Darwin's finches can have taste preferences, but not for human foods

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1   Abstract

2   Urbanization is rapidly changing ecological niches. On the Galapagos Islands, Darwin's finches

3   consume human-introduced foods preferentially; however, it remains unclear why. Here we

4   presented pastry with flavour profiles typical of human foods (oily, salty, sweet) to small and

5   medium ground finches to test if latent taste preferences might drive selection of human foods. If

6   human-food flavours were consumed more than a neutral or bitter control at sites with human

7   foods, then we predicted tastes were acquired after experience with human foods; however, if no

8   site-differences were found then this would indicate latent taste preferences. Contrary to both

9   predictions, we found no evidence that human-food flavours were preferred compared to control

10   flavours. Instead, medium ground finches consumed the bitter control pastry most and wiped

11   their beaks more frequently after feeding on oily and sweet pastry (post-ingestion beak wiping

12   can indicate aversions). Small ground finches showed no differences in consumption but wiped

13   their beaks most after feeding on sweet pastry. Our results suggest that unlike many species,

14   medium and small ground finches do not find bitter-tasting food aversive. Furthermore, taste

15   preferences are unlikely to play a major role in Darwin's finches adaptation to the presence of

16   human foods during increased urbanization.

17

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

19   Galapagos

20

21 **Introduction**

22 Human behaviour is now recognised to be a strong driver of local adaptation and differences

23 among populations of animals [1,2]. Urbanization [3–5], for example, can have profound effects

24 on foraging because humans often introduce novel foods to the surrounding environment either

25 intentionally (e.g. via garden bird feeding [6,7]) or unintentionally (e.g. by planting ornamental

26 plants [8,9]). This changes the diversity and availability of food items, and generates different

27 foraging landscapes from those in which most animals evolved [10–12]. However, organism's

28 responses to these altered niches vary, with some birds, for example, not only adapting more

29 readily to incorporate human-foods into their diet, but even preferentially consuming them over

30 more natural food sources [11,13–15]. These differences in if and how populations and species

31 utilise human foods can then have consequences for local adaptation [7,16], potentially affect

32 species divergence [17], or mediate the potential for invasive species to establish [18,19].

33 Furthermore, the gut microbiome, which is increasingly recognised to affect a suite of

34 physiological, immune, and cognitive functions in wild non-human animals [20,21], can also

35 vary with consumption of human foods [22–24]. Nevertheless, understanding why some species

36 in urban areas shift their diets to preferentially forage on human foods remains unclear.

37

38 Taste plays an important role in foraging as it allows individuals to detect nutritious

39 versus unprofitable substances in food items [25,26]. Although it was long assumed to be of little

40 importance for birds, they have sophisticated sensory adaptations with taste receptors identified

41 for bitter [25,27,28], sweet [25], and salt [29] flavours. Furthermore, experiments have

42 demonstrated that birds can use bitter tastes to avoid toxic foods [27,29,30], use sweet tastes to

43 detect sugars [25,29,31–34] indicating high caloric content [35], and use salty tastes to detect

2

44   salts [34,36,37] indicative of necessary minerals and proteins [38]. Preferences for certain tastes

45   can therefore evolve when flavours are linked to food quality and nutrient content [25]. For

46   example, omnivorous and frugivorous birds are able to detect sugars at low levels and prefer

47   sweet tastes compared to birds that forage on other types of food [29], presumably because this

48   facilitates optimal foraging for caloric content of nectar and ripe fruit.

49

50   Taste preferences can also be maladaptive, however, if they lead to the preferential

51   consumption of human foods. The introduction of human foods in urban areas causes changes in

52   resource availability, including calories and nutrient concentration [39] as much of the human

53   foods accessible to birds consists of discarded 'junk food' and snacks that are high in fat, sugar,

54   and salt. The availability of these foods can alter natural nutritional landscapes with detrimental

55   effects [40]. For example, hibernation in mammals is perturbed when human foods are consumed

56   [41,42], and racoons feeding on human foods in urbanised areas show greater weight and blood

57   sugar content [43]. In birds, American crow (*Corvus brachyrhynchos*) chicks are smaller [44]

58   and Canadian geese (*Branta canadensis maxima*) have higher rates of angel wing disorder in

59   urbanised areas, likely as a result of nutrient deficiency [45], and Australian magpies

60   (*Gymnorhina tibicen*) show alterations to blood chemistry following backyard provisioning [46].

