1   TITLE: Bees attend primarily to costs, not benefits, to avoid exploitation by floral mimics

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25   the data. ANN made the illustrations in Figure 1. ANN, CTH, and ALR wrote the original draft

26   of the manuscript; other authors provided editorial advice.

27

28

29   ABSTRACT

30

31   Animals are expected to weigh costs and benefits when making foraging decisions. Flowering

32   plants often offer floral food rewards to pollinators, but also frequently deceive pollinators into

33   visiting without providing rewards. Although floral mimicry, in which rewardless flowers mimic

34   rewarding (model) flowers is common, it remains unclear whether pollinators evaluate the

35   relative costs and benefits of visiting each. Using a signal detection theory (SDT) framework, we

36   investigated how bumble bee decisions respond to experimental manipulations of costs and

37   benefits within an intersexual floral mimicry system in which unrewarding female flowers

38   imperfectly mimic pollen-rewarding male flowers (models). Using a fully factorial design, we

39   increased the cost of visiting mimics (by adding quinine), increased the benefit of visiting

40   models (by adding pollen), increased both simultaneously, and made no changes (control). As

41   predicted by SDT, increasing mimic costs led to a conservative bias: bees made more correct

42   rejections, but fewer correct detections. Contradicting SDT predictions, enhancing model reward

43   did not elicit a liberal bias and decision performance remained unchanged. Our findings suggest

44   that bees prioritize avoiding costly errors under uncertainty, even when this limits potential

45   gains. Such conservative foraging decisions may help stabilize deceptive systems by allowing

46   mimics to persist despite moderate costs.

47

48   KEY WORDS: signal detection, Batesian mimicry, cognition, learning, intersexual mimicry,

49   decision making, pollen, Begonia, foraging, floral rewards

50

51

52   INTRODUCTION

53

54   Animals often make decisions under uncertainty, continually updating information about their

55   environment to reduce ambiguity and optimize choice behavior (Blumstein & Bouskila, 1996;

56   Real, 1992; Stephens, 2008). For pollinators such as bees, this ability is critical. During a single

57   day, a bee may visit thousands of flowers across multiple plant species that vary in their floral

58   traits and reward payoffs (Chittka et al., 1999; Heinrich, 1976, 1979). To maximize energetic

59   return, pollinators must rapidly and accurately assess complex and variable floral signals – yet

60   these signals are not always reliable. Because producing floral rewards is energetically costly

61   (Nicholls & Hempel De Ibarra, 2017; Pyke & Ren, 2023; Southwick, 1984), plants may use

62   floral signals to attract visitors without offering rewards. This occurs in Batesian floral mimicry,

63   in which a rewardless plant species (mimic) produces deceptive signals that overlap in sensory

64   space with those of a rewarding species (model), in one or more sensory modalities (Dafni, 1984;

65   Johnson & Schiestl, 2016; Pannell & Farmer, 2016). This form of deception is widespread,

66   having evolved repeatedly across angiosperms in more than 32 plant families and across 7,500

67   species worldwide (Johnson & Schiestl, 2016; Renner, 2006; Schiestl & Johnson, 2013). The

68   success of this strategy depends on the perceptual and learning limitations of pollinators, which

69   may fail to reliably discriminate mimic from model and thus visit both (Ferdy et al., 1998;

70   Renner, 2006; Schiestl & Johnson, 2013; Vázquez & Barradas, 2017).

71

72   Signal detection theory (SDT) offers a powerful framework for understanding why pollinators

73   sometimes visit rewardless flowers when faced with uncertainty (Lichtenberg et al., 2020). When

74   pollinators encounter deceptive mimics, they face four possible decision outcomes (Figure 1):

75   two correct decisions – visiting a model ('hit') and avoiding an unrewarding mimic ('correct

76   rejection') – and two types of decision errors – visiting a rewardless flower ('false alarm') or

77   failing to visit a rewarding one ('miss'). SDT describes the tradeoff between these two types of

78   decision errors (Green & Swets, 1966; Wiley, 2006). Because reducing one type of error

79   increases the other, pollinators must adopt a decision criterion that balances the costs and

80   benefits of these errors. While SDT has been widely used to explain the evolution and

81   maintenance of floral mimicry, most studies have focused on the ability of pollinators to

82   discriminate between model and mimics based on their perceptual similarity (e.g., Gumbert &

83   Kunze, 2001; Leonard et al., 2011; Russell et al., 2021) and on the relative frequency of each

84   within a given population (e.g., Finkbeiner et al., 2018; Lindström et al., 1997; Pfennig et al.,

85   2001; Russell et al., 2020). Much less is known about how the costs and benefits of foraging

86   outcomes shape pollinator decision criteria.

87

88   This is somewhat surprising, given a central prediction of SDT is that receivers should adjust

89   their decision thresholds according to the relative costs and benefits of foraging on models and

90   mimics (Abbott & Sherratt, 2013; Kikuchi & Sherratt, 2015; Sherratt & Peet-Paré, 2017). For

91   pollinators, foraging carries clear costs, including energetic expenditure and time investment

92   (Heyneman, 1983; Mayberry et al., 2024; Wolf et al., 1975), exposure to predators (Romero et

93   al., 2011), and sometimes contact with toxic or otherwise aversive floral rewards (Barlow et al.,

94   2017; Jones & Agrawal, 2016; Stevenson et al., 2017). The benefits of foraging are also variable,

95   depending on the nutritional value, quantity, and temporal or spatial availability of rewards

96   (Benadi et al., 2023; Hemingway, Leonard, et al., 2024; Venjakob et al., 2022). Although

97   pollinators are sensitive to these costs and benefits while foraging (e.g., Hemingway et al., 2024;

98   Richman et al., 2017), their influence on decision making in deceptive systems remains poorly

99   understood (see de Jager & Ellis, 2014; J. Ferdy et al., 1998; Gaskett, 2011; Russell et al., 2020).

100   SDT predicts plasticity in criteria: bees should be more cautious (avoid false alarms) when errors

101   are costly, or more liberal (favor hits) when rewards are high. Moreover, when both the cost of

102   visiting the mimic and the benefit of visiting the model are increased, the bias should reflect the

103   combined influence of costs and benefits (Lynn & Barrett, 2014).

