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Original article

Bees attend primarily to aversive costs, not pollen rewards, to avoid exploitation by floral mimics

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Animals are expected to weigh costs and benefits when making foraging decisions. Flowering plants often offer floral food rewards to pollinators, but also frequently deceive pollinators into visiting without providing rewards. Although floral mimicry, in which rewardless flowers mimic rewarding (model) flowers is common, it remains unclear whether pollinators evaluate the relative costs and benefits of visiting each. Using a signal detection theory (SDT) framework, we investigated how bumble bee decisions respond to experimental manipulations of costs and benefits within an intersexual floral mimicry system in which unrewarding female flowers imperfectly mimic pollen-rewarding male flowers (models). Using a fully factorial design, we increased the cost of visiting mimics (by adding quinine), increased the benefit of visiting models (by adding pollen), increased both simultaneously, and left them unchanged (control). As predicted by SDT, increasing mimic costs led to a conservative bias: bees made more correct rejections, but fewer correct detections. Contrary to SDT predictions, enhancing model reward did not elicit a liberal bias, and decision performance remained unchanged. Our findings suggest that bees prioritize avoiding costly errors under uncertainty, even when this limits potential gains. Such conservative foraging decisions may help stabilize deceptive systems by allowing mimics to persist despite moderate costs.

Keywords signal detection, Batesian mimicry, cognition, learning, intersexual mimicry, decision making, pollen, Begonia, foraging, floral rewards

Introduction

Animals often make decisions under uncertainty, continually updating information about their environment to reduce ambiguity and optimize choice behavior (Real 1992; Blumstein and Bouskila 1996; Stephens 2008). For pollinators such as bees, this ability is critical. During a single day, a bee may visit thousands of flowers across multiple plant species that vary in their floral traits and reward payoffs (Heinrich 1976, 1979; Chittka et al. 1999). To maximize energetic return, pollinators must rapidly and accurately assess complex and variable floral signals—yet these signals are not always reliable. Because producing floral rewards is energetically costly (Southwick 1984; Nicholls and Hempel De Ibarra 2017; Pyke and Ren 2023), plants may use floral signals to attract visitors without offering rewards. This occurs in Batesian floral mimicry, in which a rewardless plant species (mimic) produces deceptive signals that overlap in sensory space with those of a rewarding species (model), in 1 or more sensory modalities (Dafni 1984; Johnson and Schiestl 2016; Pannell and Farmer 2016). This form of deception is widespread, having evolved repeatedly across angiosperms in more than 32 plant families and across 7,500 species worldwide (Renner 2006; Schiestl and Johnson 2013; Johnson and Schiestl 2016). The success of this strategy depends on the perceptual and learning limitations of pollinators, which may fail to reliably discriminate mimics from models and thus visit both (Ferdy et al. 1998; Renner 2006; Schiestl and Johnson 2013; Vázquez and Barradas 2017).

Signal detection theory (SDT) offers a powerful framework for understanding why pollinators sometimes visit rewardless flowers under uncertainty (Lichtenberg et al. 2020). When pollinators encounter deceptive mimics, they face 4 possible decision outcomes (Fig. 1): 2 correct decisions—visiting a model ("hit") and avoiding an unrewarding mimic ("correct rejection")—and 2 types of decision errors—visiting a rewardless flower ("false alarm") or failing to visit a rewarding 1 ("miss"). SDT describes the tradeoff between these 2 types of decision errors (Green and Swets 1966; Wiley 2006). Because reducing 1 type of error increases the other, pollinators must adopt a decision criterion that balances the costs and benefits

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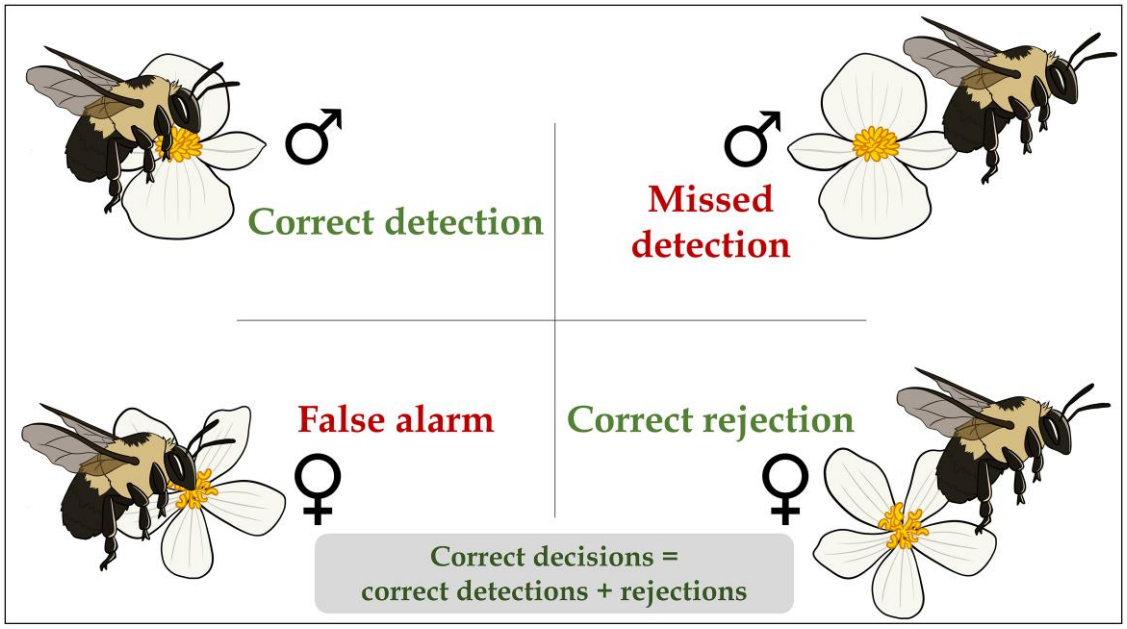

Figure 1 Sampling behavior of bees foraging on the intersexual floral mimic *Begonia odorata* can be divided into four categories in accordance with signal detection theory. Correct detections ("hits") involve the bee approaching and landing on models, whereas missed detections ("misses") involve the 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. Illustrations by Annaliese Novinger.