61   If animals are adapted to detect and prefer foods based on taste profiles that are coincidentally

62   elevated in human foods, then they could assess these foods erroneously as high quality and

63   favour consumption. On the other hand, if their taste receptors are adapted to prefer flavours

64   characteristic of human foods, then they might be better able to take advantage of this newly

65   available resource if natural foods decline (i.e. poor condition is preferable to starvation).

66   Therefore, preferential consumption of different foods due to taste preferences, especially in the

67   context of urbanization, could be either adaptive or maladaptive. However, it remains largely

68   unknown whether taste preferences actually underlie the preferential consumption of human

69   foods in urban areas.

70

71   Here, we investigate if Darwin's finches, which are known to vary in their preferential

72   consumption of human foods [11], have taste preferences for flavours associated with human

73   foods. Darwin's finches are a model system for demonstrating how foraging ecology shapes

74   adaptation into different ecological niches and results in an adaptive radiation [47,48].

75   Contemporary work has shown that the presence of humans is affecting traits such as beak

76   morphology [49] and this has been linked to the consumption of human foods [17]. Indeed, we

77   know that Darwin's finches preferentially consume human foods including crisps (potato chips),

78   biscuit (hard cookies), and rice at sites where these foods are abundant such as at tourist beaches

79   and in urban areas [11]. Indeed, urban finches can have higher nesting success than non-urban

80   finches [50], suggesting that at least some species of Darwin's finches can become locally

81   adapted to urban environments. Thus, the Darwin's finches on the Galapagos represent an

82   excellent opportunity to test whether taste preferences might underpin consumption of human

83   foods where these are available and abundant, such as in urban areas or on tourist beaches.

84

85   We assessed taste preferences in Darwin's finches in separate populations with little to no

86   movement of finches among sites [51] that varied in the availability of human foods previously

87   shown to be attractive to finches [11]. We presented flavours in the absence of visual cues

88   typical to human foods to exclude the role of learned associations with packaging (e.g. crisp

89   packets [11]). If taste preferences arise because of the consumption of human foods, we

4

90   predicted finches at sites with human foods would only prefer flavours associated with human

91   foods (e.g. sweet, salty, and oily) at sites where human foods are abundant. If taste preferences

92   are innate (i.e. latent), we predicted preferences would occur for such flavours across sites,

93   regardless of the presence or absence of human foods. Potential taste preferences can be

94   quantified as variation in feeding rate, or as variation in post-feeding beak wiping rate [25,52–

95   54]. Although beak wiping can clean the beak of debris [55], vigorous beak wiping commonly

96   occurs after feeding on something unpalatable [25,54]. Therefore, we measured taste preferences

97   in terms of consumption and beak wiping behaviour compared to two controls, neutral pastry

98   that had no flavour added and bitter-flavoured pastry as a negative control. Bitter substances are

99   aversive to many bird species, so we expected finches to consume less bitter-flavoured pastry

100   compared to neutral or other flavoured pastry across all sites as well as to elicit more beak

101   wiping behaviour [25,54] .

102

103   **Materials and Methods**

104   *Study species and location*

105   We focused on Darwin's finches, an endemic group of passerines on the Galapagos Islands, at

106   three sites on Santa Cruz Island that varied in their exposure to human foods (Supplemental

107   Figure 1). The "remote" site was a non-urban site 12 km from the main urban town with no

108   presence of human foods [22], the "beach" site was El Garrapatero beach, a non-urban site where

109   visitors often bring picnics so human food is present and abundant (de León et al. 2018, Knutie

110   et al. 2019), and the "town" site was Puerto Ayora, a fully urbanized town where humans and

111   their food are ubiquitous [11]. The two focal species were small ground finches (*Geospiza*

112   *fuliginosa*) and medium ground finches (*Geospiza fortis*). Galápagos mockingbirds (*Mimus*

113   *parvulus*) and two other finch species were also present occasionally, but rarely interacted with

114   our experiments.

