

Opinion piece



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Noisy communities and signal detection: why do foragers visit rewardless flowers?

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Floral communities present complex and shifting resource landscapes for flower-foraging animals. Strong similarities among the floral displays of different plant species, paired with high variability in reward distributions across time and space, can weaken correlations between floral signals and reward status. As a result, it should be difficult for foragers to discriminate between rewarding and rewardless flowers. Building on signal detection theory in behavioural ecology, we use hypothetical probability density functions to examine graphically how plant signals pose challenges to forager decision-making. We argue that foraging costs associated with incorrect acceptance of rewardless flowers and incorrect rejection of rewarding ones interact with community-level reward availability to determine the extent to which rewardless and rewarding species should overlap in flowering time. We discuss the evolutionary consequences of these phenomena from both the forager and the plant perspectives.

This article is part of the theme issue ‘Signal detection theory in recognition systems: from evolving models to experimental tests’.

1. Introduction

The flowers of many plants present food resources (e.g. nectar and pollen) that elicit visits from foragers. In the act of feeding on these ‘rewards’, some of these foragers transfer pollen among conspecific plants. The signals and cues (henceforth collectively referred to as ‘signals’)¹ that plants produce and the responses they induce from such foragers are thus key to the success of ecologically critical plant–pollinator mutualisms. Flower foragers² use visual, olfactory and even electrostatic signals of reward status to fine-tune their foraging decisions [3]. Most flower foragers are generalists, feeding at the flowers of several plant species in a given habitat over the course of their lives [4]. Through the use of plants’ signals (floral ‘display traits’, which include specific colours, scents and morphologies), along with past experiences of floral resource quality and quantity, flower foragers learn to focus on relatively more profitable flowers, patches and plant species. Some groups of flower foragers even share this information with conspecifics to manage real-time colony foraging strategies [5].

However, many animal-pollinated plant species produce flowers that contain no rewards at all. Over 7500 rewardless plant species have been described to date, spread widely across the angiosperms [6]. Intriguingly, however, the flowers of many rewardless species are regularly visited, and pollinated, by flower foragers. Some rewardless plant species produce sexually deceptive or brood-site mimicking flowers: they rely on signals associated with animal reproduction to lure visitors [7]. Other rewardless species advertise food rewards that do not in fact exist; these deceptive reward signals allow the flowers to attract visits and thus

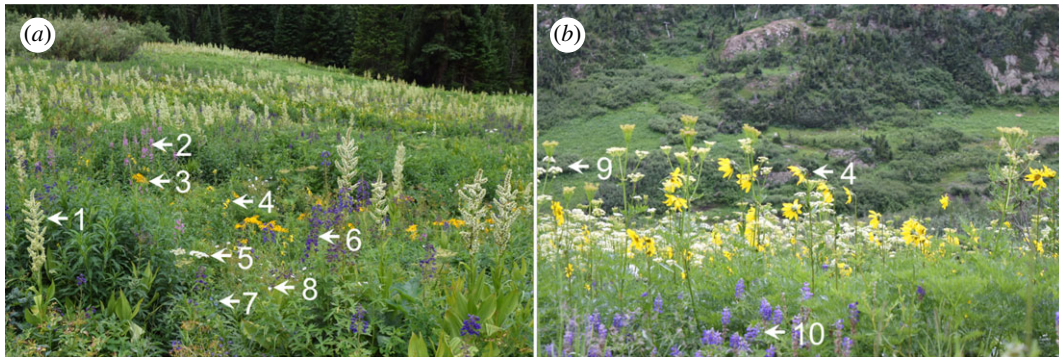


Figure 1. Example of visual similarity in floral display traits (colour and architecture) among members of neighbouring floral communities. Images are of two co-flowering (ca July) subalpine meadow communities (*a*: wet meadow; *b*: dry meadow) typical of the Elk Mountains of southwestern Colorado, USA. Such communities are often immediately adjacent and share pollinators. Plant species include: (1) *Veratrum tenuipetalum* Liliaceae, (2) *Chamaenerion angustifolium* Onagraceae, (3) *Hymenoxys hoopesii* Asteraceae, (4) *Helianthella quinquenervis* Asteraceae, (5) *Heracleum sphondylium* Apiaceae, (6) *Delphinium barbeyi* Ranunculaceae, (7) *Mertensia ciliata* Boraginaceae, (8) *Geranium richardsonii* Geraniaceae, (9) *Ligusticum porter* Apiaceae, (10) *Lupinus argenteus* Fabaceae. (Online version in colour.)

to achieve pollen transfer. These deceptive food reward signals are the focus of this article. Specifically, we ask: given foragers' capacity for learning and discrimination, why do they visit these rewardless species consistently? Often, these visits are frequent enough to maintain pollination services, apparently rendering this a viable reproductive strategy for plants.

