1   **Birds see the true colours of fruits to live off the fat of the land**

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27   **Abstract**

28   Communication is a characteristic of life, but its reliability and basic definition are hotly

29   debated. Theory predicts that trade among mutualists requires high reliability. Here, we

30   show that moderate reliability already allows mutualists to optimise their rewards. The

31   colours of Mediterranean fleshy-fruits indicate lipid rewards (but not other nutrients) to

32   avian seed dispersers on regional and local scales. On the regional scale fruits with high

33   lipid content were significantly darker and less chromatic than congeners with lower

34   lipid content. On the local scale two warbler species (*Sylvia atricapilla and S. borin*)

35   selected fruit colours that were less chromatic and thereby maximised their lipid intake,

36   a critical resource during migration and wintering. Crucially, birds were able to

37   maximise lipid rewards with moderate reliability of visual fruit colours (r^2= 0.44-0.6).

38   We suggest that mutualisms require only that any association between the quality and

39   sensory aspects of signallers is learned through multiple, repeated interactions. Because

40   these conditions are often fulfilled, also in social communication systems, we contend

41   that selection on reliability is less intense than hitherto assumed. This may contribute to

42   explaining the extraordinary diversity of signals including that of plant reproductive

43   displays.

44

Introduction

45

46 Communication is a key feature of life, structuring the interactions among partners [1,

47 2]. This explains why rapidly evolving communication systems can drive adaptive

48 radiations and outpace ecological divergence in other traits [3, 4]. However, the

49 conceptualisation of communication is contentious and hotly debated. In particular,

50 some researchers view communication as a process that evolved to facilitate

51 information transfer among signallers and perceivers [e.g., 2, 5], whereas others view

52 communication as a process of manipulating rather than informing others [6, 7]. While

53 information transfer requires reliability, it is not required for manipulation. The key

54 issues are thus how reliable communication is and how reliability (or lack thereof)

55 contributes to structuring the interactions among partners.

56   If the interests of signallers and perceivers diverge (which they commonly do),

57 reliability, a tight covariance between signal and quality, requires costs associated to

58 signalling or to cheating [8-10]. Notably, however, many ecological interactions such as

59 mutualisms appear to lack the costs of signalling or cheating that enforce reliability

60 [11]. Yet, recent studies on visual communication among fleshy-fruited plants and seed

61 dispersers concluded that fruit colours reliably indicate fruit nutritional rewards in

62 distinct communities [12, 13]. Because only one study on pollination of *Turnera*

63 *ulmifolia* demonstrated selection on the covariance between sensory traits and plant

64 rewards [14], the covariance between fruit colours and nutrients is probably best

65 explicable as by-product information originating from pleiotropy or similar biochemical

66 pathways of nutrients and pigments [12, 13]. As such, it is unclear whether animals

67 commonly select the reliability of plant-animal communication.

68   Here, we investigate the role of reliable communication in structuring seed

69 dispersal in a Mediterranean community. We analyzed a two-year dataset of fruit

70 consumption of two avian seed dispersers, blackcaps *(Sylvia atricapilla)* and garden

71 warblers *(S. borin)*, in Hato Ratón, SW Spain [15, 16]. Importantly, Jordano (1988)

72 already determined that both bird species selected fruits non-randomly and primarily to

73 maximise lipid intake because lipids provide the energy essential for long-distance

74 migration and over-wintering in Southern Spain. Here, we do not repeat that analysis

75 but rather aim to understand if birds select fruit colours indicating lipid contents.

76   We derived three predictions from the hypothesis that reliability structures seed

77 dispersal. We (i) expect fruit colour to be reliable (i.e., consistently associated with

78 nutrient rewards) both on a local and regional scale, the latter representing the

79 evolutionary setting which presumably has shaped consumers' responses. We (ii)

80 expected the nutritional rewards of foraging bouts to be consistently associated with

81 specific fruit colour combinations (Fig. 1), and (iii) the nutritional intake of consumers

82 responding to reliable signals in sequential foraging decisions (i.e., meals) should be

83 above the intake of a random forager.

84

85 **Methods**

86 **Bird diet**

87 Blackcaps and garden warblers are highly frugivorous during migration and over-

88 wintering when >90% of their diet consists of fruits [15]. The frugivorous diet of

89 blackcaps and garden warblers was obtained from September-November 1981 and 1982

90 from Hato Ratón, Doñana National Park, Southern Iberian Peninsula [16]. It is known

91 that both warblers mainly forage on fruits to maximise lipid intake at Hato Ratón [16], a

92 critical resource to fuel migration and over-wintering. All birds were mist-netted, ringed

93 and released. Based upon ring numbers we selected only the meal from the first time

94 each individual was caught for further analyses. We estimated the nutritional intake

95   resulting from a total of 1726 consumed fruits identified in 377 and 134 faecal samples

96   of blackcaps and garden warblers, respectively. These samples were obtained from the

97   faeces of birds and from flushing their digestive tract with 1% sodium chloride water

98   solution [15, 16]. The number of consumed fruits was estimated from seeds and the

99   proportion of remaining fruit skin from microhistological analysis [15, 16]. The amount

100   of fruits per species was visually estimated to the nearest 5% of an entire fruit ranging

101   from 0.05-11 fruits per sample.