115

116   *Experimental protocol and video recording*

117   We performed trials at each of the three sites (remote = 16 trials, beach = 15 trials, and

118   town = 18 trials; Supplemental Table 1) using a 'cafeteria' experiment [11]. Five cups the size of

119   ½ a plastic egg were randomly positioned in the periphery of a 3x3 egg carton and placed on the

120   ground on a white plate. The central dimple of the egg carton was weighted with a small rock,

121   and the unused dimples were left empty. The trial began when the first bird approached the tray

122   and fed, and then continued for 10 minutes [11]. If no finches fed, the trial was aborted after 20

123   minutes. All trials were performed from February 20th to March 25th, 2018, between 6am and

124   11am, or 3pm and 6pm and were filmed using a video camera (Sony HDR-CX625 Full HD

125   Compact Camcorder or Canon 7D Mark II with 100-400mm lens) positioned 10 metres from the

126   cafeteria plate. The majority of individuals were not uniquely identifiable, so we cannot be sure

127   that birds participating in different trials were independent. To reduce the potential for pseudo-

128   replication between trials, we moved the location of the cafeteria experiment for each trial by at

129   least 100 m within the study locations.

130   Each cup was filled with 2.5 g of pastry made from flour, unsalted butter, and water,

131   following methods from Speed and colleagues (2000). The pastry was flavoured according to

132   commonly available human-foods in the environment [11] and each cup was coloured (blue,

133   green, pink, purple, and yellow) to facilitate recognition of the contents: (i) blue indicated high in

134   fat (6g vegetable oil/pastry batch), (ii) green indicated bitter (0.1g quinine/pastry batch), (iii)

135   purple indicated sweet (23g sugar/pastry batch), (iv) yellow indicated salty (1.333g salt/pastry

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136   batch), and (v) pink indicated neutral or unflavoured pastry. To habituate the birds to the

137   experimental set-up, we first conducted trials at each site with only unflavoured pastry (remote =

138   17 trials, beach = 17 trials, town = 19 trials; Supplemental Materials, Supplemental Table 1).

139   Birds can have latent colour preferences, either from experience or evolutionary history.

140   However, we detected no strong biases within finch species towards, or against, any of the

141   coloured cups based on these trials (Supplemental Materials; Supplemental Table 2;

142   Supplemental Figures 2 & 3).

143

144   *Video analysis*

145   Videos were analysed using BORIS (Behavioral Observation Research Interactive Software)

146   (Friard and Gamba, 2016) and each 10-minute trial was analysed by one observer (DL). As most

147   birds (fewer than 4%) were not individually identifiable, we counted the number of feeding

148   events at the level of the trial and assigned these to each species of finch based on their body size

149   and beak morphology. We defined a feeding event as when a bird's beak was submerged into a

150   cup, lifted, and then food was consumed. If at least one cup was visited during a trial, any cups

151   not visited received a score of 0. Following each feeding event, we then recorded the number of

152   times the finch wiped its beak on a surface within 20 seconds in accordance with published

153   methods on beak wiping [54,55].

154

155   *Statistical analyses*

156   Statistical analyses were undertaken using the R environment version 4.0.2 (R Core team, 2020;

157   analyses code and data are available as Supplemental Materials). To analyse differences in taste

158   preferences, we used generalised linear mixed-effect models (GLMMs) with a negative binomial

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159   error distribution (using the glmer.nb() function in the lme4 package; Bates et al. 2015) to

160   account for overdispersion in the number of feeding events (response variable). Trial number

161   was included as a random effect to account for non-independence of feeding events within trials

162   and the fixed effects were site, pastry flavour, and their interaction. If the interaction did not

163   contribute significantly to model fit (using a likelihood ratio test to compare with a simpler

164   model containing only additive fixed effects) it was removed, but site and pastry flavour were

165   retained in all models. We then used z-tests to assess the significance of differences in

166   consumption among pastry flavour and site using 'neutral flavour (pink)' and 'town' as the

167   reference level (i.e. intercept). We report estimates and standard errors and provide incidence

168   rate or odds ratios to compare effects.