Signal detection theory provides a useful framework for investigating why foragers regularly visit rewardless flowers. The set of local plant species that flower at the same time (hereafter, the co-flowering plant community) defines the backdrop against which generalist flower foragers must decide which flowers to visit. Rewardless plant species produce deceptive display traits that may overlap in sensory space with those of rewarding plants, in one or more modalities (e.g. visual, olfactory). While floral communities are often characterized by a striking variety of signals, overlapping combinations of display traits across multiple plant species (as illustrated by the communities depicted in figure 1) are common. Such overlap may attenuate flower foragers' abilities to differentiate among the multitude of signals co-occurring in a community [6]. Further, flower foragers' responses to flowers that appear to signal rewards will depend on how frequently they encounter rewarding and rewardless flowers, as well as the fitness consequences associated with making correct and incorrect decisions about individual flowers [3,8]. Thus, flower foragers must detect signals of rewarding flowers amidst background noise from rewardless flowers, and set a threshold for acceptance that both maximizes correct acceptance of rewarding flowers and minimizes incorrect acceptance of rewardless flowers. Detecting signals from noise and setting optimal acceptance thresholds are key elements of signal detection theory as applied in behavioural ecology [8,9], but relatively few links have been made between this body of literature and that on floral display traits.

Like other foragers, animals visiting flowers integrate information on spatial and temporal reward variation, basing their foraging decisions on reward acquisition rates [10–12]. Many flower foragers exhibit a striking capacity for learning and employ complex decision rules to effectively forage in highly variable resource landscapes. They use a combination of innate preferences (e.g. for certain colours), direct and indirect assessment of flowers' reward status (including visible rewards, reward odours, flowers' electric fields and the presence or hydrocarbon footprints of other insects), and memory of

recent flower visits to decide which plant species (and indeed which individual plant) to visit, whether to probe a given flower for rewards, how much time to spend handling each flower, when to leave a given patch and when to switch between plant species. Foragers may use one or more of the above signals simultaneously. However, costs associated with decision-making (e.g. time required to learn and remember while assessing flowers, cognitive costs of memory, opportunity costs of visiting unrewarding flowers), as well as signal–reward correlations (which may be weak), should limit the degree to which animals can optimize their foraging decisions [13,14]. Previous behavioural research has shown that flower foragers often respond to rewardless flowers by visiting fewer flowers per inflorescence (e.g. [15,16]) or patch ([15], but see [17]), decreasing flower handling times (e.g. [18,19]) or flying further between inflorescences or patches [18,19]. However, such studies typically test forager responses to rewarding and rewardless flowers that are either easily distinguished from each other or else identical, and thus provide only limited insights into the constraints on forager decision-making in complex natural floral communities.

Here, we explore how display traits influence whether animals foraging for rewards, pollinators among them, will visit a flower. We argue that two community-level patterns, floral resource heterogeneity (variation in floral resource availability among flowers) and floral trait overlap (similarity in floral display traits across species), limit flower foragers' abilities to identify and discriminate against deceptive signals used by rewardless species. Below, we first use the systematic framework of signal detection theory to describe foragers' recognition of and responses to rewarding versus rewardless flowers. We then explore how floral community patterns might be driving flower foragers' responses to rewardless flowers, and the ecological implications for both foragers and plants.

2. Floral community patterns

Two common plant community patterns limit foragers' ability to discriminate among flowers in ways that may facilitate the evolution and maintenance of the rewardless character state. These are: (i) floral reward heterogeneity, which includes both spatial and temporal heterogeneity of floral reward availability; and (ii) floral trait overlap among subsets of plant

Table 1. Mechanisms contributing to patchy floral reward availability and the spatial and temporal scales at which they operate.

mechanism	spatial scale	temporal scale
intra-individual variation in production	individual	seasonal–decadal
removal/replenishment	individual–landscape	hourly–daily
intraspecific variation in production	patch	hourly–decadal
interspecific variation in production	patch–landscape	seasonal–evolutionary
plant phenology	patch–landscape	seasonal–evolutionary
plant population density	landscape	seasonal–decadal

species within a community. Renner [6] articulated this argument in some detail (see also [18,20,21]). We summarize these patterns here, and place them in the context of signal detection theory in §3.

(a) Floral reward heterogeneity

The availability of rewards within any community of flowering plants is patchy in space, from within an inflorescence to the scale of an entire landscape (table 1), as well as in ecological and evolutionary time [22]. While the flowers of some plant species are constitutively rewardless, other flowers are only transiently empty, having been drained by foragers. Variation in reward availability has numerous proximate causes, including patchy availability of resources that plants require to make rewards (e.g. water, nitrogen, light) [23], genetic variation [24,25] and unequal removal of rewards by visitors [26]. Further, floral reward availability varies among the plant species within a community [27], among patches within a population [28], among individuals within a species [25,29] and even among flowers within individual plants [30]. Each of these levels of variation typically has some temporal element, operating on diurnal [29], seasonal [31,32] or inter-annual time scales [33]. The net result is an intrinsically dynamic floral resource landscape in which a large proportion of the flowers are empty at any given point in time.