104

105   Here we used a powerful system to empirically test these predictions of SDT within the context

106   of floral deception. *Begonia odorata* is a monoecious species bearing both male and female

107   flowers on the same plant, and these flowers are visually similar, with showy white tepals

108   presented together within inflorescences (Russell et al., 2020). This system exhibits intersexual

109   floral mimicry, in which unrewarding female flowers mimic pollen-producing male flowers – a

110   phenomenon known as pseudoanthery (Johnson & Schiestl, 2016). Pollinators, typically pollen-

111   collecting bees, learn to associate male-phase traits (such as color, scent, and shape) with pollen

112   rewards, creating a signal-reward mismatch that requires them to discriminate between visually

113   similar morphs. Previous work has shown that naïve bees exhibit a sensory bias toward mimics

114 but rapidly learn to avoid them, and that model-mimic frequency has little effect on

115 discrimination performance (Russell et al., 2020). Subsequent experiments tested whether

116 variation in flower size influenced the rate of discrimination learning and found that although

117 bees quickly learned to distinguish between rewarding males and unrewarding females, this

118 learning was not significantly affected by size variation (Russell et al., 2021). While clearly bees

119 can readily learn to discriminate models from mimics, it remains unclear how discrimination is

120 shaped by the relative rewards of models and the costs of visiting mimics. *Begonia odorata*

121 therefore provides an ideal system for testing how variation in costs and benefits influences

122 pollinator decision-making.

123

124 In a fully factorial experiment, we manipulated the rewards of male flowers (via addition of

125 pollen) and the punishments of female flowers (via addition of aversive quinine powder) to vary

126 the payoffs of hits and false alarms. We asked how these manipulations, and pollinator

127 experience, affect bees' decision biases and discrimination abilities. Consistent with SDT, we

128 predicted a conservative bias in bee decision making when the cost of visiting mimics was

129 increased and a liberal bias when the benefit of visiting models was increased, and that bias

130 would reflect the sum of the cost plus the benefit when both costs and benefits of mimics and

131 models were increased, respectively. As a result, we predicted that when mimic cost increased,

132 bees would make relatively more correct rejections at the cost of making fewer correct detections

133 ('hits') and would be less likely to buzz flowers, an energetically expensive attempt to extract

134 pollen (Rossi et al., 2025). Likewise, we predicted that when model benefit increased, bees

135 would make relatively more correct detections, at the cost of fewer correct rejections, and would

136 be more likely to buzz flowers. Finally, as naïve pollinators are initially unfamiliar with the

137   phenotypic distribution and costs and benefits of visiting models and mimics, we expected bees'

138   responses to models and mimics to increasingly fit these predictions of SDT as foraging bees

139   gained experience (e.g., (Russell et al., 2020, 2021).

140

141

142   METHODS

143

144   *Test subjects*

145

146   We maintained 3 colonies (Plant Products: Biobest Group, Canton, MI, U.S.A.) of the common

147   eastern bumble bee *Bombus impatiens* following Russell et al., 2020. In brief, we allowed

148   colonies to forage freely on 2 M sucrose solution and pulverized honeybee-collected pollen

149   (Koppert Biological Systems) from artificial feeders within enclosed foraging arenas (length,

150   width, height: $82 \times 60 \times 60$ cm) set to a 14 h : 10 h light : dark cycle.

151

152   We used fresh male and female flowers with mature anthers and styles, respectively, from 10

153   simultaneously monoecious *Begonia odorata* plants raised in a university greenhouse with

154   supplemental halogen lights to extend day length to a 14 : 10 h cycle and with fertilizer

155   applications every other week (Plant Tone, NPK 5 : 3 : 3). While female *B. odorata* flowers are

156   rewardless and do not produce pollen or nectar, male *B. odorata* flowers offer pollen, their only

157   reward to their primary pollinators, bees; bumble bees are among the bee genera that visit closely

158   related *Begonia* species (De Avila et al., 2017; Pemberton & Wheeler, 2006; Schemske et al.,

159   1996; Wyatt & Sazima, 2011). Female *B. odorata* flowers closely resemble male flowers in

160   bumble bee color vision (Russell et al., 2020, 2021) and scent (unpublished data); both flower

161   sexes have creamy white dissected petals, and the female flower's yellow and highly divided

162   styles closely resemble the male flower's numerous yellow stamens.

163

164   *Experimental overview*

165   We tested how the benefits of visiting models (male flowers) and the costs of visiting mimics

166   (female flowers) influenced learning in initially flower-naïve bees ($N = 97$). We examined how

167   bees learned to sample between models and mimics by analyzing three primary components of

168   their sampling behavior during visits to arrays of 20 flowers: approaches, landings without

169   buzzing, and landing with buzzing ("buzzes"). An approach was defined as a bee in flight greatly

170   reducing its velocity while facing a flower within 3 cm. All landings (defined as 3 or more legs

171   in contact with the flower) were preceded by an approach. Landings were considered correct

172   detections when directed at models and false alarms when directed at mimics (Figure 1). Not all

173   approaches led to landings; these cases represented missed detections for models and correct

174   rejections for mimics (Figure 1). Landings without buzzing on male flowers typically involved

175   the bee collecting pollen via a behavior termed scrabbling; see Russell et al., 2017 for a

176   description. In contrast, bees never scrabbled on female flowers. Buzzes, which indicated an

177   attempt at extracting pollen whether or not it was available, were identified by their distinctive

178   sound using Zoom H2 Handy Recorders (ZOOM Corporation) to amplify and verify buzzes

179   while trials were taking place and occurred only after a bee had landed (see Russell et al. 2016a).

180   Buzzing a male flower represented a correct response, whereas buzzing a female flower

181   represented an incorrect response.

