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 ground finches (*Geospiza fuliginosa)* and medium ground finches (*Geospiza fortis)* 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 urbanization; however, if no site-differences were found then this would indicate latent taste preferences. Contrary to both predictions, we found little evidence that human-food flavours were preferred compared to control flavours at any site. Instead, finches showed a weak aversion to oily foods, but only at remote (no human foods present) sites. This was further supported by behavioural responses, with beak wiping occurring more often at remote sites after finches tasted flavours associated with human foods. Our results suggest, therefore, that while Darwin's finches may have acquired a tolerance to the flavours of human food, latent taste preferences are unlikely to have played a major role in their dietary response to 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

44 demonstrated that birds can use bitter tastes to avoid toxic foods [32,34,35], use sweet tastes to
45 detect sugars [30,34,36–39] indicating high caloric content [40], and use salty tastes to detect
46 salts [39,41,42] indicative of necessary minerals and proteins [43]. Preferences for certain tastes
47 can therefore evolve when flavours are linked to food quality and nutrient content [30]. For
48 example, omnivorous and frugivorous birds are able to detect sugars at low levels and prefer
49 sweet tastes compared to birds that forage on other types of food [34], potentially because this
50 facilitates optimal foraging for caloric content of nectar and ripe fruit.
51
52 Taste preferences can also be maladaptive, however, if they lead to the preferential
53 consumption of human foods. The introduction of human foods in urban areas causes changes in
54 resource availability, including calories and nutrient concentration [44,45] as much of the human
55 foods accessible to birds consists of discarded 'junk food' and snacks that are high in fat, sugar,
56 and salt. The availability of these foods can alter natural nutritional landscapes with detrimental
57 effects [24,46]. For example, hibernation in mammals is perturbed when human foods are
58 consumed [47,48], and racoons feeding on human foods in urbanised areas show greater weight
59 and blood sugar content [49]. In birds, American crow (*Corvus brachyrhynchos*) chicks are
60 smaller [50] and Canadian geese (*Branta canadensis maxima*) have higher rates of angel wing
61 disorder in urbanised areas, likely as a result of nutrient deficiency [51], and Australian magpies
62 (*Gymnorhina tibicen*) show alterations to blood chemistry following backyard provisioning [52].
63 If animals are adapted to detect and prefer foods based on taste profiles that are coincidentally
64 elevated in human foods, then they could assess these foods erroneously as high quality and
65 favour consumption [24,45]. On the other hand, if their taste receptors are adapted to prefer
66 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), biscuits (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 [14,27], 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 large 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.

136 Each cup was filled with 2.5 g of pastry made from flour, unsalted butter, and water,
137 following methods from Speed and colleagues (2000). The pastry (335 g flour, 135 g unsalted
138 butter, and 30 g water) was flavoured according to commonly available human-foods in the
139 environment [14] and each cup was coloured (blue, green, pink, purple, and yellow) to facilitate
140 recognition of the contents: (i) blue indicated high in fat (6g vegetable oil/pastry batch), (ii)
141 green indicated bitter (0.1g quinine/pastry batch), (iii) purple indicated sweet (23g sugar/pastry
142 batch), (iv) yellow indicated salty (1.333g salt/pastry batch), and (v) pink indicated neutral or
143 unflavoured pastry. To habituate the birds to the experimental set-up, we first conducted trials at
144 each site with only unflavoured pastry (remote = 17 trials, beach = 17 trials, town = 19 trials;
145 Supplemental Materials, Supplemental Table 1). Birds can have latent colour preferences, either
146 from experience or evolutionary history [e.g., 62]. However, we detected no strong biases within
147 finch species towards, or against, any of the coloured cups based on these trials (Supplemental
148 Materials; Supplemental Table 2; Supplemental Figures 3 & 4). Therefore, any preferences
149 detected using flavoured pastry were most likely due to taste and not visual preferences.
150
151 *Video analysis*
152 Videos were analysed using BORIS (Behavioral Observation Research Interactive Software)
153 (Friard and Gamba, 2016) and each 10-minute trial was analysed by one observer (DL). Species
154 identification was done based on bill and body size in comparison to the size of the cafeteria tray.
155 The observer was trained by KMG to first identify still images of birds (taken from videos
156 collected during trials), and then by using the videos. We counted the number of feeding events
157 at the level of the trial and assigned these to each species of finch. We defined a feeding event as
158 when a bird's beak was submerged into a cup, lifted, and then food was consumed