169   The number of beak wipes following a feeding event were low (5 or fewer) and highly

170   right-skewed (medium ground finch = 3.69, small ground finch = 3.44; calculated using the

171   'moments' package; Komsta and Novomestky 2015) so we therefore we modelled the

172   occurrences of beak wipes using a binomial distribution, where the denominator in the response

173   variable was the number of feeding events when no beak wipes occurred. Assumptions of

174   homogeneity of variance and uniformity of the residuals for all models were checked using

175   Kolmogorov-Smirnov tests for uniformity, simulation tests for dispersion, and a binomial test for

176   outliers (implemented using the 'DHARMa' package [58]). The cactus finch and small tree finch

177   rarely came to the experimental trays so only medium and small ground finches were included in

178   the data set. Furthermore, attendance of medium ground finches at beach trials was very low and

179   they did not feed from all cups in any trial. Therefore, data from this location were excluded for

180   medium ground finches and the two species were analysed separately.

181

182   **Results**

183   A total of 53 taste preference trials were conducted across three sites. Both medium and

184   small ground finches varied in their propensity to participate in experimental trials at different

185   locations. Medium ground finches participated at 16 of the 16 trials conducted at remote sites, 0

186   of the 15 trials conducted at beach sites, and in 10 of the 18 trials conducted at town sites. Small

187   ground finches participated at 10 of the 16 trials conducted at remote sites, 15 of the 15 trials

188   conducted at beach sites, and 14 of the 18 trials conducted at town sites (Supplemental Table 1).

189

190   *Medium ground finches*

191   Medium ground finches engaged in significantly more feeding events at the remote site

192   than the town site (Table 1, Figure 1C, Supplemental Table 1b), but we found no evidence that

193   taste preferences differed according to location (location*flavour-type: $\chi^2 = 4.687$, d.f. = 4, p =

194   0.321). Medium ground finches did, however, differ in their feeding events with respect to

195   flavour-type (flavour-type: $\chi^2 = 11.810$, d.f. = 4, p = 0.019), with significantly more feeds

196   occurring on the bitter (green) pastry than the neutral flavoured pastry (Table 1; Figure 1A &

197   1C). No other flavour-types were consumed more frequently than the neutral pastry (Table 1;

198   Figure 1A & 1C). We next assessed behavioural wiping responses to each flavour-type (Figure

199   1B &1D). However, as there were fewer than 10 trials at town sites where each flavour was

200   consumed (neutral (pink): N = 5, oily (blue): N = 5, bitter (green): N = 8, sweet (purple): N = 3,

201   salty (yellow): N = 6); we could not test whether responses to specific flavour-types differed

202   among the locations. Overall, medium ground finches were more likely to wipe their beaks after

203   consuming oily (blue; 14.7% of feeding events) or sweet (purple; 15.5% of feeding events)

204   flavours than after consuming neutral flavoured pastry (pink; Table 1; Figure 1B & 1D) and

9

205 wiped their beaks the least after consuming bitter (green; 5% less than after consuming neutral

206 pastry (Figure 1D)). Beak wiping also tended to occur more often after feeding events at town

207 sites compared to remote sites, although this was not significant (Table 1, Figure 1B & 1D).

208 Together, these results suggest that medium ground finches consumed bitter-flavoured pastry the

209 most (at both town and remote sites) yet wiped their beaks the least after feeding on this flavour.

210

211 *Small ground finches*

212 Small ground finches, on the other hand, showed no significant differences in their feeding

213 preferences (Figure 2), either among flavour-types ($\chi^2 = 1.160$, d.f. = 4, p = 0.885, Table 1;

214 Figure 2A & 2C), among the three sites ($\chi^2 = 2.866$, d.f. = 2, p = 0.239; town vs. beach estimate

215 $= 0.424 \pm 0.319$, z = 1.329, p = 0.184; town vs. remote estimate = -0.112 $\pm$ 0.357, z = -0.315, p =

216 0.753; Table 1; Figure 2A & 2C), or in interaction ($\chi^2 = 4.728$, d.f. = 8, p = 0.786; Table 1;

217 Figure 2A &2C). Overall, while there were no differences among locations in the proportion of

218 feeding events that led to beak wiping ($\chi^2 = 2.298$, d.f. = 2, p = 0.317; Table 1; Figure 2B & 2D),

219 small ground finches were 63% more likely to wipe their beaks after consuming sweet-flavoured

220 (purple) rather than neutral pastry (pink; Figure 2D). There were no significant differences

221 between other flavours and neutral-flavoured pastry (Table 1; Figure 2B & 2D). The number of

222 feeding trials where each flavour was consumed were too few to statistically test for location-

223 specific differences in beak-wiping responses to flavours. Nevertheless, together the feeding

224 events and beak wiping data suggest that small ground finches show little discrimination of foods

225 based on human-food flavours, regardless of location.