102   Our samples reveal the short-term sequence of fruits ingested by freely foraging

103   warblers (i.e., meals). Meals reflect fruit choice within less than an hour before birds

104   were captured owing to their very short retention times of ingesta, on average <45 min

105   [15-17]. We envision these samples as instantaneous "probes" into the feeding sequence

106   of individual foraging birds (Fig. 1A). Because the majority of faeces contained seeds or

107   fruit remains from more than one plant species, any relationship between the nutritional

108   intake of birds and the colour of consumed fruits is not a simple consequence of the

109   traits of a single fruit species but a consequence of birds mixing different fruits. We

110   estimated the total nutritional intake per meal as the sum of the product of the number

111   of consumed fruits across all fruit species in a meal, the amount of fruit pulp per fruit

112   and the percentage of nutrients relative to the dry fruit mass.

113   Null models describing random foraging are based on direct counts of fruit

114   production (on 15 15m x 1.5m plots) and availability during the study period as well as

115   weekly counts on fruit phenology [15, 16].

116

117   **Fruit traits**

118   The information about pulp nutrients and fruit colours used in this study was obtained

119   from the Western Mediterranean fleshy-fruit dataset [13]. Briefly, the contents of crude

120   lipids of fruit pulp (percentage of pulp dry mass) were analysed by Soxhlet extraction.

121   Protein contents are based upon nitrogen extraction with Kjeldahl using the conversion

122   factor of 6.25. Non-structural carbohydrates were estimated as difference between dry

123   fruit mass and the contents of lipids, protein and fiber.

124   Fruits traits are at least partly determined by plant phylogeny. Previously, we

125   have shown that --independent of plant phylogeny-- fruit colour is associated with the

126   lipid contents of fruits and fruit brightness is associated with the contents of non-

127   structural carbohydrates across 111 species of fleshy-fruited plants in Southern Spain

128   [13]. More specifically, phylogenetically independent contrasts (PICs) of lipid and

129   sugar contents correlated most closely with hue and brightness, whereas morphological

130   and other nutritional traits (e.g., protein contents) did not correlate with visual traits.

131   The pervasive association between nutritional rewards and visual traits indicates that

132   fruit colour could qualify as a reliable signal of rewards. Fruits lipids are hydrophobic

133   and thus negatively correlated with the contents of hydrophilic carbohydrates in this

134   data set (Pearson correlation $r = -0.47$, $df = 103$, $p < 0.0001$). The contents of lipids and

135   carbohydrates are unrelated to the protein contents of fruits (Pearson correlation $r < 0.10$,

136    $df = 108$, $p > 0.27$).

137   Our previous analysis does not resolve, however, whether seed disperser can

138   perceive the association between fruit colour and nutritional rewards as it was done

139   based on human colour vision. Also, our analysis was based on a tree of species which

140   occur within different communities or which fruit at different times of the year. Thus, it

141   remains unclear whether reliability occurs regionally and locally and whether

142   frugivorous animals could select for it. Additionally, the tree used does not resolve

143   intrageneric relationships. We therefore assessed whether the covariance between

144   nutritional rewards and fruit colour also persists if (i) analysed within the avian colour

145   space and (ii) whether it is consistently found within genera across the entire tree of 111

146   species.

147   We thus selected 46 congeneric species belonging to 23 genera that are broadly

148   distributed throughout the phylogeny of Mediterranean species [13] (Table S1). For

149   each genus, we selected the species with the highest and lowest content of each main

150   nutrient (lipid, sugar, protein). These fruits encompass a broad variation in colour and

151   brightness, ranging from white to black, and nutritional contents (e.g. mean lipid

152   content 7% dry fruit-pulp mass, ranging between 0.8-58%) [13]. Using paired t-tests on

153   log-transformed variables we then analysed whether the colour variables differed

154   between the groups of relative high and relative low nutritional contents, respectively.

155   These tests thus show whether fruit colour transmit reliable information on the

156   nutritional quality of fruits, i.e., whether there is a consistent trend, independent of

157   phylogenetic affinity, for visual parameters (x, y, z coordinates and the excitation of the

158   double cone) to differ in relation to the nutrient content of the pulp.

159

160   **Vision modelling**

161   We tested our first prediction on the reliability of fruit colours using models of avian

162   vision. In general, most animals are able to extract information from colours using two

163   different aspects: achromatic and chromatic information on colour. Animals process

164   chromatic and achromatic information by distinct neuronal mechanisms. Variation in

165   brightness is perceived on the scale of black to white; high brightness values indicate

166   white because they are caused by a high reflectance from a surface. Chromatic

167   information results from variation in the saturation and peak wavelengths of the colour

168   spectra; the latter is related to human colour categories (red, green).

169   Fruit colours were quantified in 2007-2008 by measuring their reflectance

170   spectra with an Ocean Optics USB-2000 spectrometer and a Top Sensor System

171   Deuterium-Halogen DH-2000 lamp as a standardized light source (DT-MINI-GS-2) and

172   calculated in 5-nm-wide spectral intervals over the range of 300–700 nm [13]. We

173   measured the reflectance of 20 fruits per species and calculated a mean reflectance

174   spectrum for further analyses.