159 (Supplemental Figure 2). Following each feeding event, we then recorded the number of times
160 the finch wiped its beak on a surface within 20 seconds in accordance with published methods on
161 beak-wiping [60,61].
162
163 *Statistical analyses*
164 Statistical analyses were undertaken using the R environment version 4.0.2 (R Core team, 2020;
165 data and code for analyses are available as Supplemental Materials). To analyse differences in
166 taste preferences, we used generalised linear mixed-effect models (GLMMs) with a negative
167 binomial error distribution (using the glmer.nb() function in the lme4 package; [63] to account
168 for overdispersion in the number of feeding events per trial (response variable). Species nested
169 within trial was included as a random effect to account for non-independence of feeding events,
170 and the fixed effects were species, site, and pastry flavour. The reference level (i.e. the model
171 intercept) was 'neutral flavour (pink)' and 'town'. We included an interaction between site and
172 pastry flavour, and assessed whether it contributed significantly to model fit using a likelihood
173 ratio test (compared to a simpler model with the same random effect structure, but containing
174 only additive fixed effects). We then used z-tests to assess the significance of differences in
175 consumption among pastry flavours. We report estimates and standard errors and provide
176 incidence rate or odds ratios (negative binomial and binomial models, respectively) to compare
177 effects.
178 The number of beak wipes following a feeding event were low (5 or fewer) and highly
179 right-skewed (medium ground finch = 3.69, small ground finch = 3.44; calculated using the
180 'moments' package; [64] so we therefore modelled the occurrences of beak wipes using a
181 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 dataset (see Supplemental Figures 3 & 4).

Results

A total of 49 taste preference trials were conducted across three sites. Participation was similar for both species (medium ground finch = 16 remote trials and 10 town trials, small ground finch = 10 remote trials and 14 town trials) except for trials conducted at beach sites where medium ground finches participated in only 4 of the 15 trials whereas small ground finches participated in all trials (Supplemental Table 1).

Taste preferences

The overall consumption of pastry among ground finch species did not differ (1089 feeding events by medium ground finches versus 1186 feeding events by small ground finches; estimate = -0.102 ± 0.163, z = -0.625, p = 0.532). However, we found some evidence that ground finches preferred some flavour types more than others at different sites (flavour-type * site, χ^2 = 16.352, d.f. = 8, p = 0.0376; Figure 1A & 1B; Supplemental Table 3). To investigate this interaction further, we explored differences among flavour-types in separate models for each site. At beach sites, there was no significant difference in the number of feeding events according to flavour-type (χ^2 = 2.025, d.f. = 4, p = 0.731, N = 15 trials). However, at remote (χ^2 = 20.090, d.f.

205 = 4, p = 0.0005, N = 16 trials) and town (χ^2 = 10.595, d.f. = 4, p = 0.032, N = 18 trials) sites we
206 detected significant variation in consumption and the preferred flavours differed. Ground finches
207 at remote sites fed less often on oily (blue) pastry than either the neutral or the bitter control
208 whereas at sites in town, finches fed more often on sweet (purple) pastry, but only in comparison
209 to the bitter control (Table 1, Figure 1A & 1B).
210
211 We next assessed behavioural wiping responses to each flavour-type (Figure 2). Overall,
212 small ground finches were much more likely to wipe their beak after feeding than medium
213 ground finches (estimate = 0.528 ± 0.198, z = 2.672, p = 0.008; Supplemental Table 4). Again,
214 however, we detected that beak-wiping was more likely to occur after consuming some flavours
215 at some sites (flavour-type * site, χ^2 = 28.132, d.f. = 8, p = 0.0005; Figure 2; Supplemental Table
216 4). On further inspection (as above), at town sites ground finches showed no difference in their
217 propensity to wipe their beak after feeding on flavoured pastry (Table 1, Figure 2, N = 18 trials).
218 However, at beach sites ground finches wiped their beaks less often after consuming oily (blue)
219 or bitter (green) flavoured pastry compared to neutral (pink) pastry and less often after eating
220 salty (yellow) compared to bitter pastry (Table 1, Figure 2, N = 15 trials). At remote sites,
221 ground finches were more likely to wipe their beaks after consuming pastry containing any
222 'human-food' flavour as compared to either the neutral or the bitter control (Table 1, Figure 2, N
223 = 16 trials). Taken together, these results suggest that ground finches in town showed little
224 preference to human-food flavours whereas at remote sites, all human-food flavours evoked
225 more behavioural reactions than controls, and oily flavoured pastry was preferred the least.
226
227 **Discussion**