182

183   We assigned flower-naïve bees approximately evenly across five treatments: an unmodified

184   control treatment, a modified control treatment ('control treatment'), an increased model benefit

185   treatment ('benefit treatment'), an increased mimic cost treatment ('cost treatment'), and an

186   increased model benefit and mimic cost treatment ('both treatment'). In the unmodified control

187   treatment, both male flowers (which offer on average 0.18 mg of pollen) and female flowers

188   were presented to bees without modification. In all other treatments, anthers of male flowers

189   were supplemented with pollen. Because collecting pollen from male *Begonia* flowers to

190   supplement other flowers was extremely time intensive, we used cherry pollen for all

191   supplementation (*Prunus avium*; Pollen Collection and Sales, Lemon Cove, California, USA),

192   which bumble bees readily collect (e.g., Russell et al., 2017). In the 'control treatment', male

193   flowers were each supplemented with 0.9 mg pollen (to control for the effect of adding a novel

194   pollen type across treatments) and female flowers were unmodified. To increase the benefit to

195   bees when visiting models, in the 'benefit treatment', male flowers received double the pollen

196   supplement (1.8 mg pollen added to the anthers of each flower), while female flowers were

197   unmodified. To increase the cost to bees when visiting mimics, in the 'cost treatment', the styles

198   of female flowers were supplemented with 0.5 mg of powdered quinine (99% anhydrous,

199   ACROS Organics, Fisher Scientific, Hampton, NH, USA), a stimulus that bees perceive as

200   aversive (Muth et al., 2016), while male flowers received the base supplement (0.9 mg pollen).

201   In the 'both treatment', male flowers received the double pollen supplement (1.8 mg), while

202   female flowers received the quinine supplement. Across all treatments, 20 flowers were arranged

203   in a 5 x 4 Cartesian grid, with flowers spaced 7 cm apart. Male and female flowers were

204   alternated by position and presented in equal numbers. To prevent desiccation, freshly cut live

205 flowers were placed into custom water tubes (Russell et al., 2017). We systematically alternated

206 trials among treatments to control for potential effects of time and day.

207

208 To initiate a behavioral trial, flowers were set up and a single flower-naïve worker bee was

209 gently captured from the foraging arena using a 40 dram vial (Bioquip) and immediately released

210 in the center of the test arena following (Russell et al., 2017). We terminated the trial after 60

211 visits (or earlier if the bee stopped visiting flowers for 5 minutes) to avoid bees depleting models

212 of pollen rewards (mean 47 visits; range 4-60 visits). To terminate the trial, we captured the bee

213 in a 40-dram vial and euthanized it. For each trial we used a new flower-naïve bee and new

214 freshly clipped flowers; we tested bees individually and never reused flowers or bees across

215 trials. The test arena was cleaned after each trial. For analyses, we excluded one bee with fewer

216 than five visits and no flower landings.

217

218 *Data analyses*

219

220 All data were analyzed using R v.4.4.0 (Developmental Core Team R, 2024). To analyze how

221 experience and the costs of visiting mimics and benefits of visiting models affected sampling

222 behavior, we fit generalized linear mixed models (GLMMs) with a binomial distribution using

223 the glmmTMB() function (glmmTMB package; Brooks, 2025), specifying type II Wald chi-

224 squared ($\chi2$)-tests via the Anova() function (car package; Fox et al., 2023). We checked model

225 assumptions for all models (DHARMa package; Hartig, 2024).

226

227   For the first set of GLMMs, the response variable was sampling behavior (either 'correct

228   decisions' vs 'incorrect decision', 'correct detection' vs 'missed detection', 'correct rejection' vs

229   'false alarm', 'buzz given landing' vs 'land without buzzing', or 'landing on male' vs 'landing

230   on female') and the explanatory variables were 'treatment' (modified control ('Control'),

231   increased model benefit ('Benefit'), increased mimic cost ('Cost'), and increased mimic cost and

232   model benefit ('Both') and experience ('visit number'). We included 'bee' as a random factor,

233   with 'visit number' as repeated measures within bee, within colony (except for two models, in

234   which bee within colony would not converge; we therefore excluded the colony random effect

235   for these two models). In cases of significant effects, we ran Tukey's post hoc test using the

236   emmeans() function (emmeans package; Length, 2025) to determine which pairs were

237   significant. For the second set of GLMMs, in which we examined how pollen reward

238   supplementation specifically affected sampling behavior, the explanatory variable 'treatment'

239   was either the unmodified control or the modified control.

240

241   To determine whether pollen or quinine supplementation affected flower-naïve bees' initial

242   landing preference for models (male flowers) versus mimics (female flowers), we used G-tests

243   (DescTools package; Signorell et al., 2025) to examine choice of first flower landing. There were

244   no significant differences in model versus mimic preference for any treatment (modified control:

245    $G = 0.430$, $N = 21$, $P = 0.512$; increased model benefit: $G = 1.33$, $P = 0.249$, $N = 19$; increased

246   mimic cost: $G = 0.00$, $P = 1.000$, $N = 20$; increased mimic cost and model benefit: $G = 0.20$, $P =$

247   0.655, $N = 21$).

248

249

250   RESULTS

251

252   *Correct decisions and detections are affected primarily by mimic cost*

253

254   Flower-naïve bees overall learned to make proportionally more correct decisions (combining

255   correctly rejecting mimics and correctly detecting models) with experience, but this pattern

256   depended on treatment: increasing the cost of mimics modestly reduced the proportion of correct

257   decisions with experience (Figure 2a; GLMM: treatment effect: χ^2_3 = 19.71, *P* < 0.0002;

258   experience effect: χ^2_1 = 6.38, *P* < 0.012; treatment × experience effect: χ^2_3 = 10.06, *P* < 0.019).

259   Bees made proportionally fewer correct detections with experience and the rate of correct

260   detections decreased much more quickly when mimics were relatively more costly to visit

261   (Figure 2b; GLMM: treatment effect: χ^2_3 = 45.79, *P* < 0.0001; experience effect: χ^2_1 = 96.97, P <

262   0.0001; treatment × experience effect: χ^2_3 = 8.57, *P* < 0.036). Bees made proportionally more

263   correct rejections with experience, and this pattern did not depend on the cost of mimics and

264   benefit of models (Figure 2c; GLMMs: treatment effect: χ^2_3 = 6.94, *P* = 0.074; experience effect:

265   χ^2_1 =130.07, *P* < 0.0001; treatment × experience effect: χ^2_3 = 0.67, *P* = 0.880).