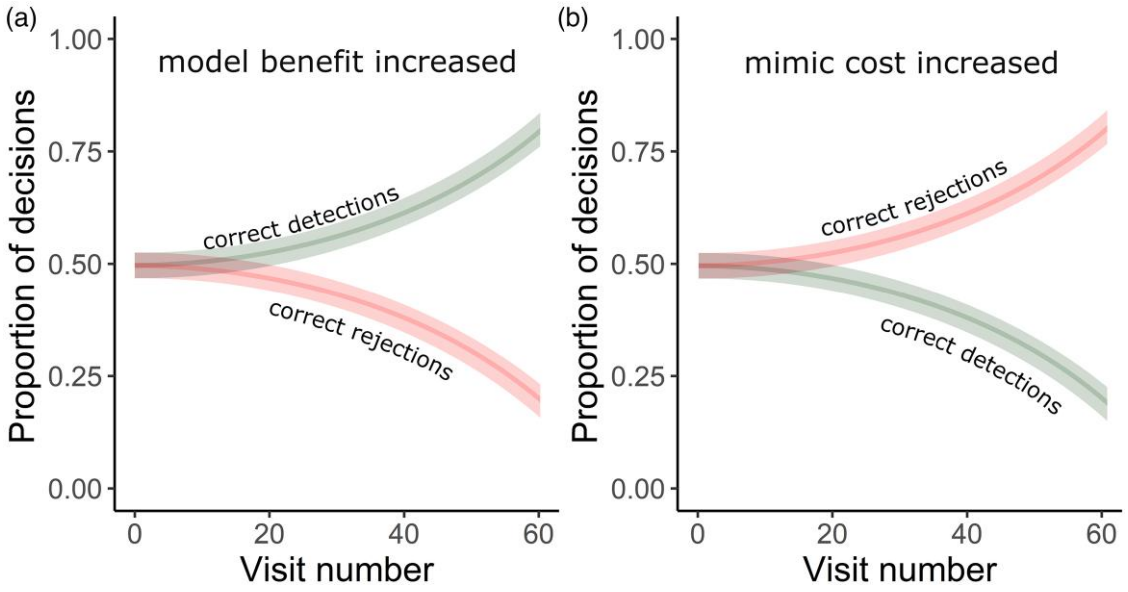

Figure 2 Conceptual diagram illustrating the key predictions when mimic costs or model benefits are increased. We predicted that (a) enhancing model reward would elicit a liberal bias, and thus bees would make relatively more correct detections, at the cost of fewer correct rejections. We also predicted that (b) when mimic cost increased, bees would be more risk aversive and thus make relatively more correct rejections at the cost of making fewer correct detections ("hits"). Differences in responses are expected to become more pronounced with experience ("visit number"), but liberal and conservative biases need not be symmetric (as they depend on the relative nature of the cost and benefit).

of these errors (Fig. 2). While SDT has been widely used to explain the evolution and maintenance of floral mimicry, most studies have focused on the ability of pollinators to discriminate between models and mimics based on their perceptual similarity (eg Gumbert and Kunze 2001; Leonard et al. 2011; Russell et al. 2021) and on the relative frequency of each within a given population (eg Lindström et al. 1997; Pfennig et al. 2001; Finkbeiner et al. 2018; Russell et al. 2020). Much less is known about how the costs and benefits of foraging outcomes shape pollinator decision criteria (Latty and Trueblood 2020; Hemingway, Leonard, et al. 2024).

This is somewhat surprising, given a central prediction of SDT is that receivers should adjust their decision thresholds according to

the relative costs and benefits of foraging on models and mimics (Abbott and Sherratt 2013; Kikuchi and Sherratt 2015; Sherratt and Peet-Paré 2017). For pollinators, foraging carries clear costs, including energetic expenditure and time investment (Wolf et al. 1975; Heyneman 1983; Mayberry et al. 2024), exposure to predators (Romero et al. 2011), and sometimes contact with toxic and/or aversive scents and components of floral rewards (Jones and Agrawal 2016; Barlow et al. 2017; Stevenson et al. 2017). The benefits of foraging are also variable, depending on the nutritional value, quantity, and temporal or spatial availability of rewards (Venjakob et al. 2022; Benadi et al. 2023; Hemingway, Leonard, et al. 2024). Although pollinators are sensitive to the costs and benefits of foraging discussed above (eg Richman et al. 2017; Hemingway et al. 2024), their influence on decision making in deceptive systems remains poorly understood (see Ferdy et al. 1998; Gaskett 2011; de Jager and Ellis 2014; Russell et al. 2020). SDT predicts plasticity in criteria: bees should be more cautious (avoid false alarms) when errors are costly, or more liberal (favor hits) when rewards are high (Fig. 2). Moreover, when both the cost of visiting the mimic and the benefit of visiting the model are increased, the bias should reflect the combined influence of costs and benefits (Lynn and Barrett 2014).

Here we used a powerful system to empirically test these predictions of SDT within the context of floral deception. *Begonia odorata* is a monoecious species bearing both male and female flowers on the same plant, and these flowers are visually similar, with showy white tepals presented together within inflorescences (Russell et al. 2020). This system exhibits intersexual floral mimicry, in which unrewarding female flowers mimic pollen-producing male flowers—a phenomenon known as pseudoanthery (Johnson and Schiestl 2016). Pollinators, typically pollen-collecting bees, learn to associate male-phase traits (such as color, scent, and shape) with pollen rewards, creating a signal-reward mismatch that requires them to discriminate between visually similar morphs. Previous work has shown that flower-naïve bees exhibit a sensory bias toward mimics but rapidly learn to avoid them, and that the frequency of model-mimics has little effect on discrimination performance (Russell et al. 2020). Subsequent experiments tested whether variation in flower size influenced the rate of discrimination learning and found that although bees quickly learned to distinguish between rewarding males and unrewarding females, this learning was not significantly affected by size variation (Russell et al. 2021). While it is clear that bees can readily learn to discriminate models from mimics, it remains unclear how discrimination is shaped by the relative rewards of models and the costs of visiting mimics. *Begonia odorata*, therefore, provides an ideal system for testing how variation in costs and benefits influences pollinator decision-making.