175   Birds use four cone types for colour vision. To calculate fruit colours according

176   to the visual perception of birds, we modelled the probability of photon capture of each

177   cone by multiplying the mean fruit reflectance spectra from each species with the

178   spectral sensitivities of the cones using the avian eye model developed by Vorobyev and

179   Osorio [18]. We calculated perception of fruit brightness according to the excitation of

180   the avian double cone according to Schaefer et al. [19]. In general, the avian eye model

181   assumes that discrimination is determined by thresholds that are set by noise originating

182   in the cones [18].

183   We converted cone excitation values for the four avian cone types used for

184   colour vision into the relative cone excitation values by dividing the excitation of each

185   cone by the sum of all cone outputs. Because these values are not independent from

186   each other, we transformed the cone excitation values into the tetrahedral colour space

187   of birds [4, 20] where each of the vertices represents the sole excitation of a single cone

188   (Figure 1B). The colour space within the tetrahedron is characterised by three Cartesian

189   coordinates {x,y,z} that define the location of each spectrum [4, 20]. The origin of the

190   coordinates is the achromatic point where all cones are stimulated equally.

191   Chromaticity, or the strength of a colour signal, is proportional to the Euclidean distance

192   from any point within the tetrahedron to the achromatic point [20]. The x coordinates

193   range from blue fruits with negative scores to red fruits with positive scores, y

194 coordinates range from purple fruits (negative scores) to green fruits (positive scores),

195 whereas positive scores on z are indicative of UV reflectance.

196   In general, the visual system of birds is relatively conservative. The spectral

197 sensitivities of most frugivorous birds including *Sylvia* warblers are unknown. Similar

198 to most other passerine families, Sylviidae belong to the UVS type of colour vision,

199 where the sensitivity of the short-wavelength cone is biased towards the ultraviolet. We

200 therefore used the well-known UVS spectral sensitivities of blue tits (*Cyanistes*

201 *caeruleus*) [21] to model fruit colour perception. However, if spectral sensitivities of the

202 other, VS, type of avian vision are employed, the results remain unaltered (e.g., fruit

203 colours indicate equally lipids: paired t-test, t= 2.67, df= 22, p< 0.05).

204

205 **Analysing reliability**

206 We tested our first prediction on the reliability of fruit colours on two spatial scales: in

207 the Western Mediterranean area (the regional scale) and in the fruits actually consumed

208 by Sylvia warblers at Hato Ratón (the local scale). To test our second and third

209 prediction on how birds respond to fruit colour as reliable cue of nutritional rewards, we

210 calculated the colour profile of a meal. The colour profile is the sum of the species-

211 specific {x,y,z} coordinates of all fruit species found in a meal weighted by their

212 relative abundance (in %) in that meal. Visual parameters and nutritional intake are thus

213 both compound variables that include the number of fruits in a meal as a weighting

214 factor to estimate the total 'visual' and 'nutritional' profile of each meal. This means

215 that the colour profile of a meal is independent of the number of fruits eaten in a meal

216 but dependent on the species composition in that meal. We then analysed the correlation

217 between total intake of lipids, sugars, and proteins and the colour profile as well as

218 brightness values across individual faecal samples of warbler species. We found a

219 consistent pattern in both years and therefore included samples from different years in

220 our analyses.

221

222 **Statistical analyses**

223 On the local scale of Hato Ratón we analysed the relationship between visual and

224 nutritional fruit traits in multiple regression with permutation test. In this analysis, the

225 variables of each species (nutritional contents, x, y, z coordinates) were weighted by

226 their relative fruit abundance in Hato Ratón (according to the data on fruit production

227 see [16] to account for the fact that seed dispersers encounter some species more

228 frequently than others.

229   We analysed the relationship between the colour profile and the overall intake of

230 sugars, lipids, and proteins in meals using multiple regressions with nutritional intake as

231 dependent variable and the colour coordinates {x,y,z} and brightness as well as the

232 number of fruits consumed per each meal as independent variables. The results

233 remained qualitatively identical if we analysed the residuals of the regression between

234 fruit number and nutritional rewards of meals showing that the association between

235 nutritional profiles and visual profiles is not a simple autocorrelation caused by the

236 number of fruits eaten.

237   To analyse whether the two Sylvia warblers choose fruit colours non-randomly

238 we used Monte Carlo simulations to sample combinations of fruit species within meals

239 according to the number of fruits (1-11) present in each meal. We ran separate

240 simulations for each month and year because Monte Carlo simulations are weighted by

241 the availability of each fruit species i.e., the number of fruits of each species present in

242 Hato Ratón at a given time based on the fruit counts. In other words, the likelihood that

243 a fruit species is represented in the simulated meals is a function of its abundance in a

244   given month. For each month, we ran 5000 simulations of each number of fruits (1-11)

245   in the meals where the {x,y,z} coordinates of each meal are determined by summing the

246   values of each species represented in the meal according to its proportion. We used

247   MANOVA analyses with Wilk's test to test for differences in {x,y,z} coordinates as

248   dependent variables between the observed and simulated meals for each species, month

249   and year separately. We determined whether the observed colour profile of meals was

250   within the 95% CI of simulated meals expected under the assumption that birds forage

251   randomly.