266

267   *Decision to buzz is affected primarily by mimic cost*

268

269   Bees did not alter how often they buzzed models with experience, but overall buzzed models

270   significantly less when the cost of visiting mimics was increased (Figure 3a; GLMM: treatment

271   effect: χ^2_3 = 66.49, *P* < 0.0001; experience effect: χ^2_1 = 1.56, *P* = 0.213; treatment × experience

272   effect: χ^2_3 = 3.57, *P* = 0.313). Bees altered how often they buzzed mimics with experience, but

273   this pattern depended on the cost of visiting mimics (Figure 3b). When the cost of mimics was

274   unmodified, bees initially buzzed frequently, but less so with experience; when the cost of

275   mimics was increased, bees initially rarely buzzed, but increased buzzing somewhat with

276   experience (Figure 3b; GLMM: treatment effect: $\chi^2_3 = 43.56$, $P < 0.0001$; experience effect: $\chi^2_1 =$

277   20.07, $P < 0.0001$; treatment $\times$ experience effect: $\chi^2_3 = 31.29$, $P < 0.0001$). Finally, the

278   proportion of landings on models changed with experience, but this relationship was complex

279   (Figure 3c). Landings on models increased the most when only the benefit of visiting models was

280   increased; landings on models decreased the most when costs of mimics and benefits of models

281   were increased simultaneously (Figure 3c; GLMM: treatment effect: $\chi^2_3 = 4.94$, $P = 0.177$;

282   experience effect: $\chi^2_1 = 2.96$, $P < 0.086$; treatment $\times$ experience effect: $\chi^2_3 = 8.41$, $P < 0.039$).

283

284   *Decision making is modestly improved when models are pollen supplemented*

285

286   Bees made proportionally more correct decisions with experience but made consistently more

287   correct decisions (15% more on average) when models were supplemented with pollen (Figure

288   4a; GLMM: treatment effect: $\chi^2_1 = 11.55$, $P < 0.0007$; experience effect: $\chi^2_1 = 3.96$, $P < 0.047$;

289   treatment $\times$ experience effect: $\chi^2_1 = 0.13$, $P = 0.719$). Bees decreased their proportion of correct

290   detections with experience but made consistently more correct detections (7.5% more on

291   average, though this difference was not statistically significant) when models were supplemented

292   with pollen (Figure 4b; GLMM: treatment effect: $\chi^2_1 = 2.57$, $P = 0.110$; experience effect: $\chi^2_1 =$

293   18.80, $P < 0.0001$; treatment $\times$ experience effect: $\chi^2_1 = 3.55$, $P = 0.060$). Bees increased their

294   proportion of correct rejections with experience but made consistently more correct rejections

295   (30% more on average) when models were supplemented with pollen (Figure 4c; GLMM:

296   treatment effect: $\chi^2_1 = 6.40$, $P < 0.0099$; experience effect: $\chi^2_1 = 43.05$, $P < 0.0001$; treatment $\times$

297   experience effect: $\chi^2_1 = 2.58$, $P = 0.108$). Bees in both treatments slightly improved their

298   proportions of landings on models with experience, with bees making consistently more landings

299   on models (13% more on average) when supplemented with pollen (Figure 4d; GLMM:

300   treatment effect: $\chi^2_1 = 5.82$, $P < 0.016$; experience effect: $\chi^2_1 = 0.60$, $P = 0.438$; treatment $\times$

301   experience effect: $\chi^2_1 = 0.044$, $P = 0.834$).

302

303

304   DISCUSSION

305

306   When encountering floral mimicry, pollinators must continually discriminate between rewarding

307   and unrewarding flowers, often under conditions of incomplete information and uncertainty

308   (Johnson & Schiestl, 2016). Using a framework derived from signal detection theory (SDT), we

309   asked how increasing decision costs and benefits influenced bees' decision criteria. We found

310   that bees adjusted their decision thresholds in response to increased costs, but not to increased

311   benefits. When the cost of encountering a mimic was elevated by adding quinine, bees exhibited

312   a conservative bias, producing more correct rejections and fewer correct detections; bees also

313   made far fewer costly attempts to collect pollen (Rossi et al., 2025) on models and mimics.

314   However, increasing rewards associated with male flowers by providing extra pollen did not

315   elicit a corresponding liberal shift. This asymmetry suggests that bees are more responsive to

316   potential costs than to benefits. This pattern only partially aligns with the predictions of signal

317   detection theory, which predicts that receivers should adjust their decision thresholds according

318   to the relative costs and benefits of foraging on models and mimics (Abbott & Sherratt, 2013;

319   Kikuchi & Sherratt, 2015; Sherratt & Peet-Paré, 2017).

320

321   More broadly, these findings align with published evidence that bees tend to minimize costly

322   errors, even when this strategy limits potential gains. In many contexts, when foraging decisions

323   are made under uncertainty, individuals must balance the expected payoff of each option with the

324   variability in outcomes – commonly referred to as risk-sensitivity (Kacelnik & Bateson, 1996;

325   McNamara & Houston, 1992). Such models predict that animals evaluate both the mean and

326   variability of rewards, with risk-averse individuals favoring consistent outcomes and risk-prone

327   individuals favoring variability when average gains are equivalent. Many animals exhibit risk-

328   prone behavior when facing delays but are generally risk-averse or risk-neutral when outcomes

329   differ in magnitude or probability, including cases where rewards may be absent (Kacelnik &

330   Bateson, 1996). Bumble bees exhibit risk aversion when nectar volumes vary (Harder & Real,

331   1987), but individuals may shift toward being risk-prone when the colony's energetic reserves

332   are low (Cartar & Dill, 1990). Similarly, honey bees become more risk-averse when

333   discrimination among rewards becomes more difficult, suggesting that uncertainty may amplify

334   avoidance of costly mistakes (Shafir et al., 2008). Considered together with our findings, bees

335   may generally prioritize minimizing costly errors, such as visiting unrewarding or punishing

336   mimics, over maximizing potential gains, potentially reflecting a broader conservative bias in

337   their decision-making under uncertainty.