226

227 **Discussion**

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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 [11]. 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, the only evidence we detected for a taste preference was

238   that medium ground finches favoured the bitter-flavoured control. Medium ground finches fed

239   most often on the bitter-flavoured pastry and wiped their beaks the least following its ingestion.

240   This was surprising, given that bitter-tasting foods often elicit increased beak wiping in birds

241   [25,54]. It is possible that our sample sizes were too small to detect preferences for human-food

242   flavours, or that we did not add sufficient flavour to the pastry to be detectable. However,

243   previous work detecting taste preferences had smaller sample sizes than our study ([e.g. 31 (n =

244   6/group), 32 (n = 11), 33 (n = 6 and 10)], and the amount of flavour we added to the pastry

245   emulated human foods as closely as possible. It therefore seems unlikely that our results can only

246   be explained by methodological issues. Since Darwin's finches consume human foods

247   preferentially when available, why did we not find preferences for flavours associated with

248   commonly available human foods?

249

250   It could be that Darwin's finches have not evolved a preference for tastes associated with

251   human foods because these species are generalist feeders, especially during periods of non-

252   drought [10]. Taste preferences evolve when they allow animals to identify food items that offer

253   important nutrients (e.g., high in lipids, salts, or sugars)[25,26,29,40]. Yet for generalists, it

254   might not be adaptive to have latent taste preferences if these limit individuals from consuming a

255   wide variety of dietary items [10] or they might not need to discern specific foods that are high in

256   lipids, salts, or sugars. Indeed, many studies that have found taste preferences in birds have been

257   conducted with specialists [32,33]. Another possibility is that Darwin's finches have not yet

258   acquired preferences for flavours associated with human foods. At the tourist beach site, easy

259   access to the public only became available around 2010 (J. Podos, personal communication), and

260   the town of Puerto Ayora was established in 1926 [59; E. Hennessey, personal communication],

261   so perhaps not enough generations have passed from when finches gained access to human foods

262   for finches to acquire taste preferences.

263

264   For the medium ground finch, we found that the bitter taste is preferred across sites

265   (Figure 1; Table 1), suggesting a latent taste preference for bitter, and the presence or absence of

266   human foods did not correlate with different taste preferences as predicted. We also found a lack

267   of aversion to bitter pastry in both species with finches not wiping their bills more after

268   consuming bitter pastry. This was unexpected because we know birds possess TAS2R bitter taste

269   receptors [28], and often discriminate against toxic prey via bitterness. In fact, of the species

270   studied by Wang and Zhao [28], medium ground finches had the second most TAS2R genes. So

271   why would medium ground finches prefer bitter tastes as opposed to being averse? If the natural

272   foods found at remote sites are bitter in taste, that might explain why medium ground finches

273   have a latent preference for bitter tastes. Bitter tastes are often associated with aposematic prey,

274   and the relative lack of aposematic prey on the Galapagos [60] suggests finches do not need to

275   develop an aversion to bitter tastes as shown by the preferential consumption of bitter tastes and

276   not wiping their bills after consuming bitter pastry. Another possibility is zoopharmacognosy,

277   where animals eat medicinally advantageous foods, despite possible aversive qualities. This is

278   common in birds; great bustards (*Otis tarda*) ingest toxic blister beetles to control digestive tract

279   parasites [61] , and house sparrows (*Passer domesticus*) ingest leaves containing quinine (our

280   bittering agent) during malaria outbreaks [62], alleviating symptoms. Quinine is an invasive

281   plant found on the Galapagos. However, no finch has ever been observed consuming quinine

282   (Heinke Jäger, personal communication), so this possibility is unlikely.