252

253   **Results**

254   Avian seed dispersers can visually evaluate the lipid rewards of Western Mediterranean

255   fruits but not their sugar or protein rewards. Fruits with higher lipid contents were

256   significantly darker than congeneric fruits with lower lipid contents (sister species

257   comparison to eliminate biases caused by phylogenetic relatedness, paired t-test, n=23,

258   t= 2.71, df= 22, p< 0.05), a relationship significantly consistent across the congeneric

259   comparisons (19 out of 23 contrasts showing higher lipid content in the congener with

260   darker fruits; binomial test, p= 0.003). Fruits with higher lipid contents differed also in

261   their chromatic properties, scoring lower (mean= 0.063) on the x-axis of avian colour

262   space --that captures variation from blue (negative values) to red (positive values) in our

263   fruits-- than congeners with lower lipid content (mean=0.155; paired t-test, t= 2.27, df=

264   22, p< 0.05). Again, this relationship was consistent across the congeneric comparisons

265   (binomial test, p= 0.003). There were no differences in the relationship between other

266   parameters of avian colour space (y, z coordinates) and lipid (p>0.2). The contents of

267   carbohydrates and protein did not correlate with any parameter of avian colour space

268   (x,y,z axes and perceived brightness all p> 0.3). Thus, the previously reported

269   association between carbohydrates and fruit brightness [13] does not hold within plant

270   genera. Overall, lipid-rich fruits were darker and significantly, and consistently, less

271   chromatic on the Iberian Peninsula compared to fruits with low lipid content that were

272   redder.

273   Because fruit colour is related to lipid contents in the Western Mediterranean

274   area, we then asked whether the colours of fruits simultaneously present in a local

275   community consistently indicate lipid contents. Variation in fruit brightness indicated

276   very reliably the lipid contents of 16 fleshy-fruited species (table S2) that blackcaps and

277   garden warblers consumed in Hato Ratón (Regressions with permutation test, $F_{1,14}=$

278   53.5, $r^2= 0.778$; $p< 0.001$). Colour variation was likewise associated with the lipid

279   contents of these fruits. This association was strongest for the y-axis of avian colour

280   space, which ranges from purple (negative values) to green (positive values) ($F_{1,14}=$

281   29.7, $r^2= 0.606$; $p= 0.0002$). UV reflectance was also associated with lipid contents (z-

282   axis: $F_{1,14}= 20.7$, $r^2= 0.567$, $p= 0.0004$) as was, albeit to a lesser extent, variation in the

283   reflectance in the blue part of the spectrum relative to the red part of the spectrum (x-

284   axis: $F_{1,14}= 13$, $r^2= 0.445$, $p= 0.003$). None of the colour parameters of the 16 fleshy-

285   fruited species indicated the contents of sugars and proteins (Regressions with

286   permutation test, $F_{1,14}= r^2< 0.11$, $p> 0.1$) revealing that these nutritional rewards are not

287   indicated at Hato Ratón. Now that we have shown a reliable relationship between lipids

288   and fruit colours in the fruits ingested by birds, we tested our second prediction that

289   birds use fruit colour as a reliable advertisement to optimise foraging.

290   Birds responded to fruit colours non-randomly (Table 1), and that response

291   predicted the total lipid intake in their meals (blackcap $F_{5, 398}= 763.2$, adjusted $r^2= 0.90$,

292    $p< 0.0001$, garden warbler $F_{5, 144}= 406.5$, adjusted $r^2= 0.93$, $p< 0.0001$), which was

293   above the one of random foragers (blackcap, $t= 301$, $p< 0.0001$; garden warbler $t= 154$,

294   p< 0.0001). Lipid-rich fruits did not differ in size or other parameters from less

295   rewarding fruits in Hato Ratón. Although the variation in the reflectance in the blue part

296   of the spectrum relative to the red part (x axis) was a less reliable indicator of the lipid

297   contents of fruits in Hato Ratón than other colour parameters, this variation was the best

298   predictor of the lipid rewards of the meals of both warblers (blackcap: x axis: t= -16.34,

299   p< 0.0001; y axis: t= 0.4 p> 0.6; z-axis: t= 7.65, p< 0.0001; brightness profile: t= 0.3,

300   p> 0.7, number of fruits: t = 16.52, p< 0.0001; garden warbler: x axis: t= -21.22, p<

301   0.0001, y axis: t= 12.2, p< 0.0001; z-axis: t= 7.52, p< 0.0001; brightness profile: t= 172,

302   p< 0.0001, number of fruits: t=-4.64, p< 0.0001). This result shows that the colour

303   profile of meals predicted their lipid reward as much (in blackcaps) or more (in garden

304   warblers) as the number of fruits eaten per meal (mean =2). Birds preferentially

305   consumed fruits that were less chromatic than randomly expected (Fig. 2) and those

306   colour combinations predicted lipid rewards but not the rewards of carbohydrates or

307   proteins.

308

309   **Discussion**

310   Here, we have shown for the first time that communication in a fruit-dispersal

311   mutualism is regionally and locally reliable and that mutualistic seed dispersers

312   apparently forage using fruit colours as indicators of lipid rewards and thereby

313   maximise their lipid intake. These results highlight that (i) frugivorous animals could

314   use colour to optimise foraging returns and hence partner choice in seed dispersal

315   mutualism; (ii) reliability does not need to be very strong to structure the consumer-

316   resource interactions that characterise mutualisms.