338

339   Here, we made female (mimic) flowers more aversive by adding quinine. It remains unclear

340   whether similar patterns of discrimination would emerge if the costs associated with floral

341   deception were altered in different ways; however, we suspect that such manipulations could

342   produce even stronger effects. In natural foraging environments, pollinators encounter a range of

343   costs associated with decision errors, including energetic, time, and missed opportunities, all of

344   which likely have fitness consequences (de Jager & Ellis, 2014; Nakazawa et al., 2024; Raine &

345   Chittka, 2008; Zurbuchen et al., 2010). Pollinators are also susceptible to predator attacks while

346   foraging, which can have serious fitness consequences (Romero et al., 2011). Increasing any of

347   these costs may shift pollinator decision-making toward a more conservative strategy in which

348   they avoid potential mimics, even at the expense of occasionally rejecting rewarding models.

349   Under conditions where costs become sufficiently high, such as when deceptive flowers are

350   abundant (Duffy & Johnson, 2017; Ferdy et al., 1999) or rewards are consistently poor,

351   pollinators may even stop visiting either flower type altogether.

352

353   Conversely, what if the benefits were enhanced? For pollinators, the primary rewards offered by

354   flowers are nectar and pollen, and increases in either their quantity or quality generally promote

355   higher visitation rates and greater resource collection (Cartar, 2004; Hemingway et al., 2024;

356   Nachev et al., 2017; Robertson et al., 1999; Ruedenauer et al., 2016). Here, we increased the

357   reward value of male (model) flowers by supplementing them with pollen. It seems unlikely that

358   adding even more pollen would increase the perceived benefits associated with male flowers, as

359   bees did not deplete all pollen in most trials. Pollen supplementation relative to flowers in their

360   natural state however did increase bee performance overall, suggesting that pollen odor acts as

361   an honest cue of reward presence, potentially explaining why male *Begonia* offer so little pollen

362   per flower. Changes in reward quantity may be perceived as less beneficial than changes in

363   quality (see Cnaani et al., 2006), and these patterns may further depend on the type of floral

364   reward being evaluated. Whether similar enhancements in nectar reward quantity or quality

365   would generate comparable patterns of response, or even encourage a more liberal acceptance

366   bias, remains unclear. One key aspect of nectar quality - sugar concentration - can be assessed

367   immediately when bees sample nectar (Bitterman, 1976; De Brito Sanchez, 2011; Hemingway &

368   Muth, 2022) and bees can also taste pollen, which may provide some indication of its quality

369   (Mayberry et al., 2024; Muth et al., 2016; Ruedenauer et al., 2016). Future experiments that

370   manipulate the type and magnitude of floral rewards in different ways will be important for

371   testing whether these behavioral patterns generalize across other forms of floral deception.

372

373   Aside from the observed asymmetry in decision criteria, we found that learning played an

374   important role in shaping performance over time, with bees adjusting their responses as they

375   became familiar with models and mimics. When mimic costs were increased, bees made

376   proportionally fewer correct decisions and detections overall with experience. In contrast, correct

377   rejections increased with experience regardless of the relative costs or benefits. Buzzing of

378   mimics also diminished with experience when mimic costs were unmodified, indicating bees

379   learned to reduce the energetic cost of false alarms; buzzing of mimics likely did not decline with

380   experience when mimic costs were increased, due to the initially very low incidence of buzzing.

381   Overall, bees showed marginal improvements with experience when models were supplemented

382   with pollen. Pollinator learning is often proposed to mitigate exploitation by floral Batesian

383   mimics (Anderson & Johnson, 2006; Dafni, 1984; Dukas, 1987; Gigord et al., 2001; Jersáková et

384   al., 2006; Schiestl & Johnson, 2013), although the mechanisms underlying this remain poorly

385   understood (de Jager & Ellis, 2014; Gigord et al., 2001, 2002). Naïve pollinators are initially

386   unfamiliar with the phenotypic distribution and payoffs of models and mimics and are therefore

387   expected to initially visit both randomly. With experience they learn to use distinctive cues to

388   target rewarding flowers (Clarke et al., 2013; Rands et al., 2023; Russell & Ashman, 2019;

389   Whitney et al., 2009). Signal detection theory predicts that such learning should lead pollinators

390   to increasingly avoid mimics, even at the cost of some missed rewards, thus maximizing foraging

391   efficiency (Abbott & Sherratt, 2013; Guilford & Dawkins, 1991; Oaten et al., 1975). Our results

392   support this prediction, particularly when mimic costs were high, and align with previous

393   findings that discrimination performance improves with experience (de Jager & Ellis, 2014;

394   Internicola & Harder, 2012; Kunze & Gumbert, 2001; Russell et al., 2020, 2021).

395

396   Mimicry occurs across a range of decision-making contexts beyond floral deception, with one of

397   the most well-studied examples involving predators encountering defended prey. In such

398   systems, predators must decide whether to attack or avoid prey that may resemble defended

399   species (Skelhorn et al., 2016). As with pollinators facing deceptive flowers, these decisions

400   entail a trade-off. Being overly cautious may reduce foraging opportunities, whereas being

401   overly liberal may increase risk of exposure to chemically or physically defended prey.

402   Theoretical work has examined how predators evaluate risk in the face of such deceptive signals,

403   exploring how uncertainty and the potential costs of mistakes shape decision rules (Holen &

404   Sherratt, 2021; Kikuchi & Sherratt, 2015; Sherratt, 2011; Speed & Ruxton, 2010). Empirical

405   studies similarly demonstrate that when the costs of attacking defended prey are high, predators

406   tend to adopt more conservative strategies, by avoiding more broadly and sampling less

407   frequently (reviewed in Skelhorn et al., 2016), or relying more heavily on social information

408   (e.g., Hämäläinen et al., 2021). Together, these findings align with the results found in our

409   current study, suggesting that as the costs of errors and the degree of uncertainty increase,

410   decision-makers may favor conservative strategies that minimize potential losses, even at the

411   expense of foregoing greater potential rewards.

412

413   In conclusion, bumble bees appear to prioritize avoiding exploitation over maximizing potential

414   gains, revealing an asymmetry in how they evaluate risk when encountering uncertainty with

415   floral mimics. Our findings thus may offer new insight into the evolutionary persistence of floral

416   deception and the ecological dynamics that maintain it. Because pollinators did not substantially

417   increase visits to more profitable models over time, deceptive mimics may persist even in the

418   presence of more rewarding flowers. However, as the costs of visiting deceptive flowers

419   increase, pollinators are expected to adopt even more conservative decision criteria, further

420   reducing visits to potential mimics. If these costs become too high, pollinators may ultimately

421   abandon the entire floral system, decreasing reproductive success for both mimics and models.