283

284   The Galapagos Islands are experiencing an exponential increase in urbanization and

285   tourism, including permanent human residents [63], and we know Darwin's finches

286   preferentially consume human foods over natural food sources when readily available [11].

287   However, here we found no taste preferences for flavours associated with human foods. It

288   therefore seems likely that finches do not have latent preferences for these flavours, nor acquired

289   a preference through repeated exposure to human foods. Why then have Darwin's finches

290   adapted rapidly to changing food availability and incorporated human foods into their diet? One

291   possibility is that they could be attracted to other sensory cues such as aural or visual cues

292   associated with human foods. For example, in town and on the beach (but not in remote areas),

293   finches respond to brightly coloured visual cues of human food packaging and are attracted to

294   the 'crinkle' sound associated with foil and plastic food packaging [Supplemental Figure 4; 11].

295   Alternatively, it could be driven by availability itself at the beach and town sites. While the food

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296   sources Darwin's finches normally feed upon are available within town and at the beach [11], the

297   abundance of human foods at these sites simply make these more accessible to finches, and

298   therefore, finches did not need to discriminate between different flavours typically associated

299   with human foods and aversive flavours to expand their diet diversity [11]. Further work is

300   required to understand the mechanisms underlying how Darwin's finches developed a preference

301   for consuming human foods at sites where human foods are readily available.

302

303   Humans, through processes such as urbanization, can have a major impact on foraging ecology

304   by introducing novel foods that can become preferentially consumed by birds [13,14]. However,

305   the mechanisms leading to changes in foraging ecology remain largely unknown. Although we

306   cannot yet explain *why* Darwin's finches prefer human foods, our results help to rule out the

307   possibility that taste preferences play an important role in incorporating human foods into their

308   diets. Similarly, our finding that ground finches do not find bitter tastes aversive expands the

309   increasing knowledge on variation in response to tastes among species. As the adoption of

310   human foods into animals' diets can have cascading effects on health, reproduction, and fitness

311   [6,12,16,41,43], it remains of paramount importance to elucidate why some species integrate

312   these foods while others do not.

313

314   **Author contributions**

315   KMG and RT designed the study, KMG and LVR collected the field data, DL analyzed the

316   videos, RT, DL, and KMG analyzed the data, and all authors wrote and edited the manuscript.

317

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487

488   Tables

489   Table 1. Mean differences (± S.E.) in the (I) number of feeding events and (II) proportion of

490   feeding events followed by beak wiping by (a) medium ground finches and (b) small ground

491   finches from coloured cups containing pastry flavoured to be salty (yellow), sweet (purple),

492   bitter (green), or oily (blue). Differences in (I) were estimated using generalised linear mixed

493   effects models with a negative binomial error distribution and where trial and site were included

494   as random effects. Differences in (II) were estimated using a similar model but with a binomial

495   error distribution to account for proportional response data. 'Neutral', unflavoured pastry was set

496   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
Location	0.424 ± 0.319	1.329	0.184	0.144 ± 0.255	0.563	0.573
	-0.112 ± 0.357	-0.315	0.753	0.438 ± 0.291	1.508	0.132

497

498   Figure Legend

499   Figure 1. Differences in the (A,C) number of feeding events and (B,D) proportion of feeding

500   events that were followed by beak-wiping by Medium ground finches presented with pastry in

501   coloured cups with neutral (pink), oily (blue), bitter (green), sweet (purple), or salty (yellow)

502   flavours common to human-foods in either town (●, N = 10 trials) or remote (▲, N = 16 trials)

503   locations. A and B present the raw data, C and D present the effect sizes of the differences

504   between each flavour and the neutral pastry, or between town and remote locations, computed

505   from generalised linear mixed effects models (see Methods for more details). Effects that were

506   significantly different from zero (dashed pink vertical line) are indicated by asterisks (* $0.01 < p$

