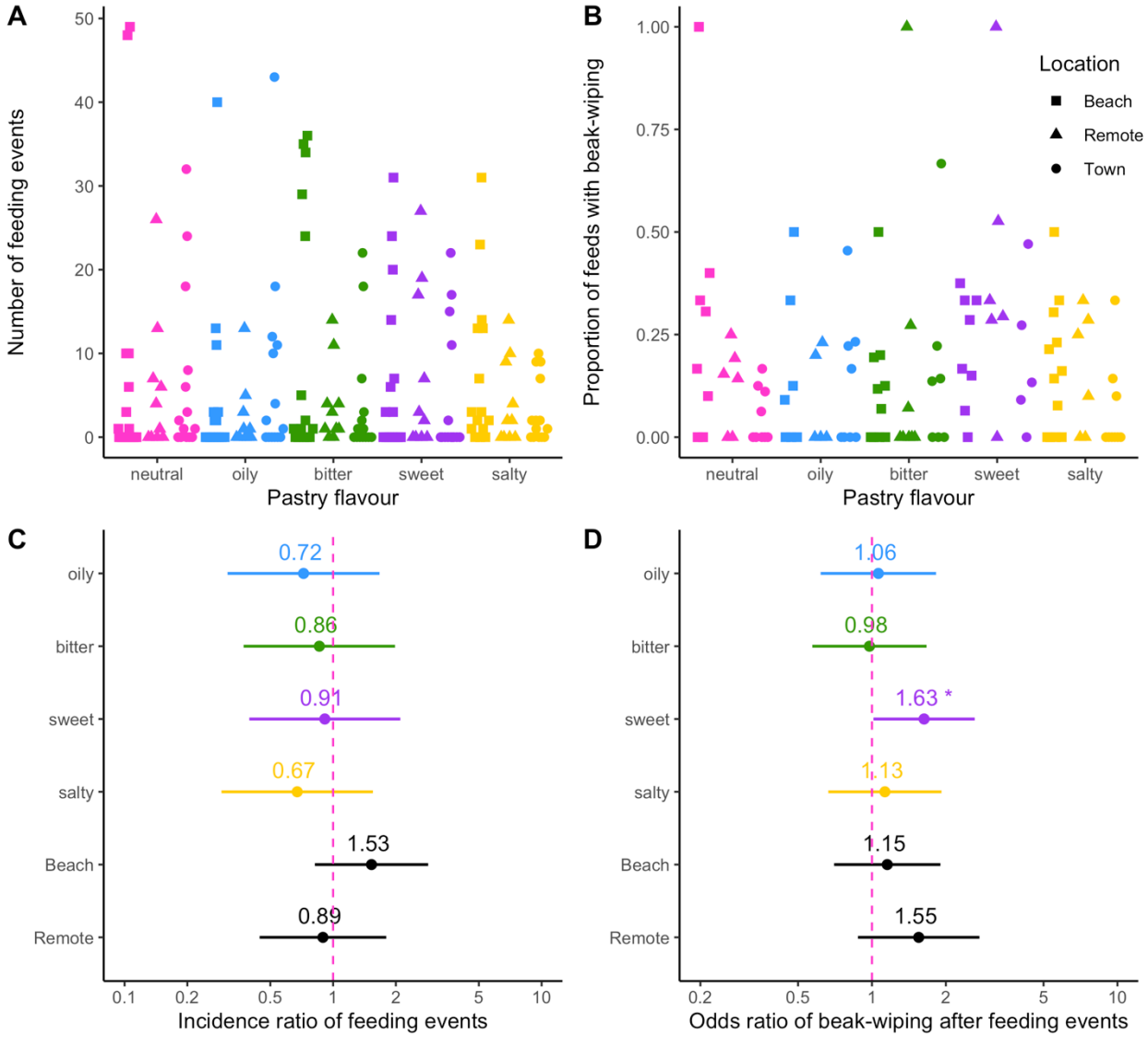


Figure 2.


A
Number of feeding events
50
40
30
20
10
0
neutral
oily
bitter
sweet
salty
Pastry flavour
B
Proportion of feeds with beak-wiping
1.00
0.75
0.50
0.25
0.00
Location
Beach
Remote
Town
neutral
oily
bitter
sweet
salty
Pastry flavour
C
oily
bitter
sweet
salty
Beach
Remote
0.72
0.86
0.91
0.67
1.53
0.89
0.1
0.2
0.5
1
2
5
10
Incidence ratio of feeding events
D
oily
bitter
sweet
salty
Beach
Remote
1.06
0.98
1.63 *
1.13
1.15
1.55
0.2
0.5
1
2
5
10
Odds ratio of beak-wiping after feeding events