In a fully factorial experiment, we manipulated the rewards of male flowers (via addition of pollen; see Cresswell and Robertson 1994; Robertson et al. 1999; Burkart et al. 2014) and the punishments of female flowers (via addition of odorless aversive quinine powder; used frequently as an aversive stimulus in bee behavioral studies; see Avarguès-Weber et al. 2010; Tiedeken et al. 2014; Muth et al. 2016) to vary the payoffs of hits and false alarms. Given the widespread occurrence of aversive secondary metabolites in floral scents, nectar, and particularly pollen, this approach provides an ecologically grounded way of increasing foraging costs for pollinators (Junker and Blüthgen 2010; Stevenson et al. 2017; Palmer-Young et al. 2019; Hemingway, Leonard, et al. 2024). We asked how these manipulations and pollinator experience affect bees' decision biases and discrimination abilities. Under SDT, changes in the costs and benefits associated with decisions are expected to alter the decision threshold (criterion) used to classify stimuli. Increasing the costs of false alarms should shift the threshold in a conservative direction, making bees less likely to classify a flower as rewarding, whereas increasing the benefit of hits should shift the threshold in a liberal direction, making bees more likely to do so. Consistent with these predictions, we expected a conservative bias in bee decision making when the cost of visiting mimics was increased, and a liberal bias when the benefit of visiting models was increased (Fig. 2), and that bias would reflect the sum of the cost plus the benefit when both costs and benefits of mimics and models were increased, respectively. As a result, we predicted that when mimic cost increased, bees would make relatively more correct rejections at the cost of making fewer correct detections ("hits") and would be less likely to buzz flowers, an energetically expensive attempt to extract pollen (Rossi et al. 2026). Likewise, we predicted that as model benefit increased, bees would make relatively more correct detections, at the cost of fewer correct rejections, and would be more likely to buzz flowers. Finally, as naïve pollinators are initially unfamiliar with the phenotypic distribution and costs and benefits of visiting models and mimics, we expected bees' responses to models and mimics to increasingly fit these predictions of SDT as foraging bees gained experience (eg Russell et al. 2020, 2021).

Materials and methods

Test subjects

We maintained 3 colonies (Plant Products: Biobest Group, Canton, MI, USA) of the common eastern bumble bee *Bombus impatiens* following Russell et al. (2020). In brief, we allowed colonies to forage freely on 2 M sucrose solution and pulverized honeybee-collected pollen (Koppert Biological Systems) from artificial feeders within enclosed foraging arenas (length, width, height: $82 \times 60 \times 60$ cm) set to a 14 h:10 h light:dark cycle.

We used fresh male and female flowers with mature anthers and styles, respectively, from 10 simultaneously monoecious *B. odorata* plants raised in a university greenhouse with supplemental halogen lights to extend day length to a 14:10 h cycle and with fertilizer applications every other week (Plant Tone, NPK 5:3:3). While female *B. odorata* flowers are rewardless and do not produce pollen or nectar, male *B. odorata* flowers offer pollen, their only reward to their primary pollinators, bees; although bumble bees have not been observed visiting *B. odorata*, they are among the bee genera that visit closely related *Begonia* species (Schemske et al. 1996; Pemberton and Wheeler 2006; Wyatt and Sazima 2011; de Avila et al. 2017). Female *B. odorata* flowers closely resemble male flowers in bumble bee color vision (Fig. S1; see Russell et al. 2020, 2021) and scent (unpublished data); both flower sexes have creamy white dissected tepals, and the female flower's yellow and highly divided styles closely resemble the male flower's numerous yellow stamens.

Experimental overview

We tested how the benefits of visiting models (male flowers) and the costs of visiting mimics (female flowers) influenced learning in initially flower-naïve bees ($N = 97$). We examined how bees learned to discriminate between models and mimics by analyzing 3 primary components of their sampling behavior during visits to arrays of 20 flowers: approaches, landings without buzzing, and landing with buzzing ("buzzes"). An approach was defined as a bee in flight greatly

reducing its velocity while facing a flower within 3 cm. All landings (defined as 3 or more legs in contact with the flower) were preceded by an approach. Landings were considered correct detections when directed at models and false alarms when directed at mimics (Fig. 1). Not all approaches led to landings; these cases represented missed detections for models and correct rejections for mimics (Fig. 1). Sampling behaviors were visually assessed during trials, which were video recorded as backup. Landings without buzzing on male flowers typically involved the bee collecting pollen via a behavior termed scrabbling, which involved the bee manipulating the anthers with the mandibles and legs, knocking pollen onto the thorax and abdomen, whereupon it was groomed into the pollen baskets; (Russell et al. 2017). In contrast, bees never scrabbled on female flowers. Bees that landed on flowers with quinine touched it with their antennae and/or their extended proboscis and nearly always took flight immediately, whereupon they proceeded to groom while in flight (suggesting bees were removing any residual quinine from their bodies). Buzzes, which indicated an attempt at extracting pollen, whether or not it was available, were identified by their distinctive sound using Zoom H2 Handy Recorders (ZOOM Corporation) to amplify and verify buzzes while trials were taking place and occurred only after a bee had landed (see Russell et al. 2016). Buzzing a male flower represented a correct response, whereas buzzing a female flower represented an incorrect response.

We assigned flower-naïve bees approximately evenly across 5 treatments: an unmodified control treatment, a modified control treatment ("control treatment"), an increased model benefit treatment ("benefit treatment"), an increased mimic cost treatment ("cost treatment"), and an increased model benefit and mimic cost treatment ("both treatment"). In the unmodified control treatment, both male flowers (which offer on average 0.18 mg of pollen) and female flowers were presented to bees without modification. In all other treatments, anthers of male flowers were supplemented with pollen. Because collecting pollen from male *Begonia* flowers to supplement other flowers was extremely time intensive, we used cherry pollen for all supplementation (*Prunus avium*; Pollen Collection and Sales, Lemon Cove, CA, USA), which bumble bees readily collect (eg Russell et al. 2017). In the "control treatment," male flowers were each supplemented with 0.9 mg pollen (to control for the effect of adding a novel pollen type across treatments), and female flowers were unmodified. To increase the benefit to bees when visiting models, in the "benefit treatment," male flowers received double the pollen supplement (1.8 mg pollen added to the anthers of each flower), while female flowers were unmodified. To increase the cost to bees when visiting mimics, in the "cost treatment," the styles of female flowers were supplemented with 0.5 mg of powdered quinine (99% anhydrous, ACROS Organics, Fisher Scientific, Hampton, NH, USA), a stimulus that bees perceive as aversive (Muth et al. 2016), while male flowers received the base supplement (0.9 mg pollen). In the "both treatment," male flowers received the double pollen supplement (1.8 mg), while female flowers received the quinine supplement. Across all treatments, 20 flowers were arranged in a 5×4 Cartesian grid, with flowers spaced 7 cm apart. Male and female flowers were alternated by position and presented in equal numbers. To prevent desiccation, freshly cut live flowers were placed into custom water tubes (Russell et al. 2017). We alternated trials sequentially among all treatments to control for potential effects of time and day.