228 Taste preferences have often been overlooked in understanding animals' foraging decisions, yet
229 in human-modified environments, latent taste preferences could explain why some species are
230 able to readily adapt to novel foods while others do not. Here we investigated if taste preferences
231 can explain preferential consumption of human foods by Darwin's finches [14]. We predicted
232 that if finches at sites with more exposure to human foods (i.e. at the tourist beach or in town)
233 showed greater consumption and reduced aversive behavioural responses to flavours typical of
234 these foods (salty, oily, sweet), then taste preferences could have developed from experience
235 with the changed foraging landscape. However, if finches across sites preferred these 'human-
236 food flavours' then latent taste preferences could have facilitated rapid adoption of human foods
237 into the diet. Against both predictions, however, the only evidence we detected for a taste
238 preference was that ground finches at remote sites showed a weak aversion to oily foods. This
239 was further supported by behavioural responses, with beak wiping (an aversive response
240 common across birds [30,60]) occurring more often at remote sites after finches tasted flavours
241 associated with human foods. This suggests that ground finches do not have latent taste
242 preferences for human foods or have acquired preferences from contact with human foods.
243 However, ground finches might now be more tolerant of oily flavours. It is possible that our
244 sample sizes were too small to detect preferences for human-food flavours, or that we did not
245 add sufficient flavour to the pastry for these to be detectable. However, previous work detecting
246 taste preferences had smaller sample sizes than our study (e.g., n = 6 per group [36]; n = 11 [37];
247 n = 6 and 10 [38]), and the amount of constituents that we added to the pastry emulated human
248 foods as closely as possible. It therefore seems unlikely that our results can only be explained by
249 methodological issues. Since Darwin's finches consume human foods preferentially when

250 available, why did we not find preferences for flavours associated with commonly available
251 human foods?
252
253 It could be that Darwin's finches have not evolved a preference for tastes associated with
254 human foods because these species are generalist feeders, especially during periods of non-
255 drought [13]. We conducted our trials during the traditional rainy season when the finches would
256 be more generalist. Taste preferences evolve when they allow animals to identify food items that
257 offer important nutrients (e.g., high in lipids, salts, or sugars)[30,31,34,46]. Yet for generalists, it
258 might not be adaptive to have latent taste preferences if these limit individuals from consuming a
259 wide variety of dietary items [13] or they might not need to discern specific foods that are high in
260 lipids, salts, or sugars. Indeed, many studies that have found taste preferences in birds have been
261 conducted with specialists [37,38]. Another possibility is that Darwin's finches have not yet
262 acquired preferences for flavours associated with human foods. Tourism has grown
263 exponentially only relatively recently [66]. At the tourist beach site, easy access to the public
264 only became available around 2010 [J. Podos, personal communication], and the town of Puerto
265 Ayora was established in 1926 [67; E. Hennessey, personal communication], so perhaps not
266 enough generations have passed from when finches gained access to human foods for finches to
267 acquire taste preferences.
268
269 For the finches, we found that the presence or absence of human foods did not correlate
270 with different taste preferences as predicted. Surprisingly, we also found little evidence that the
271 bitter-tasting control elicited beak wiping. This was unexpected because we know birds possess
272 TAS2R bitter taste receptors [33], and often discriminate against toxic prey via bitterness. In

273 fact, of the species studied by Wang and Zhao [33], medium ground finches had the second most
274 TAS2R genes. So why did we not find a lack of aversion to bitter tastes? If the natural foods
275 found at remote sites are bitter in taste, then perhaps finches are accustomed to bitter tastes.
276 Bitter tastes are often associated with aposematic prey, and the relative lack of aposematic prey
277 on the Galapagos [68] suggests finches may not need to discriminate against bitter tastes.
278 Another possibility is zoopharmacognosy, where animals eat medicinally advantageous foods,
279 despite possible aversive qualities. This is common in birds; great bustards (*Otis tarda*) ingest
280 toxic blister beetles to control digestive tract parasites [69] , and house sparrows (*Passer*
281 *domesticus*) ingest leaves containing quinine (our bittering agent) during malaria outbreaks [70],
282 alleviating symptoms. Quinine is an invasive plant found on the Galapagos. However, no finch
283 has ever been observed consuming quinine (Heinke Jäger, personal communication), so this
284 possibility is unlikely.
285
286 The Galapagos Islands are experiencing an exponential increase in urbanization and
287 tourism, including permanent human residents [66], and we know Darwin's finches
288 preferentially consume human foods over natural food sources when readily available [14].
289 However, here we found little evidence for taste preferences for flavours associated with human
290 foods during the traditional rainy season, although finches at remote sites showed a small
291 aversion towards oily foods. It therefore seems likely that finches do not have latent preferences
292 for these flavours, nor acquired a preference through repeated exposure to human foods. Why
293 then have Darwin's finches adapted rapidly to changing food availability and incorporated
294 human foods into their diet when human foods are readily available? One possibility is that they
295 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 5,14]. 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 types of food 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.