317

318   **Reliability and selection by mutualists**

319   Because visual discrimination is the first of several steps in hierarchical decision-

320   making by frugivorous birds [22], the striking covariance of the visual and lipid profiles

321   of the meals of the two Sylvia warblers facilitates birds' maximization of lipid intake, a

322   critical nutrient for their survival during autumn and winter [16]. Interestingly, neither

323   carbohydrate nor protein rewards were associated with variation in fruit colour even

324   though our previous study found an association between carbohydrates and fruit

325   brightness in 111 species from Southern Spain [13]. The lack of an association between

326   carbohydrates and fruit brightness within the community indicates that broad-scale

327   comparisons including species from different areas and seasons can over-estimate the

328   reliability that animals can use while foraging.

329   Our conclusion that birds used dark and less chromatic fruit colours to optimise

330   lipid rewards is supported by two facts. First, the relationship between less chromatic

331   colours and lipid rewards was stronger in the meals of birds than among the fruits

332   available at Hato Ratón illustrating that birds preferentially consumed fruits with a tight

333   association between fruit colour and lipid rewards. Second, varying fruit availability

334   among different months and years represents a natural experiment to examine birds'

335   preferences. That birds' non-random selection remained significant even if analysed

336   separately over monthly periods (Table 1), indicates very consistent choices

337   independent of temporal variations in the fruit supply.

338   Our analyses revealed congruent associations between fruit colour and lipid

339   rewards on the regional and local scale. Yet, we expect the reward-colour association to

340   vary according to spatial and temporal variation in fruit abundance and ripening

341   phenology. Importantly, such variation does not prevent birds to respond to (and

342   potentially select) reliable plant communication. Experiments manipulating colour-

343   reward associations have shown that garden warblers associate colours with their

344 specific rewards in 1-2 days [23] allowing birds to develop quickly preference rankings

345 according to the local fruit supply. Thus, in repeated interactions mutualists can cope

346 with variation in signal-reward associations because they necessarily evaluate the

347 quality of a resource by taste and post-ingestive feedbacks enabling them to learn the

348 quality of rewards.

349 Reliability in plant-animal communication can arise as a by-product of a shared

350 biochemistry of fruit pigments and nutrients [12, 13]. For example, covariance between

351 carotenoids and lipid molecules is explicable because carotenoids depend on a

352 phospholipid environment [24]. However, the covariance in our study is not explicable

353 by fruit biochemistry because the dark and less chromatic fruits associated with lipid

354 contents are mainly pigmented by anthocyanins, a hydrophilic class of pigments

355 unrelated to lipids.

356 Animals can also select for reliability in mutualism as part of a self-serving

357 strategy. For example, hawkmoths reduce probing time on less rewarding Petunia

358 flowers to increase their foraging efficiency and thereby reduce the pollination and seed

359 set of relatively unrewarding flowers [25]. It is currently unknown whether seed

360 dispersers remove more fruits from more rewarding plants on an intra-specific level but

361 birds possess fine-tuned discrimination abilities for variation in the concentration of the

362 main nutrients [26]. Because fruit colours and nutrients are both evolutionary labile

363 traits [13], the covariance between both can evolve according to selection by mutualists

364 if these remove less fruits of less rewarding plant individuals.

365

366 **Communication in mutualisms**

367 We suggest that communication could structure mutualisms even if its reliability is

368 limited. We suggest limited reliability to be a very general mechanism structuring the

369 consumer-resource interactions that characterise mutualisms where partners repeatedly

370 exchange resources to their mutual benefit. This is because fair trade among mutualists

371 can always ensue if the summed effects of repeated interactions have pronounced

372 influence on the fitness of each partner, but a single interaction does not strongly

373 determine their fitness. This occurs not only among members of a social group as in

374 cooperation and dominance but also in mutualisms such as pollination and seed

375 dispersal.

376   Conversely, selection for reliability is more pronounced in one-time

377 communication systems like mate choice and prey-predator interactions, where a single

378 error of choice can have dramatic fitness consequences. The current debate on the

379 general reliability of communication [5, 7] does not reflect that selection upon reliability

380 will vary depending on the interaction frequency among communicators. Finally, we

381 note that our results explain why the colouration of fruit products influences how

382 humans perceive their nutritional quality [27, 28].

383

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458

459   **Table 1.** MANOVA analyses showed that the colour patterns in the meals of the two

460   warbler species differed from simulated random compositions in all months except for

461   one in blackcaps (see also Fig 3). Columns indicate the frequencies of observed meals

462   (in %) which are outside the 2.5% and 97.5% percentiles of the simulated values for the

463   achromatic, x, y, and z components of the color space.