To initiate a behavioral trial, flowers were set up, and a single flower-naïve worker bee was gently captured from the foraging arena using a 40-dram vial (Bioquip) and immediately released in the center of the test arena (following Russell et al. 2017). We terminated the trial after the bee made 60 flower visits (or earlier if the bee stopped visiting flowers for 5 min) to avoid bees depleting models of pollen rewards (mean 47 visits; range 4 to 60 visits). To terminate the trial, we captured the bee in a 40-dram vial and euthanized it by freezing at −20 °C. For each trial, we used a new flower-naïve bee and new, freshly clipped flowers; we tested bees individually and never reused flowers or bees across trials. The test arena was cleaned after each trial. For analyses, we excluded 1 bee with fewer than 5 visits and no flower landings.

Data analyses

All data were analyzed using R v.4.4.0 (Developmental Core Team R 2024). To analyze how experience and the costs of visiting mimics and benefits of visiting models affected sampling behavior, we fit generalized linear mixed models (GLMMs) with a binomial distribution using the glmmTMB() function (glmmTMB package; Brooks 2017), specifying type II Wald chi-squared (χ^2)-tests via the Anova() function (car package; Fox et al. 2019). We checked model assumptions for all models (DHARMa package; Hartig 2024).

For the first set of GLMMs, the response variable was sampling behavior (either "correct decisions" vs "incorrect decisions," "correct detection" vs "missed detection," "correct rejection" vs "false alarm," "buzz given landing" vs "land without buzzing," or "landing on male" vs "landing on female") and the explanatory variables were "treatment" (modified control ("Control"), increased model benefit ("Benefit"), increased mimic cost ("Cost"), and increased mimic cost and model benefit ("Both") and experience ("visit number"), specified with interaction terms in case bee responses changed more quickly with experience in 1 or another treatment. We included "bee" as a random factor, with "visit number" as repeated measures within bee, within colony (except for 2 models, in which bee within colony would not converge; we therefore excluded the colony random effect for these 2 models). In cases of significant effects, we ran Tukey's post hoc test using the emmeans() function (emmeans package; Lenth 2025) to determine which pairs were significant.

For the second set of GLMMs, in which we examined how pollen reward supplementation specifically affected sampling behavior (response variables as above: either "correct decisions" vs "incorrect decision," "correct detection" vs "missed detection," "correct rejection" vs "false alarm"), the explanatory variable "treatment" was either the unmodified control or the modified control. Random factors were specified as above.

To determine whether pollen or quinine supplementation affected flower-naïve bees' initial landing preference for models (male flowers) vs mimics (female flowers), we used *G*-tests (DescTools package; Signorell et al. 2025) to examine choice of first flower landing. There were no significant differences in model vs mimic preference for any treatment (modified control: $G = 0.430$, $N = 21$, $P = 0.512$; increased model benefit: $G = 1.33$, $P = 0.249$, $N = 19$; increased mimic cost: $G = 0.00$, $P = 1.000$, $N = 20$; increased mimic cost and model benefit: $G = 0.20$, $P = 0.655$, $N = 21$), suggesting our manipulations did not strongly influence at least initial preference.

Results

Correct decisions and detections are affected primarily by mimic cost

Flower-naïve bees overall learned to make proportionally more correct decisions (combining correctly rejecting mimics and correctly