422   These dynamics may help explain the stability of automimetic systems like those found in

423   *Begonia*, where deceptive and rewarding flowers coexist with moderate costs (Agren &

424   Schemske, 1991; Schemske et al., 1996; Wyatt & Sazima, 2011). More broadly, a conservative

425   pollinator bias may carry population-level consequences by lowering pollen transfer efficiency

426   and constraining plant reproductive success, thereby shaping the coevolutionary balance between

427   attraction, deception, and learning in plant-pollinator interactions. These dynamics could be

428   tested in both a field and lab setting to shed light on fitness consequences of these decision rules

429   under different cost-benefit regimes. Linking signal detection theory with pollinator behavior in

430   plant–pollinator interactions thus provides a powerful approach for understanding how animals

431   navigate uncertainty and deception in their environments and how these decision-making

432   processes shape ecological and evolutionary outcomes.

433

434

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DECLARATIONS

CONFLICTS OF INTEREST

Not applicable

ETHICS APPROVAL

All bumble bee experimentation was carried out in accordance with the legal and ethical standards of the USA.

DATA ACCESSSIBILITY

The datasets supporting this article are available as electronic supplementary material.

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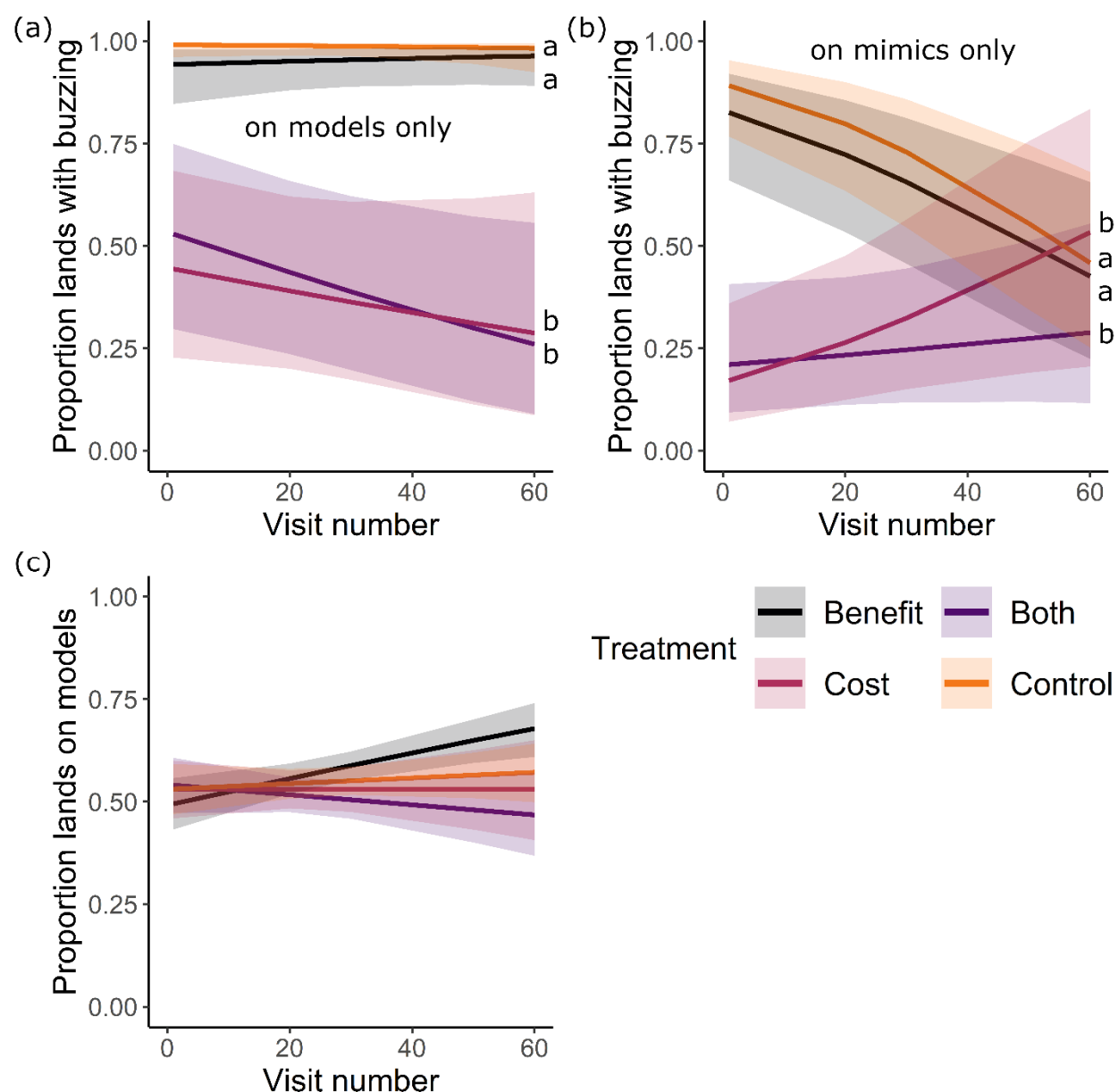
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FIGURES and FIGURE LEGENDS