Acknowledgements

We thank Lotte Skovmand for their assistance with field work and Nick Davies for their assistance with the research project. During this study, RT was supported by an Independent Research Fellowship from the Natural Environment Research Council UK (NE/K00929X/1) and a start-up grant from the Helsinki Institute of Life Science (HiLIFE), University of Helsinki. KMG was funded by Christ's College and Clare Hall at the University of Cambridge and was supported by Banting Postdoctoral Fellowship from the Natural Sciences and Engineering Research Council of Canada.

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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 at (a) Town sites, (b) Beach sites, and (c) Remote sites that vary in exposure to human foods. Medium ground finches (I: N = 130 observations from 26 trials, II: N = 95 observations from 26 trials) and small ground finches (I: N = 195 observations from 39 trials, II: N = 114 observations from 39 trials) were presented with coloured cups containing pastry flavoured to be oily (blue), sweet (purple), or salty (yellow), and two controls: neutral (pink, set as model intercept) and bitter (green). 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. Significant differences are indicated in bold font.

	I. Feeding events			II. Beak-wiping		
	Mean difference ± S.E.	Z	p	Mean difference ± S.E.	Z	p
(a) Town sites:						
intercept(neutral)	1.872 ± 0.290	6.447	<0.001	-2.696 ± 0.345	-7.489	<0.001
Oily (blue)	0.118 ± 0.347	0.340	0.734	0.905 ± 0.433	2.090	0.146
Bitter (green)	-0.435 ± 0.345	-1.262	0.207	-0.053 ± 0.403	-0.131	0.393
Sweet (purple)	0.519 ± 0.397	1.310	0.190	0.936 ± 0.368	2.541	0.070
Salty (yellow)	-0.591 ± 0.348	-1.699	0.089	0.593 ± 0.399	-1.486	0.369
Species(small)	0.446 ± 0.236	1.888	0.059	0.565 ± 0.320	-0.180	0.857
(b) Beach sites:						
intercept(neutral)	3.120 ± 0.554	5.635	<0.001	-1.396 ± 0.429	-3.255	0.001
Oily (blue)	-0.300 ± 0.513	-0.582	0.560	**-0.820 ± 0.414**	**-1.980**	**0.048**
Bitter (green)	0.018 ± 0.477	0.038	0.970	**-0.733 ± 0.347**	**-2.112**	**0.035**
Sweet (purple)	-0.249 ± 0.492	-0.506	0.613	-0.647 ± 0.375	-1.725	0.085
Salty (yellow)	-0.512 ± 0.463	-1.107	0.268	-0.030 ± 0.341	-0.089	0.929
Species(small)	-0.348 ± 0.418	-0.832	0.406	0.253 ± 0.352	0.720	0.471
(c) Remote sites:						
intercept(neutral)	2.241 ± 0.240	9.328	<0.001	-2.969 ± 0.324	-9.172	<0.001
Oily (blue)	**-0.766 ± 0.291**	**-2.638**	**0.008**	**0.874 ± 0.436**	**2.006**	**0.045**
Bitter (green)	0.328 ± 0.270	1.216	0.224	0.210 ± 0.380	0.553	0.580
Sweet (purple)	0.427 ± 0.271	1.575	0.115	**1.314 ± 0.334**	**3.915**	**<0.001**
Salty (yellow)	-0.033 ± 0.276	-0.119	0.905	**0.982 ± 0.365**	**2.689**	**0.007**
Species(small)	-0.385 ± 0.247	-1.558	0.119	**1.020 ± 0.240**	**4.257**	**<0.001**