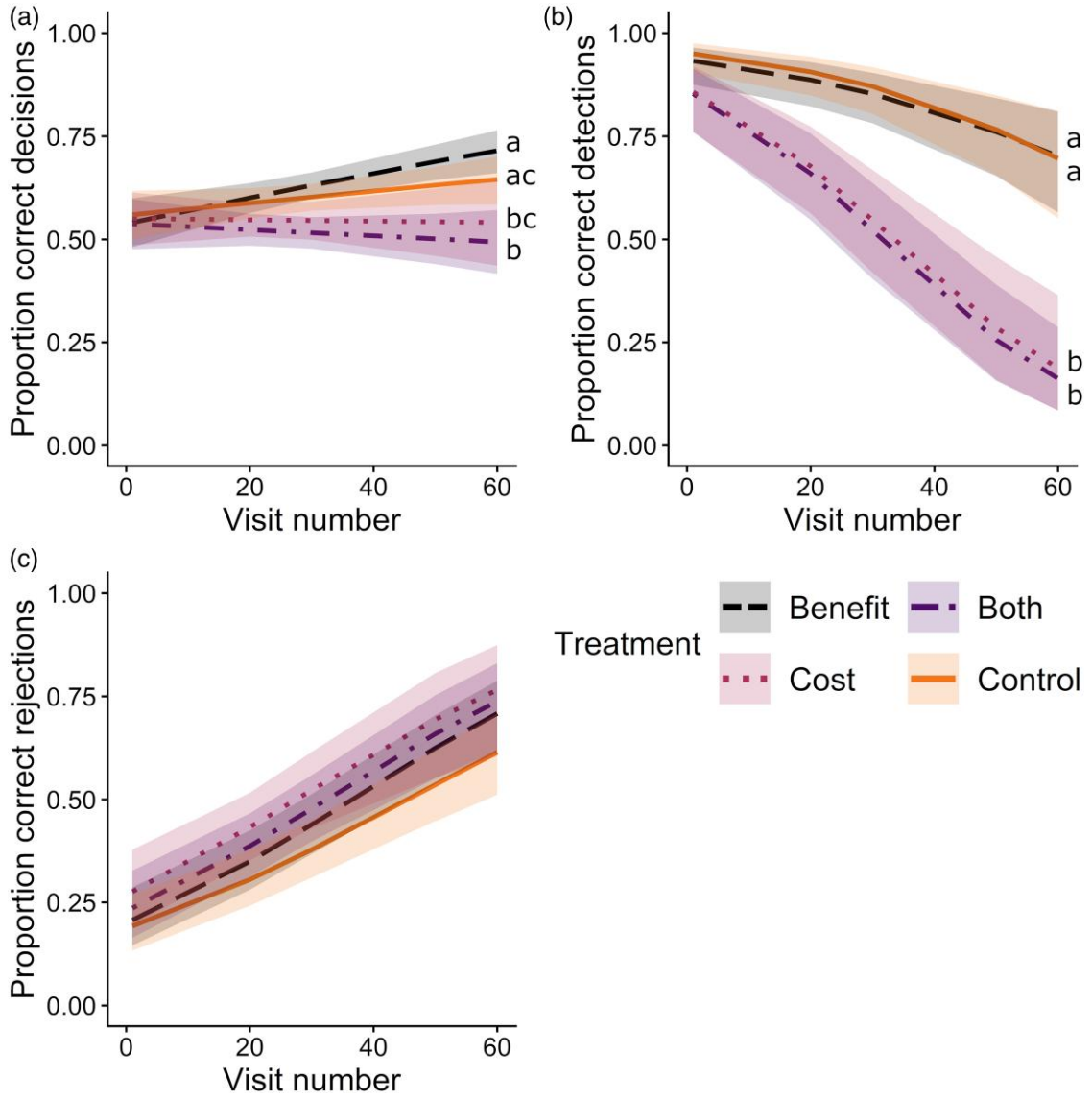

Figure 3 Sampling behavior of initially naïve bees foraging in treatments (indicated by line color and and dash style) that differed in terms of the relative costs and benefits of mimics and models, respectively. The mean proportion of (a) correct decisions, (b) correct detections, and (c) correct rejections 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 estimated means and shaded regions indicate 95% confidence intervals. Different letters next to plotted lines indicate significant differences among treatments at $P < 0.05$ according to Tukey's post hoc tests.

detecting models) with experience, but this pattern depended on treatment: increasing the cost of mimics modestly reduced the proportion of correct decisions with experience (Fig. 3a; GLMM: treatment effect: $\chi^2_3 = 19.71$, $P < 0.0002$; experience effect: $\chi^2_1 = 6.38$, $P < 0.012$; treatment × experience effect: $\chi^2_3 = 10.06$, $P < 0.019$). Bees made proportionally fewer correct detections with experience and the rate of correct detections decreased much more quickly when mimics were relatively more costly to visit (Fig. 3b; GLMM: treatment effect: $\chi^2_3 = 45.79$, $P < 0.0001$; experience effect: $\chi^2_1 = 96.97$, $P < 0.0001$; treatment × experience effect: $\chi^2_3 = 8.57$, $P < 0.036$). Bees made proportionally more correct rejections with experience, and this pattern did not depend on the cost of mimics and benefit of models (Fig. 3c; GLMMs: treatment effect: $\chi^2_3 = 6.94$, $P = 0.074$; experience effect: $\chi^2_1 = 130.07$, $P < 0.0001$; treatment × experience effect: $\chi^2_3 = 0.67$, $P = 0.880$).

Decision to buzz is affected primarily by mimic cost

Bees did not alter how often they buzzed models with experience, but overall buzzed models significantly less when the cost of visiting mimics was increased (Fig. 4a; GLMM: treatment effect: $\chi^2_3 = 66.49$, $P < 0.0001$; experience effect: $\chi^2_1 = 1.56$, $P = 0.213$; treatment × experience effect: $\chi^2_3 = 3.57$, $P = 0.313$). Bees altered how often they buzzed mimics with experience, but this pattern depended on the cost of visiting mimics (Fig. 4b). When the cost of mimics was unmodified, bees initially buzzed frequently, but less so with experience; when the cost of mimics was increased, bees initially rarely buzzed, but increased buzzing modestly with experience (Fig. 4b; GLMM: treatment effect: $\chi^2_3 = 43.56$, $P < 0.0001$; experience effect: $\chi^2_1 = 20.07$, $P < 0.0001$; treatment × experience effect: $\chi^2_3 = 31.29$, $P < 0.0001$). Finally, the