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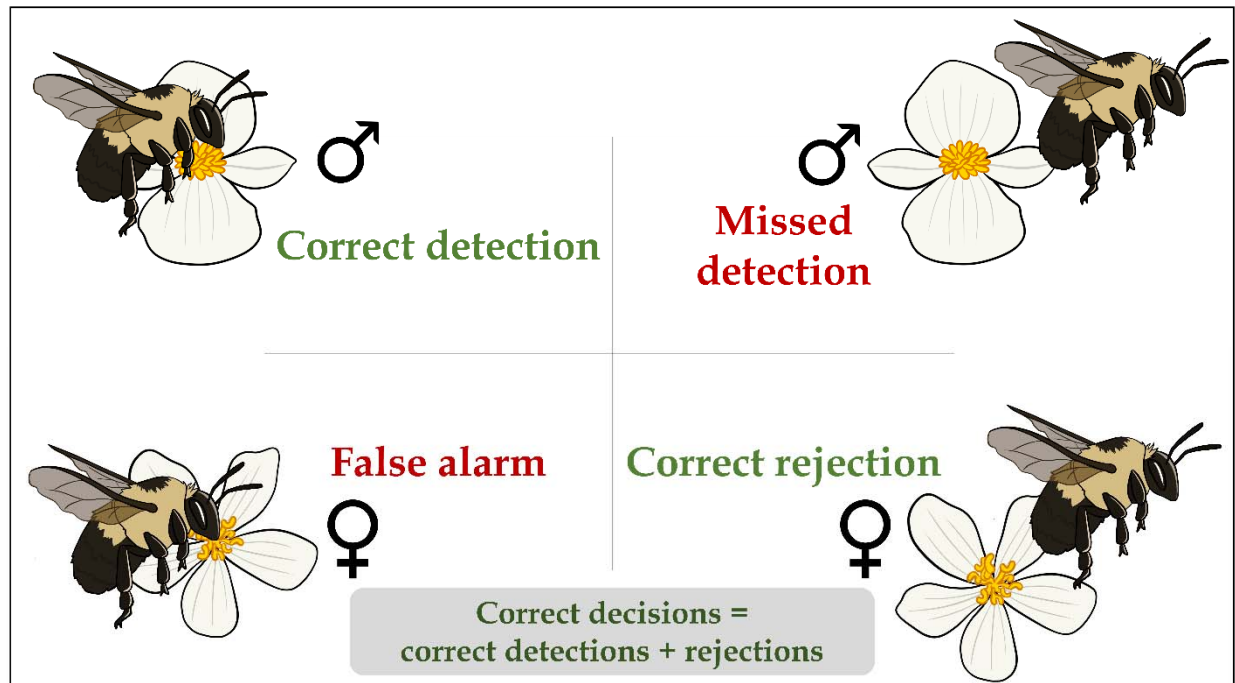
Figure 1. Sampling behavior of bees foraging on the intersexual floral mimic *Begonia odorata* can be divided into four categories in accordance with signal detection theory. **Correct detections** ('hits') involve the bee approaching and landing on models, whereas **missed detections** ('misses') involve the bee approaching, but not landing on models. **Correct rejections** involve the bee approaching, but not landing on mimics, whereas **false alarms** involve the bee approaching and landing on mimics. Thus, **correct decisions** involve the bee approaching and landing on models, and approaching, but not landing on mimics.

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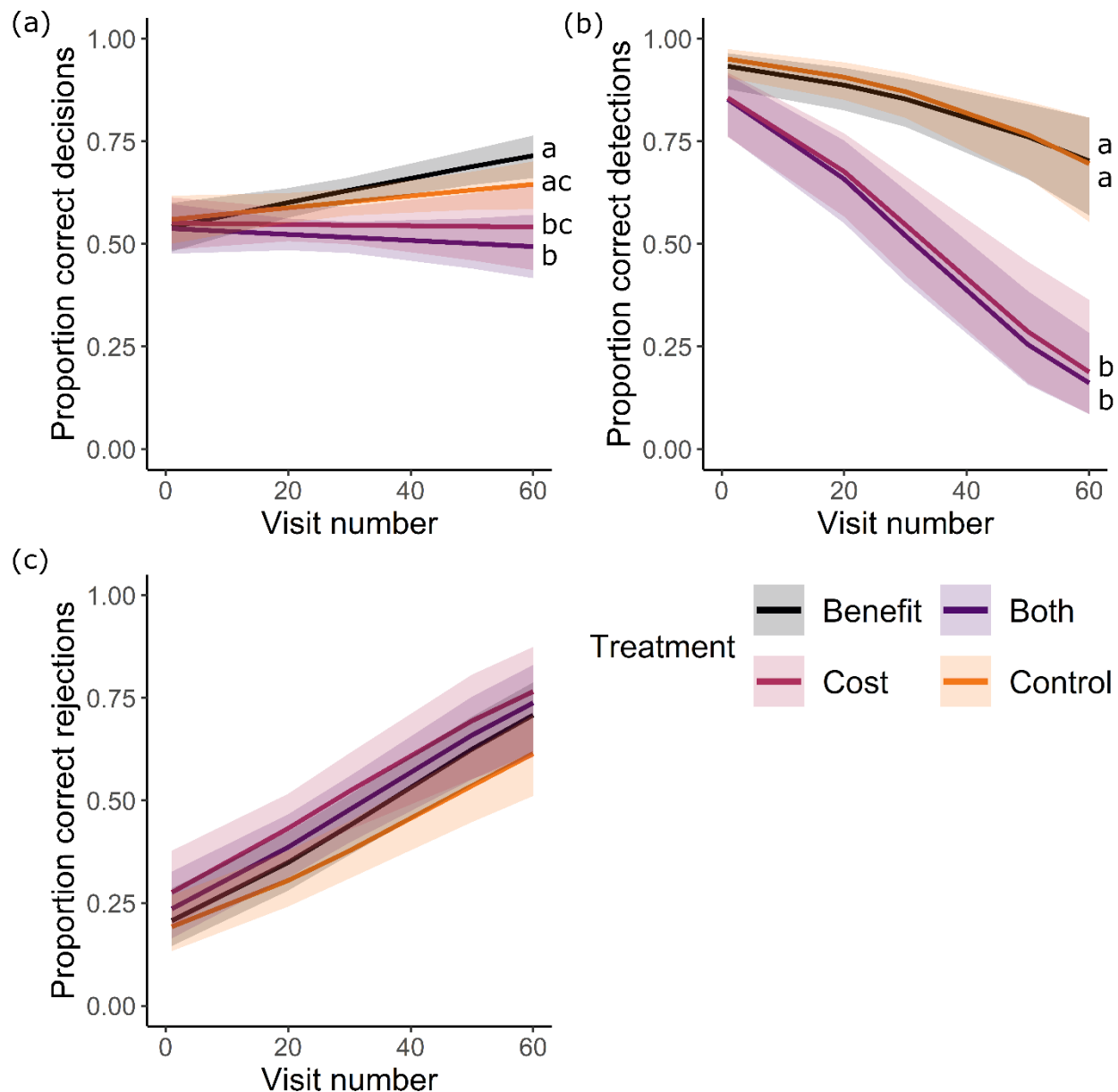
Figure 2. Sampling behavior of initially naïve bees foraging in treatments (different colored lines) that differed in terms of the relative costs and benefits of mimics and models, respectively. The mean proportion of (a) correct decisions, (b) correct detections, and (c) correct rejections made by bees over the course of up to 60 visits. N = 21, 19, 20 and 21 bees in the modified control ('Control'), increased model benefit ('Benefit'), increased mimic cost ('Cost'), and increased mimic cost and model benefit ('Both') treatments, respectively. Plotted lines indicate

727   estimated means and shaded regions indicate 95% confidence intervals. Different letters next to

728   plotted lines indicate significant differences among treatments at $P < 0.05$ according to Tukey's

729   post hoc tests.