464
465   **Species and period**

	Wilk's λ	P	%A	% x	% y	% z

466   *Sylvia atricapilla*

467	October 1981 (N= 44)					
	0.999	***	4.5	6.8	4.5	9.0
468	November 1981 (N= 36)					
	0.9999	NS	5.5	5.6	2.8	16.7
469	October 1982 (N= 91)					
	0.9837	***	26.4	34.1	4.4	14.3
470	November 1982 (N= 206)					
	0.9963	***	15.5	12.6	3.4	20.4
471						
472	*Sylvia borin*					
473	September 1981 (N= 27)					
	0.9991	***	14.8	11.1	7.4	25.9
474	October 1981 (N= 17)					
	0.9998	*	11.8	35.3	5.9	17.6
475	September 1982 (N= 73)					
	0.9272	***	26	75.3	26.2	8.2
476	October 1982 (N= 17)					
	0.9886	***	35.3	41.2	5.9	11.8

477
478 ***: P<0.0001; **: P<0.001; *: P<0.05; NS: non-significant.
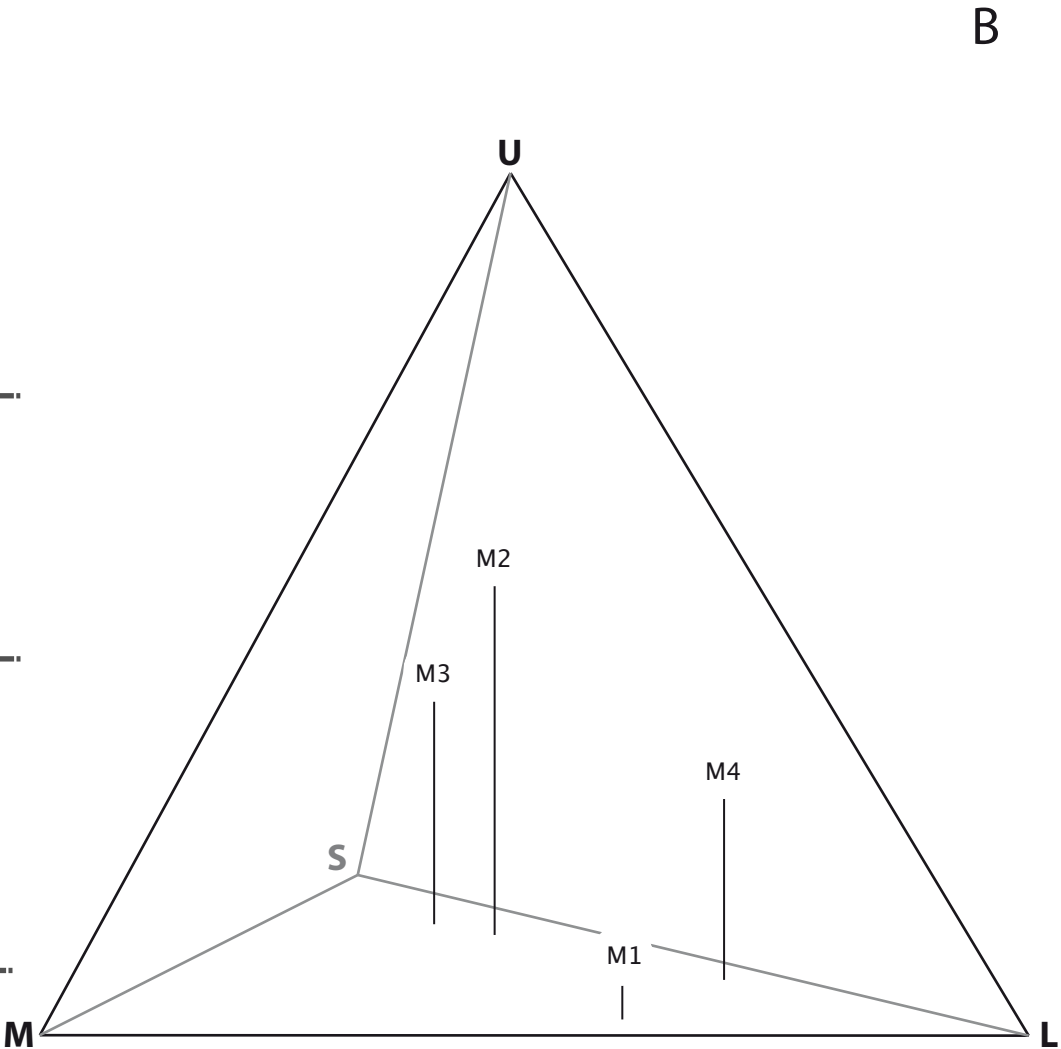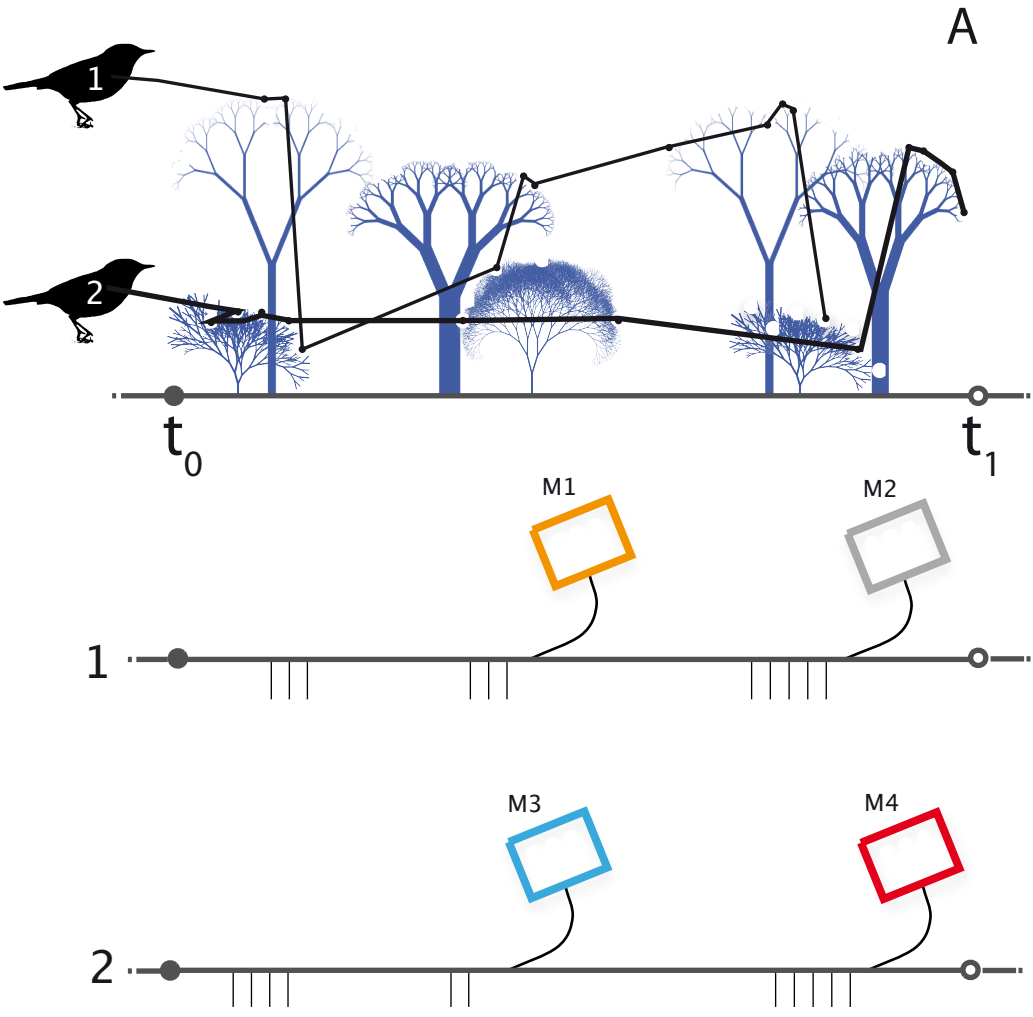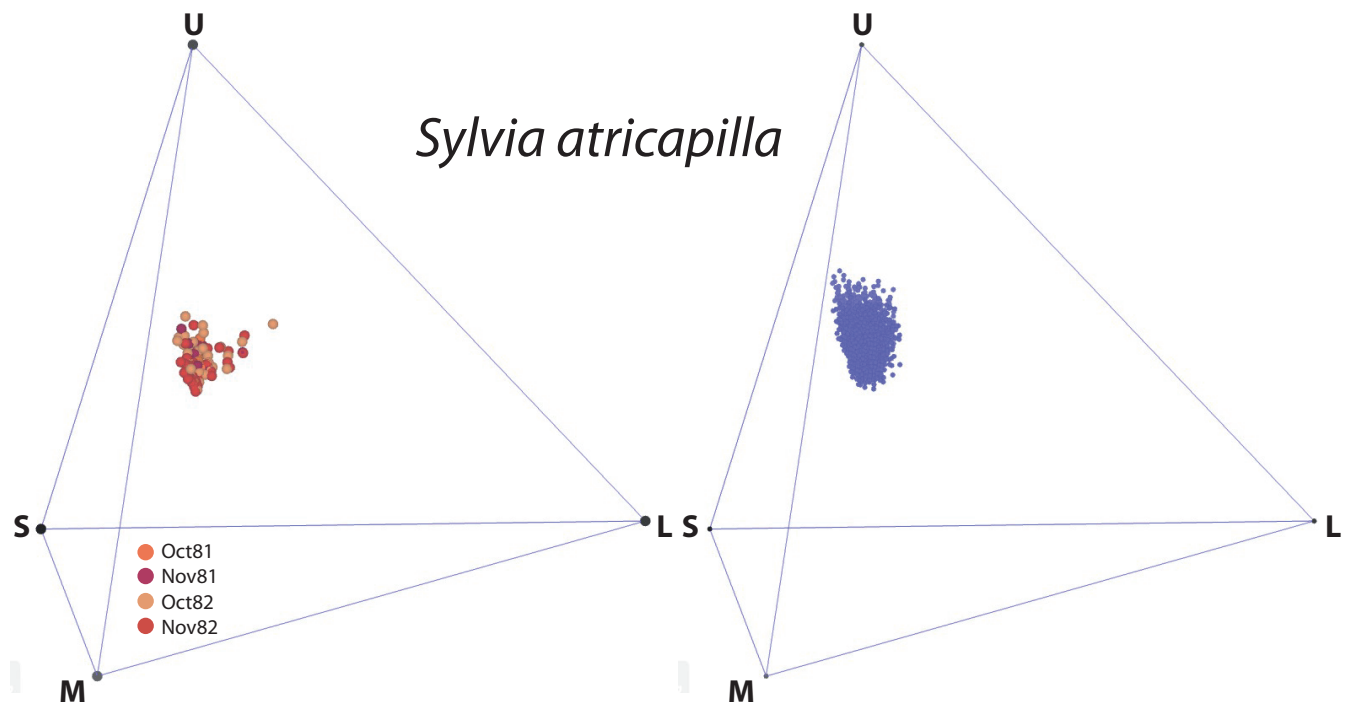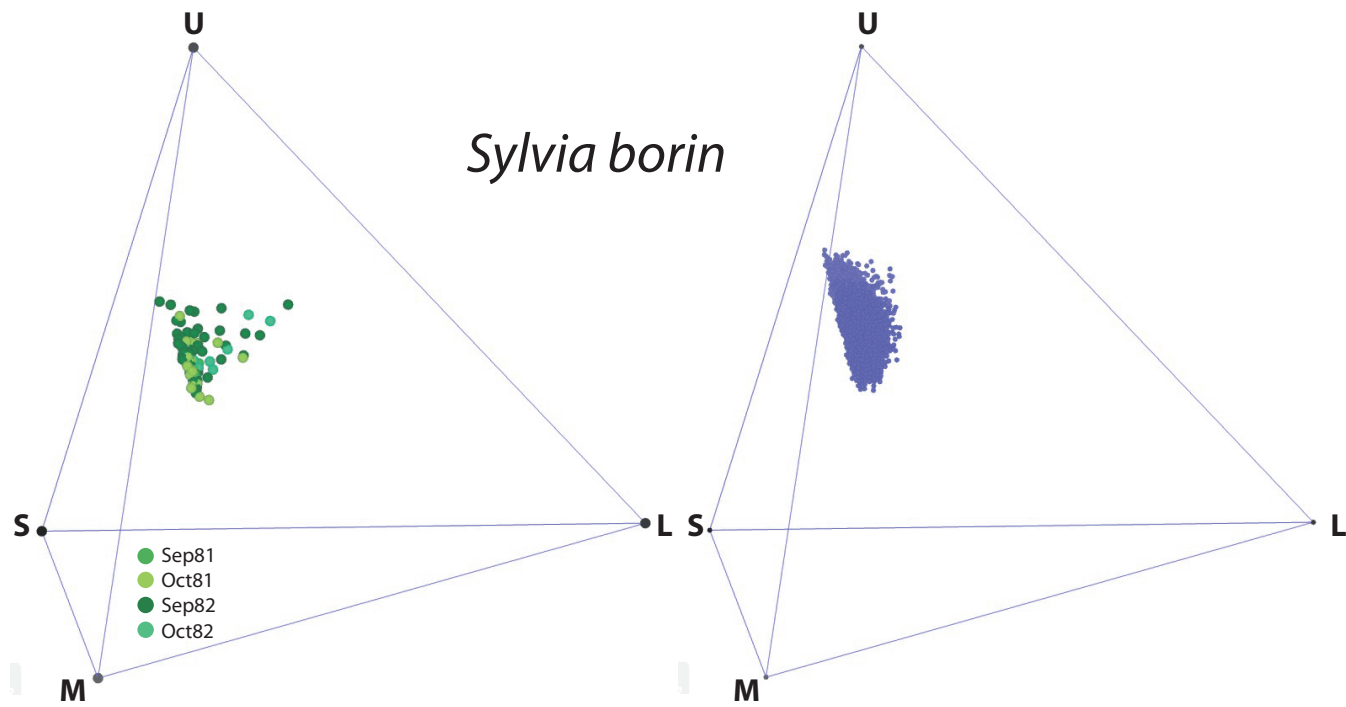479