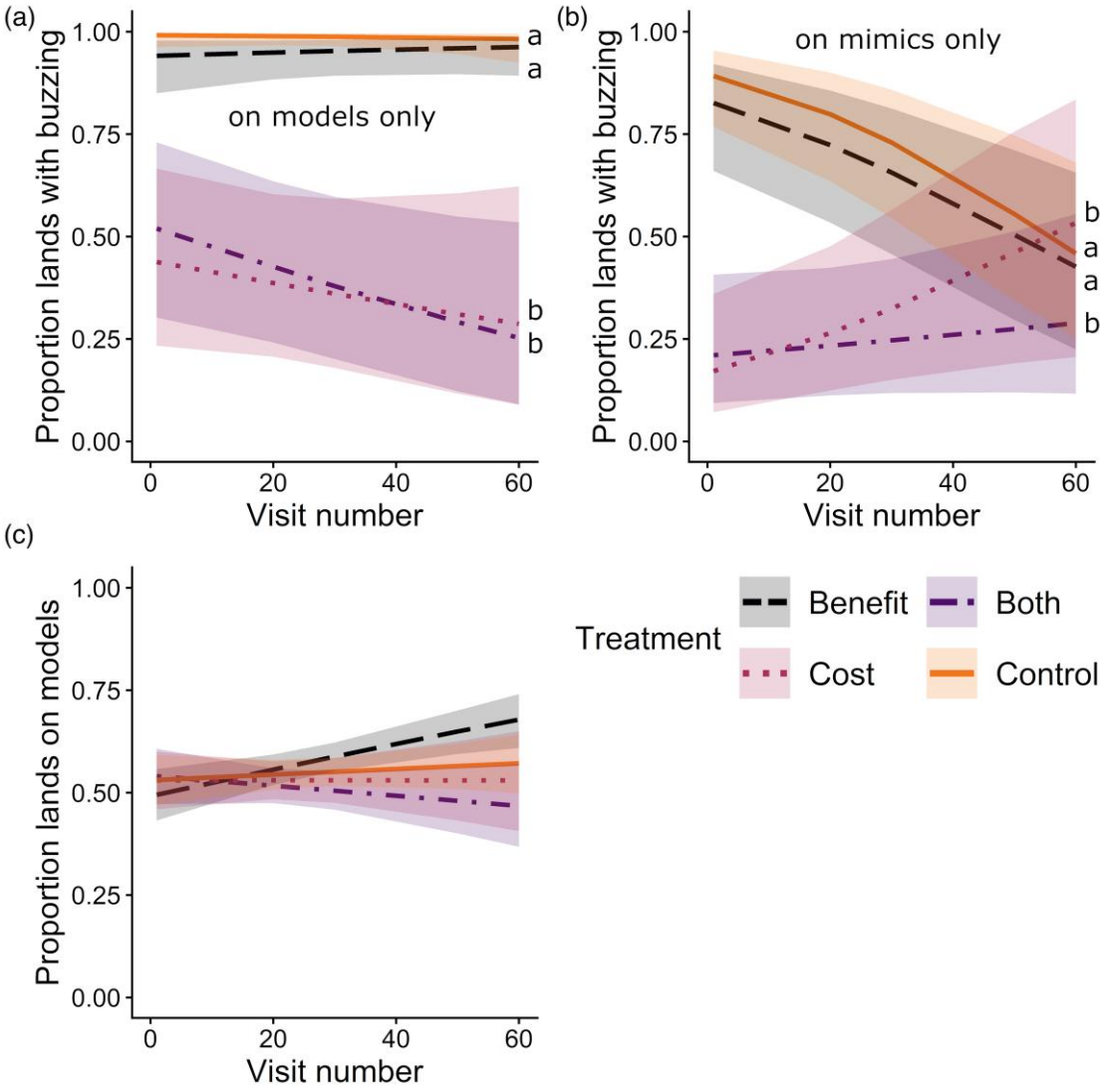

Figure 4 Landing behavior of initially naïve bees (same dataset as in Fig. 2, analyzed for different sampling behavior) foraging in treatments (indicated by line color and dash style) that differed in terms of the relative costs and benefits of mimics and models, respectively. Mean proportion of landings made on (a) models during which the bee buzzed, (b) mimics during which the bee buzzed, and on (c) models (vs mimics), 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 estimated means and shaded regions indicate 95% confidence intervals. Different letters next to plotted lines indicate significant differences among treatments at $P < 0.05$ according to Tukey's post hoc tests.

proportion of landings on models changed with experience, but this relationship was complex (Fig. 3c). Landings on models increased the most when only the benefit of visiting models was increased; landings on models decreased the most when costs of mimics and benefits of models were increased simultaneously (Fig. 4c; GLMM: treatment effect: $\chi^2_3 = 4.94$, $P = 0.177$; experience effect: $\chi^2_1 = 2.96$, $P < 0.086$; treatment × experience effect: $\chi^2_3 = 8.41$, $P < 0.039$).

Decision making is modestly improved when models are pollen supplemented

Bees made proportionally more correct decisions with experience but made even more correct decisions (15% more on average) when models were supplemented with pollen (Fig. 5a; GLMM: treatment effect: $\chi^2_1 = 11.55$, $P < 0.0007$; experience effect: $\chi^2_1 = 3.96$, $P < 0.047$; treatment × experience effect: $\chi^2_1 = 0.13$, $P = 0.719$). Bees decreased their proportion of correct detections with experience but tended to make more correct detections (7.5% more on average, though this difference was not statistically significant) when models were supplemented with pollen (Fig. 5b; GLMM: treatment effect: $\chi^2_1 = 2.57$, $P = 0.110$; experience effect: $\chi^2_1 = 18.80$, $P < 0.0001$; treatment × experience effect: $\chi^2_1 = 3.55$, $P = 0.060$). Bees increased their proportion of correct rejections with experience but made consistently more correct rejections (30% more on average) when models were supplemented with pollen (Fig. 5c; GLMM: treatment effect: $\chi^2_1 = 6.40$, $P < 0.0099$; experience effect: $\chi^2_1 = 43.05$, $P < 0.0001$; treatment × experience effect: $\chi^2_1 = 2.58$, $P = 0.108$). Bees in both treatments slightly improved their proportions of landings on models with experience, with bees making consistently more landings on models (13% more on average) when models were supplemented with pollen (Fig. 5d; GLMM: treatment effect: $\chi^2_1 = 5.82$, $P < 0.016$; experience effect: $\chi^2_1 = 0.60$, $P = 0.438$; treatment × experience effect: $\chi^2_1 = 0.044$, $P = 0.834$).