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Figure 3. Landing behavior of initially naïve bees (same dataset as in Figure 2, analyzed for

different sampling behavior) foraging in treatments (different colored lines) that differed in terms

734   of the relative costs and benefits of mimics and models, respectively. Mean proportion of lands

735   made on (a) models during which the bee buzzed, (b) mimics during which the bee buzzed, and

736   on (a) models (versus mimics), over the course of up to 60 visits. $N = 21$, 19, 20 and 21 bees in

737   the modified control ('Control'), increased model benefit ('Benefit'), increased mimic cost

738   ('Cost'), and increased mimic cost and model benefit ('Both') treatments, respectively. Plotted

739   lines indicate estimated means and shaded regions indicate 95% confidence intervals. Different

740   letters next to plotted lines indicate significant differences among treatments at $P < 0.05$

741   according to Tukey's post hoc tests.

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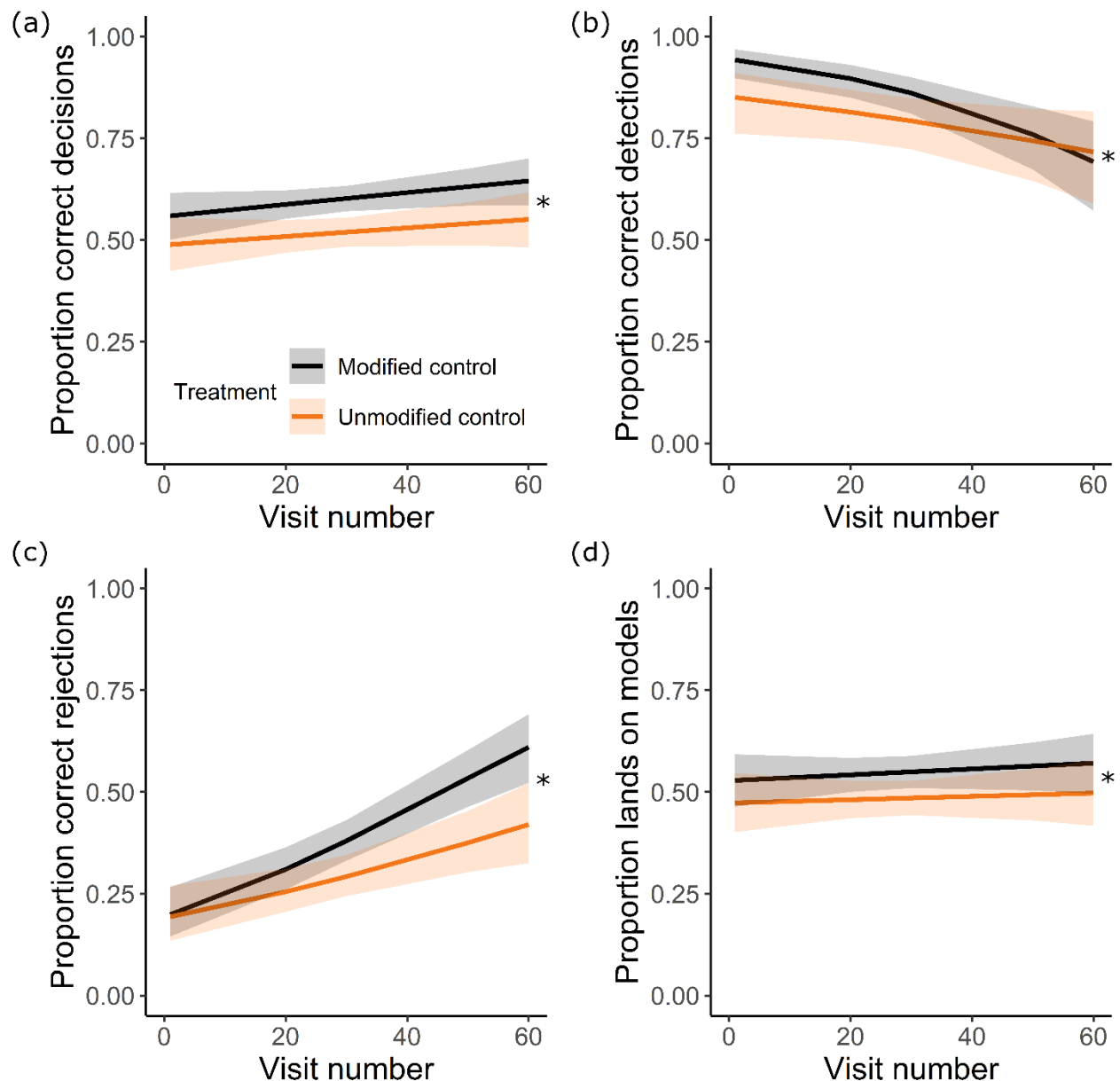
Figure 4. Sampling and landing behavior of initially naïve bees foraging in treatments differing in terms of whether we supplemented pollen to models (partially different dataset from Figures 2 and 3, analyzed for same behaviors). Mean proportion of (a) correct decisions, (b) correct detections, (c) correct rejections, and (d) lands made on models (versus mimics), over the course of up to 60 visits. $N = 21$ and 16 bees in the pollen supplemented ('Modified Control') and natural ('Unmodified Control') treatments, respectively. Plotted lines indicate estimated means

751   and shaded regions indicate 95% confidence intervals. Asterisks indicate significant differences

752   among treatments at $P < 0.05$ according to Tukey's post hoc tests.