530

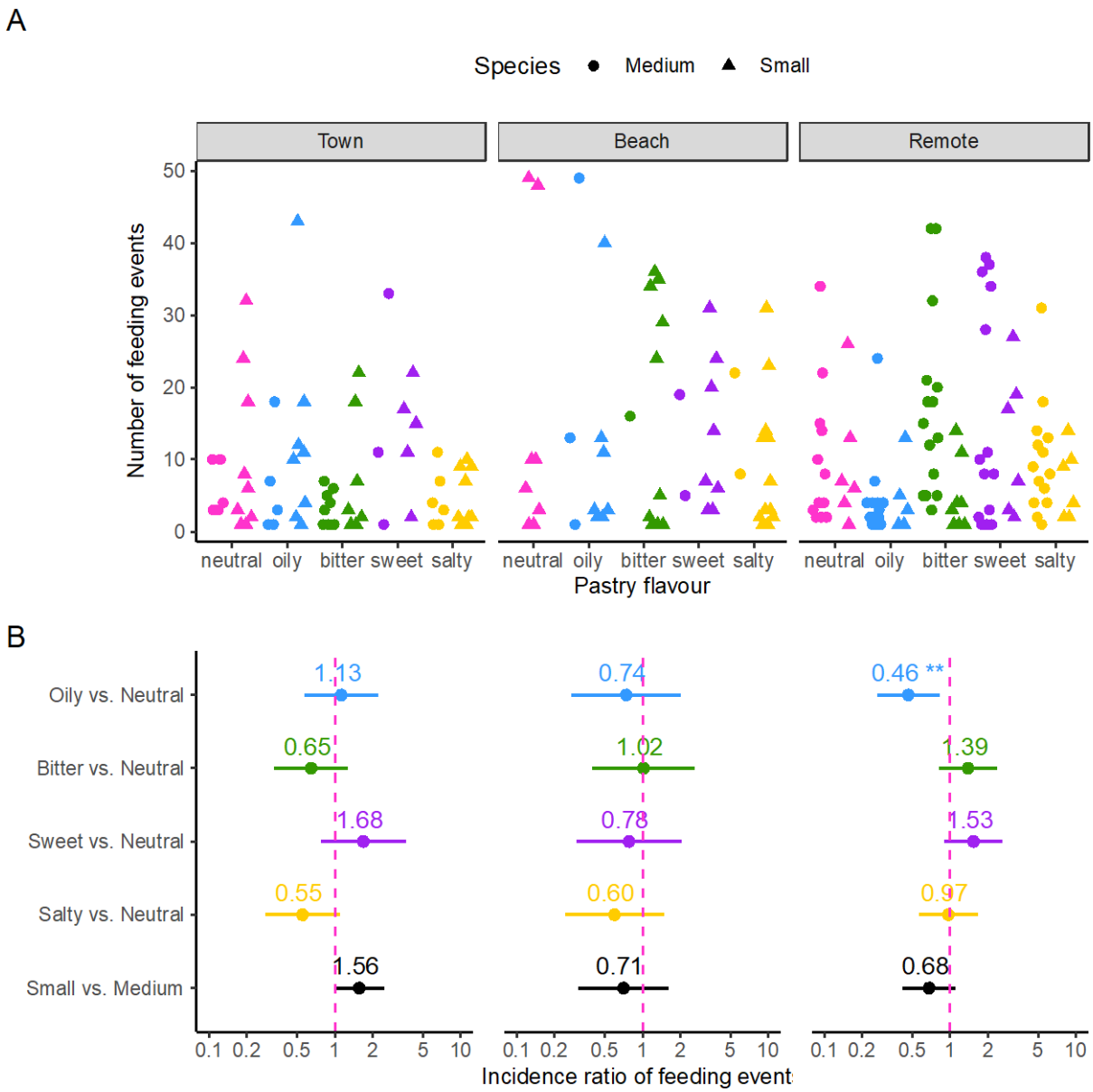
Figure Legend

Figure 1. Differences in the number of feeding events by medium and small ground finches presented with coloured cups containing pastry with neutral (pink), oily (blue), bitter (green), sweet (purple), or salty (yellow) flavours at either town (N = 18 trials), beach (N = 15 trials), or remote (N = 16 trials) sites. (A) presents the raw data, (B) presents the effect sizes of the differences between each flavour and the neutral pastry, or between species, computed from generalised linear mixed effects models (see Methods for more details). Effects 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 proportion of feeding events that were followed by beak-wiping by medium and small ground finches presented with coloured cups containing pastry with neutral (pink), oily (blue), bitter (green), sweet (purple), or salty (yellow) flavours at either town (N = 18 trials), beach (N = 15 trials), or remote (N = 16 trials) sites. (A) presents the raw data, (B) presents the effect sizes of the differences between each flavour and the neutral pastry, or between species, computed from generalised linear mixed effects models (see Methods for more details). Effects significantly different from zero (dashed pink vertical line) are indicated by asterisks (* $0.01 < p < 0.05$, ** $0.001 < p < 0.01$).