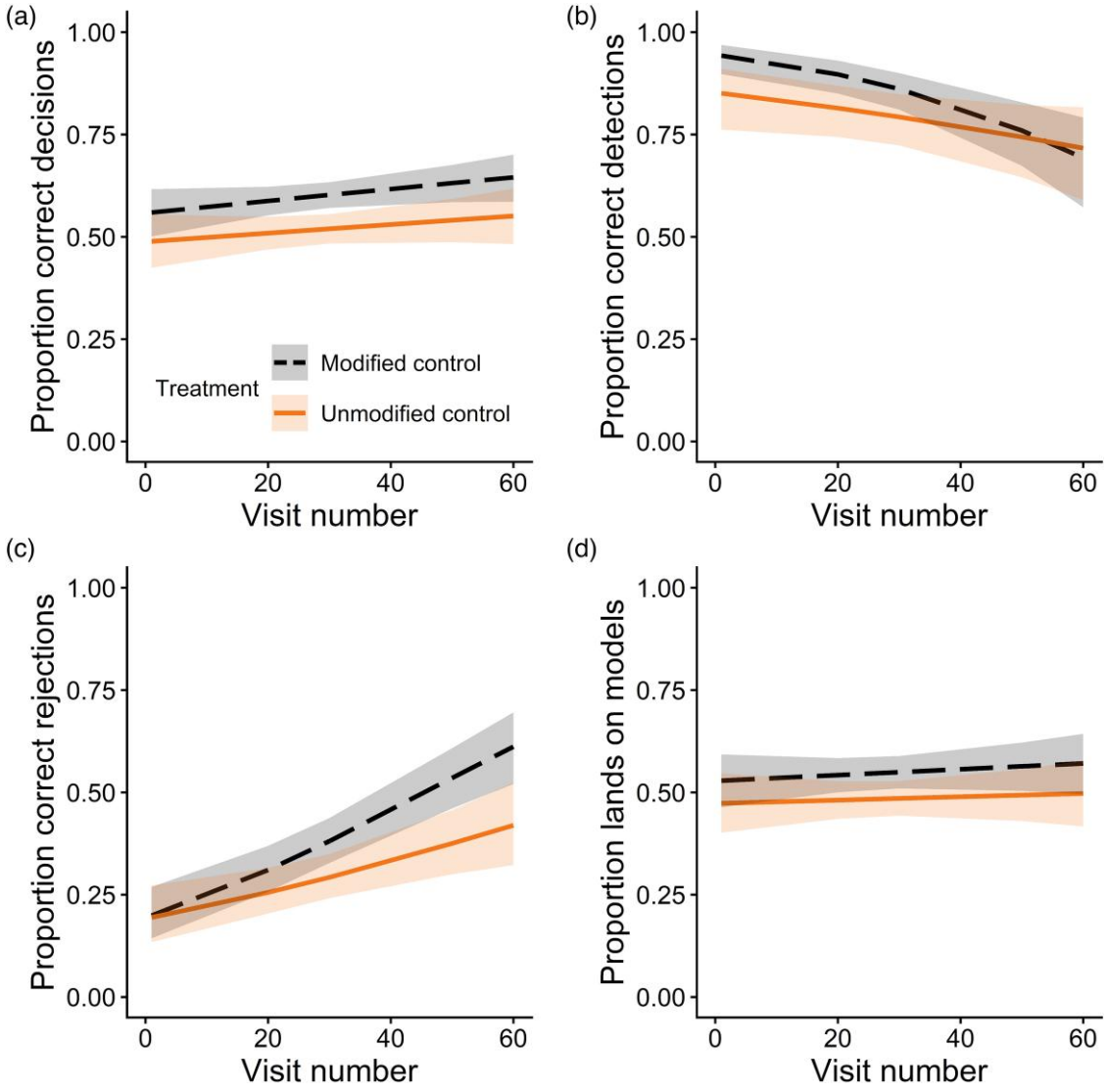

Figure 5 Sampling and landing behavior of initially naïve bees foraging in treatments differing in terms of whether we supplemented pollen to models (partially different dataset from Figs. 2 and 3, analyzed for same behaviors). Mean proportion of (a) correct decisions, (b) correct detections, (c) correct rejections, and (d) lands made on models (vs 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 and shaded regions indicate 95% confidence intervals. Asterisks indicate significant differences among treatments at $P < 0.05$ according to Tukey's post hoc tests.

Discussion

When encountering floral mimicry, pollinators must continually discriminate between rewarding and unrewarding flowers, often under conditions of incomplete information and uncertainty (Johnson and Schiestl 2016). Using a framework derived from SDT, we asked how increasing decision costs and benefits influenced bees' decision criteria. We found that bees adjusted their decision thresholds in response to increased costs, but not to increased benefits. When the cost of encountering a mimic was elevated by adding quinine, bees exhibited a conservative bias, producing more correct rejections and fewer correct detections; bees also made far fewer costly attempts to collect pollen (Rossi et al. 2026) on models and mimics. However, increasing rewards associated with male flowers by providing extra pollen did not elicit a corresponding liberal shift in decision threshold. This asymmetry suggests that, under the conditions tested here, bees are more responsive to potential aversive costs than to the potential benefits of additional pollen rewards. This pattern only partially aligns with predictions from SDT, which suggest that receivers should adjust their decision thresholds according to the relative costs and benefits of foraging on models and mimics (Abbott and Sherratt 2013; Kikuchi and Sherratt 2015; Sherratt and Peet-Paré 2017).

More broadly, these findings align with published evidence that bees tend to minimize costly errors, even when this strategy limits potential gains. In many contexts, when foraging decisions are made under uncertainty, individuals must balance the expected payoff of each option with the variability in outcomes, commonly referred to as risk-sensitivity (McNamara and Houston 1992; Kacelnik and Bateson 1996). Such models predict that animals evaluate both the mean and variability of rewards, with risk-averse individuals favoring consistent outcomes and risk-prone individuals favoring variability when average gains are equivalent. Many animals exhibit risk-prone behavior when facing delays but are generally risk-averse

or risk-neutral when outcomes differ in magnitude or probability, including cases where rewards may be absent (Kacelnik and Bateson 1996). Bumble bees exhibit risk aversion when nectar volumes vary (Harder and Real 1987), but individuals may shift toward being risk-prone when the colony's energetic reserves are low (Cartar and Dill 1990). Similarly, honey bees become more risk-averse when discrimination among rewards becomes more difficult, suggesting that uncertainty may amplify avoidance of costly mistakes (Shafir et al. 2008). Considered together with our findings, bees may generally prioritize minimizing costly errors, such as visiting unrewarding or punishing mimics, over maximizing potential gains, potentially reflecting a broader conservative bias in their decision-making under uncertainty.

Here, we increased the costs of visiting female (mimic) flowers by adding quinine. Secondary metabolites are common in floral scents, nectar, and pollen across plant species and can be aversive to bees (Junker and Blüthgen 2010; Palmer-Young et al. 2019; Stevenson 2020; Hemingway, Leonard, et al. 2024). Although quinine represents just 1 type of foraging cost, it provides an ecologically relevant manipulation of aversive floral chemistry (Tiedeken et al. 2014). It remains unclear whether similar patterns of discrimination would emerge if the costs associated with floral deception were altered in different ways; however, we suspect that such manipulations could produce even stronger effects. In natural foraging environments, pollinators encounter a range of costs associated with decision errors, including energetic and time costs, and missed opportunities, all of which likely have fitness consequences (Raine and Chittka 2008; Zurbuchen et al. 2010; de Jager and Ellis 2014; Nakazawa et al. 2024). Pollinators are also susceptible to predator attacks while foraging, which can have serious fitness consequences (Romero et al. 2011). Increasing any of these costs may shift pollinator decision-making toward a more conservative strategy in which they avoid potential mimics, even at the expense of occasionally rejecting rewarding models. Under conditions where costs become sufficiently high, such as when deceptive flowers are abundant (Ferdy et al. 1999; Duffy and Johnson 2017) or rewards are consistently poor, pollinators may even stop visiting either flower type altogether.