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481   **Figure Legends**

482   **Figure 1**: The trade of resources characterising mutualistic interactions leads to

483   multiple, repeated interactions among individual producers and consumers. For

484   example, birds use visual information to decide which fruits to consume. Two

485   individual birds combine different fruit species in their meals during a short feeding

486   bout (t_0-t_1), along their foraging sequence, in which they visited different fruiting plants.

487   M1-M4 indicate the composition of four meals i.e., the number of fruits consumed and

488   their species identity (**A**). For illustrative purposes, M1 and M2 represent two foraging

489   bouts of the same individual. In our analyses, we only considered a single meal for each

490   individual bird. The colours birds see can be represented within a three dimensional

491   chromaticity diagram characterised by the coordinates {x, y, z} (**B**). The locations of

492   different meals (A) in the visual space (B) are defined by the coordinates of the fruit

493   species each meal includes, weighted by the number of fruits from each species. In

494   other words, the visual profile of each meal is scaled given the relative contribution of

495   fruit species within that meal.

496

497   **Figure 2.-** Colour profiles of warblers' meals within the three dimensional tetrahedral

498   representation of the visual space. For each species, meals of different years and months

499   are identified by colour codes (inset). The locations of observed fruit meals colour

500   profiles are compared with the locations of simulated meals (N= 10,000), representing

501   the expected patterns for avian foragers consuming fruits in proportion to their actual

502   availability in the habitat. The 3D scatter of observed data (left) for the two warbler

503   species consistently deviates from the simulated, null model expectation (right)

504   indicating that birds were selecting highly distinctive and non-random combinations of

505   fruit colours in their meals. In turn, these fruit combinations consistently resulted in

506 higher lipid intake when compared to simulated meals, despite marked changes

507 (between years and months) in the fruit supply.

A

B

M1 M2

1

M3 M4

2

U

M2

M3

M4

S

M1

M

L

Sylvia borin

Sep81
Oct81
Sep82
Oct82

Sylvia atricapilla

Oct81
Nov81
Oct82
Nov82

Observed

Simulation