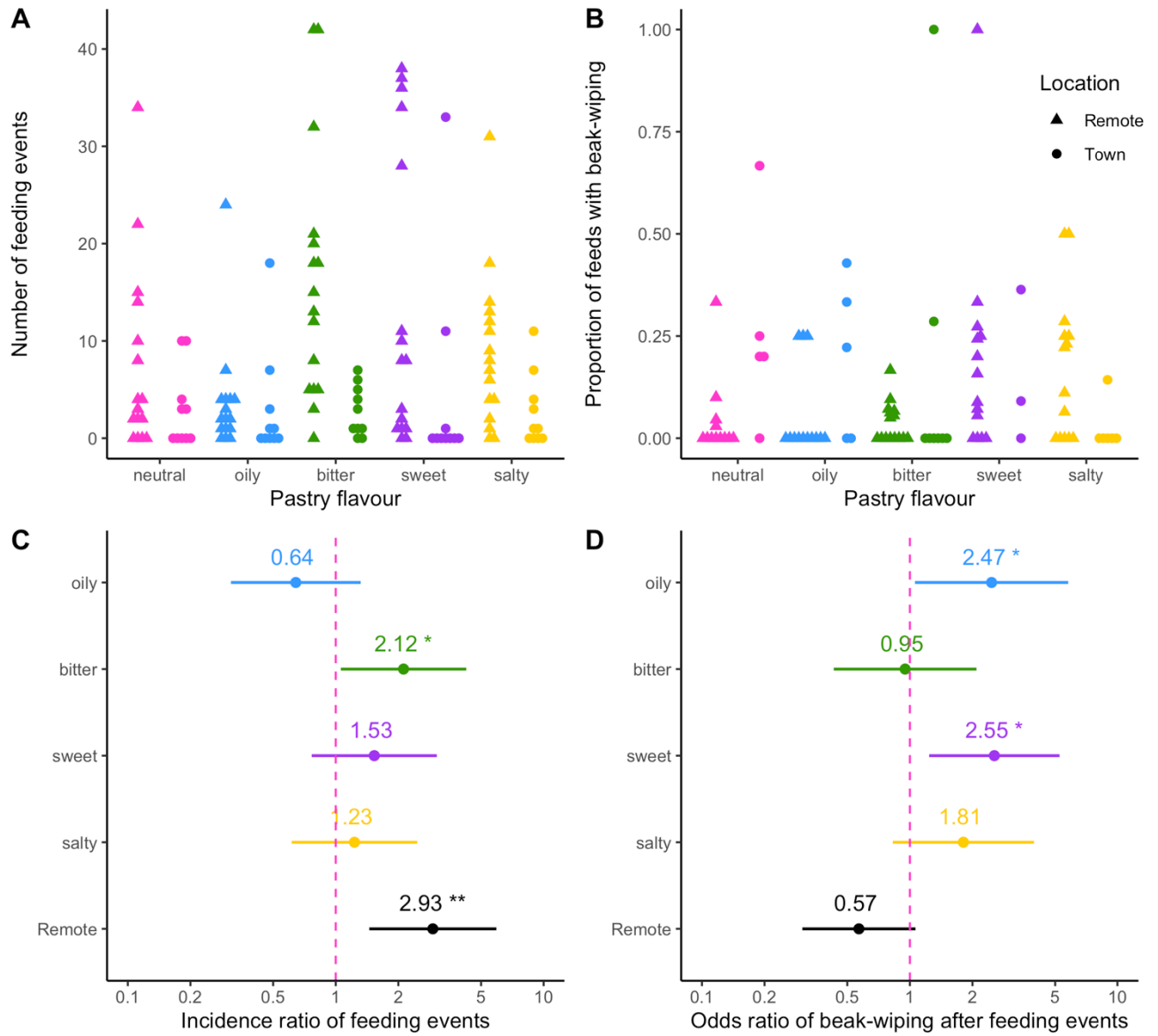507 < 0.05, ** $0.001 < p < 0.01$).