Conversely, what if the benefits were enhanced? Here, we increased the reward value of male (model) flowers by supplementing them with pollen. Nectar and pollen are the primary rewards offered by flowers and increases in either their quantity or quality generally promote higher visitation rates and greater resource collection (Robertson et al. 1999; Cartar 2004; Ruedenauer et al. 2016; Nachev et al. 2017; Hemingway et al. 2024). Although pollen supplementation increased overall bee performance, we found no evidence that increasing pollen quantity shifted bees toward a more liberal decision threshold, which may help explain why male *Begonia* can offer so little pollen per flower. Likewise, changes in reward quantity may be perceived as less beneficial than changes in quality (see Cnaani et al. 2006), and these patterns may further depend on the type of floral reward being evaluated. For example, sugar concentration, a key component of nectar quality, can be assessed immediately when bees sample nectar (Bitterman 1976; De Brito Sanchez 2011; Hemingway and Muth 2022), whereas pollen quality may require different sensory information and timescales to assess despite bees being able to taste pollen (Muth et al. 2016; Ruedenauer et al. 2016; Mayberry et al. 2024). Stronger or qualitatively different reward manipulations may produce different outcomes and future experiments that manipulate the type and magnitude of floral rewards in different ways will be important for testing whether these behavioral patterns generalize across other forms of floral deception.

Aside from the observed asymmetry in decision criteria, we found that learning played an important role in shaping performance over time, with bees adjusting their responses as they became familiar with models and mimics. When mimic costs were increased, bees made proportionally fewer correct decisions and detections overall with experience. In contrast, correct rejections increased with experience regardless of the relative costs or benefits. Buzzing of mimics also diminished with experience when mimic costs were unmodified, indicating bees learned to reduce the energetic cost of false alarms; buzzing of mimics likely did not decline with experience when mimic costs were increased, due to the initially very low incidence of buzzing. Overall, bees showed marginal improvements with experience when models were supplemented with pollen.

Pollinator learning is often proposed to mitigate exploitation by floral Batesian mimics (Dafni 1984; Dukas 1987; Gigord et al. 2001; Anderson and Johnson 2006; Jersáková et al. 2006; Schiestl and Johnson 2013), although the mechanisms underlying this remain poorly understood (Gigord et al. 2001; Gigord et al. 2002; de Jager and Ellis 2014). Naïve pollinators are initially unfamiliar with the phenotypic distributions and payoffs of models and mimics and are therefore expected to initially visit both randomly. With experience, they learn to use distinctive cues to target rewarding flowers (Whitney et al. 2009; Clarke et al. 2013; Russell and Ashman 2019; Rands et al. 2023). Although our experiment was not designed to identify which cues bees learned, they likely relied on the natural multimodal *Begonia* floral display (eg differences in pollen, gynecium, androecium, and perianth shape, size, and scent) and potentially differences introduced by our experimental manipulations (ie differences in quinine and pollen color and scent). SDT predicts that such learning should lead pollinators to increasingly avoid mimics, even at the cost of some missed rewards, thus maximizing foraging efficiency (Oaten et al. 1975; Guilford and Dawkins 1991; Abbott and Sherratt 2013). Our results support this prediction, particularly when mimic costs were high, and align with previous findings that discrimination performance improves with experience (Kunze and Gumbert 2001; Internicola and Harder 2012; de Jager and Ellis 2014; Russell et al. 2020; Russell et al. 2021).

Mimicry occurs across a range of decision-making contexts beyond floral deception, with one of the most well-studied examples involving predators encountering defended prey. In such systems, predators must decide whether to attack or avoid prey that may resemble defended species (Skelhorn et al. 2016). As with pollinators facing deceptive flowers, these decisions entail a trade-off. Being overly cautious may reduce foraging opportunities, whereas being overly liberal may increase the risk of exposure to chemically or physically defended prey. Theoretical work has examined how predators evaluate risk in the face of such deceptive signals, exploring how uncertainty and the potential costs of mistakes shape decision rules (Speed and Ruxton 2010; Sherratt 2011; Kikuchi and Sherratt 2015; Holen and Sherratt 2021). Empirical studies similarly demonstrate that when the costs of attacking defended prey are high, predators tend to adopt more conservative strategies, by avoiding more broadly and sampling less frequently (reviewed in Skelhorn et al. 2016), or relying more heavily on social information (eg Hämäläinen et al. 2021). Together, these findings align with the results found in our current study, suggesting that as the costs of errors and the degree of uncertainty increase, decision-makers may favor conservative strategies that

minimize potential losses, even at the expense of foregoing greater potential rewards. Future experiments manipulating a broader range of costs and benefits will be important for determining how general this pattern is across pollination systems.

In conclusion, bumble bees appear to prioritize avoiding exploitation over maximizing potential gains, revealing an asymmetry in their risk evaluation when encountering uncertainty with floral mimics. Our findings may thus offer new insights into the evolutionary persistence of floral deception and the ecological dynamics that maintain it. Because pollinators did not substantially increase visits to more profitable models over time, deceptive mimics may persist even in the presence of more rewarding flowers. However, as the costs of visiting deceptive flowers increase, pollinators are expected to adopt even more conservative decision criteria, further reducing visits to potential mimics. If these costs become too high, pollinators may ultimately abandon the entire floral system, decreasing reproductive success for both mimics and models. These dynamics may help explain the stability of automimetic systems like those found in *Begonia*, where deceptive and rewarding flowers coexist with moderate costs (Agren and Schemske 1991; Schemske et al. 1996; Wyatt and Sazima 2011). More broadly, a conservative pollinator bias may have population-level consequences by reducing pollen transfer efficiency and constraining plant reproductive success, thereby shaping the coevolutionary balance among attraction, deception, and learning in plant-pollinator interactions. These dynamics could be tested in both field and lab settings to shed light on the fitness consequences of these decision rules under different cost-benefit regimes. Linking SDT with pollinator behavior in plant–pollinator interactions thus provides a powerful approach for understanding how animals navigate uncertainty and deception in their environments and how these decision-making processes shape ecological and evolutionary outcomes.

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Author contributions

Annaliese N. Novinger (Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Validation, Visualization, Writing—original draft, Writing—review & editing [equal]), Claire T. Hemingway (Conceptualization, Visualization, Writing—original draft, Writing—review & editing [equal]), Jenny K. Burrow (Data curation, Investigation, Methodology, Writing—review & editing [equal]), Charlotte C. Davis (Data curation, Investigation, Methodology, Writing—review & editing [equal]), and Avery L. Russell (Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing—original draft, Writing—review & editing [equal])

Supplementary material

Supplementary material is available at *Behavioral Ecology* online.

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Conflicts of interest

None declared.

Data availability

Analyses reported in this article can be reproduced using the data and R code provided by Novinger et al. (2026).

Ethics approval

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

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