550 **Figures**

551 Figure 1.



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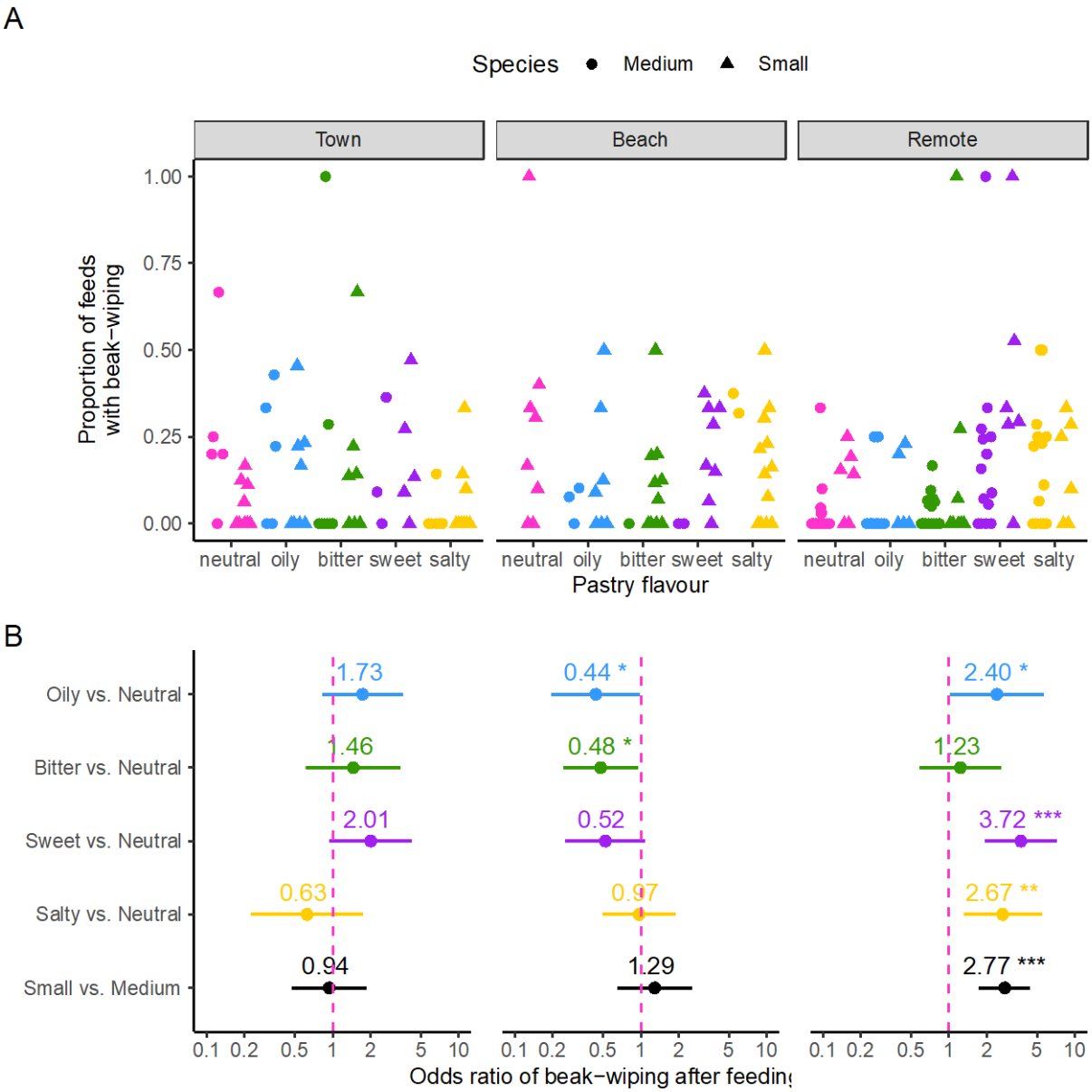
554 Figure 2.



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