508

509   Figure 2. Differences in the (A,C) number of feeding events and (B,D) proportion of feeding

510   events that were followed by beak-wiping by small ground finches presented with pastry in

511   coloured cups with neutral (pink), oil (blue), bitter (green), sweet (purple), or salty (yellow)

512   flavours common to human-foods in either town (●, N = 14 trials), beach (■, N = 15 trials), or

513   remote (▲, N = 10 trials) locations. A and B present the raw data, C and D present the effect

514   sizes of the differences between each flavour and the neutral pastry, or between town, beach, and

515   remote locations, computed from generalised linear mixed effects models (see Methods for more

516   details). Effects that were significantly different from zero (dashed pink vertical line) are

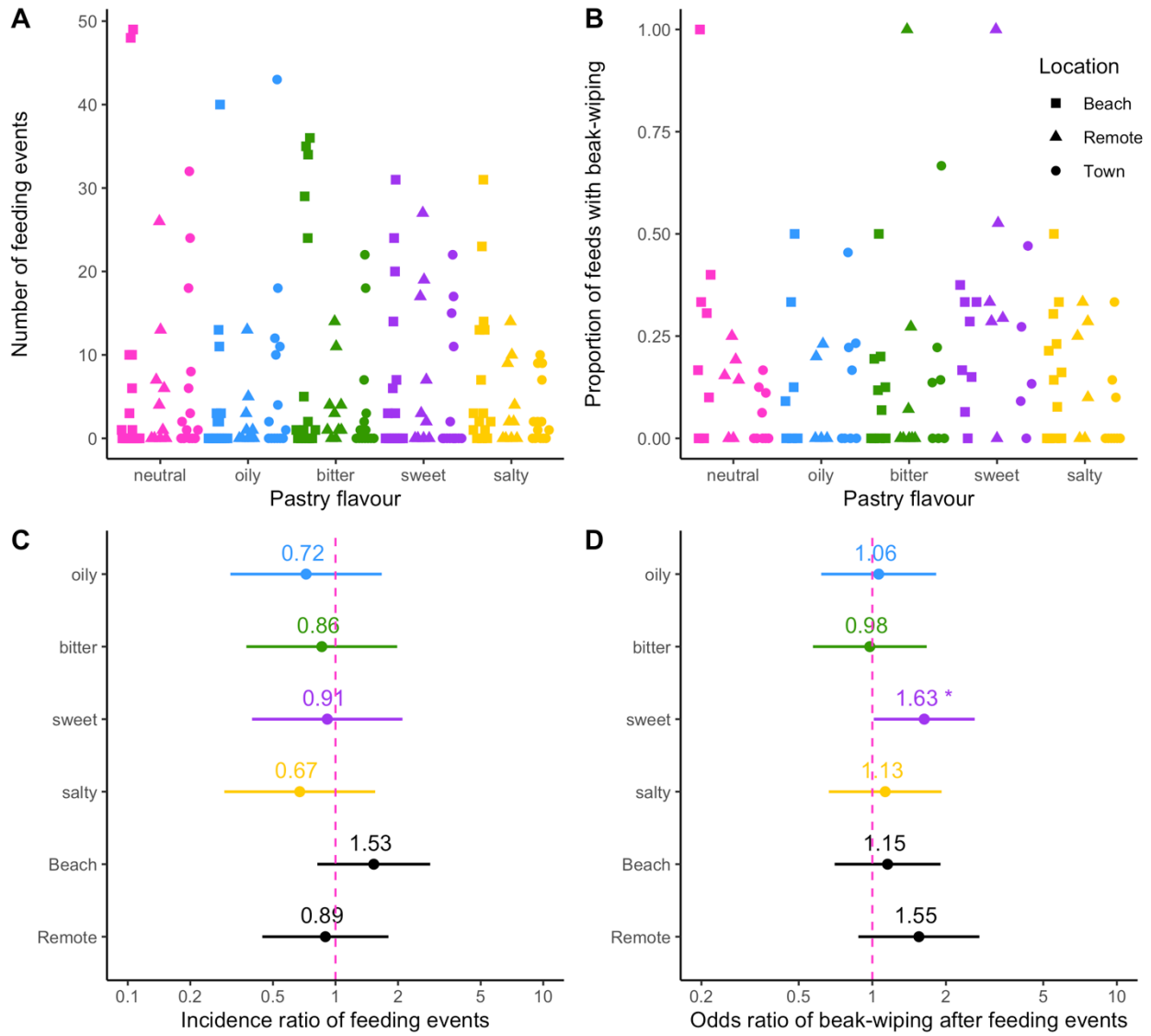517   indicated by asterisks (* $0.01 < p < 0.05$, ** $0.001 < p < 0.01$).

518

519   **Figures**

520   Figure 1.

521

522

523   Figure 2.

524