(b) Floral trait overlap

Species within plant communities can exhibit overlap in floral display traits such as colour, morphology and scent ([34–36], but see [37]). This can be, at least in part, the product of convergent floral evolution driven by a shared set of selective agents (herbivores, pollinators and abiotic factors; [34,35,38]). Indeed, subsets of species in a co-flowering community can share sets of key display traits. For example, Kantsa *et al.* [35] report that 41 forb species in a Greek scrub community can largely be reduced to seven modules describing floral scent. Further, strong coordination between scent profiles and flower colour results in the reduction of nine of these 41 species into just two integrated phenotypes: purple flowers that emit terpenes and offer nectar rewards, and red flowers that emit aliphatic

volatiles and provide other types of rewards (pollen and shelter). As a result, the range of sensory space available for a given flower-foraging species to discern among plant species may represent a relatively narrow band of the total sensory space otherwise available to that forager species. Further, such multimodal floral signals often consist of linked traits (e.g. colour, odour) that may be controlled by pleiotropic gene networks [39]. Thus, community-level convergence in floral display traits can result in higher overlap among the set of signals that foragers can use to detect and discriminate against rewardless plants and those that they can use to correctly identify rewarding species. This is carried to an extreme in cases of floral mimicry, in which constitutively rewardless plants closely resemble rewarding models, though less exaggerated resemblance is common [36].

3. How does floral reward recognition affect foraging?

Foragers must rely on detecting and learning floral signals to make foraging decisions amidst the noise in a floral community. While animals must solve many signal detection problems, including nest-mate recognition [8] and mate-quality recognition [40], the high variability of floral resource availability paired with potentially high floral trait overlap and the fact that many flowers do not signal reward status (though some do, e.g. [35,41]) make recognizing the quality and quantity of floral rewards a particularly complex challenge. Specifically, the probability that a given floral display trait signals reward presence, the relative abundance of rewarding flowers as well as the costs and benefits associated with visiting rewarding or rewardless flowers can vary, either in synchrony or at different spatial and temporal scales.

By formalizing how information about floral rewards changes, signal detection theory can help us determine the impact of these complexities on floral visitors' foraging decisions. Below, we first present an overview of signal detection theory as it applies to floral displays. We next investigate the effects on foragers of three major components of signal detection theory: overlap between the two classes of signallers (rewarding and rewardless flowers), relative frequencies of the two classes of signallers, and the costs and benefits of acceptance and rejection. We then explore how floral resource heterogeneity and floral trait overlap might affect flower foraging in the context of signal detection.

(a) Floral displays and probability density functions

Following convention in signal detection theory literature, we assume that the community of flowering plants can be represented by two simple signal sets: one representing flowers that are rewarding at any given point in time and the other those that are rewardless at that same point in time. These signal sets can be represented graphically by curves showing the probability that a signaller belongs to a certain class of individuals (here, rewarding versus rewardless flowers), given its signal level (e.g. colour hues, chemical concentrations) [8]. These curves are called probability density functions (PDFs), and we give a detailed example in figure 2. While floral signals of reward availability exist in multiple modalities and may be multimodal in a given plant [35], for ease of visualization in figure 2, we represent each signal set as varying in only one

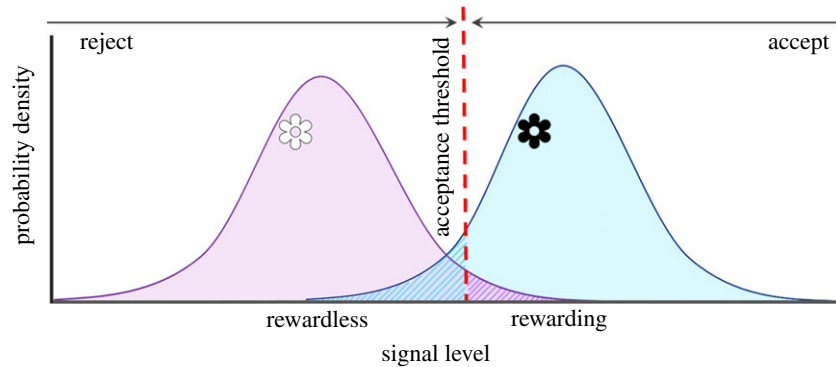


Figure 2. PDFs for the two classes of signaller we consider in this article: rewarding flowers (black icon, blue lighter curve) and rewardless flowers (white icon, purple darker curve). The *x*-axis represents the flower's 'signal level', a composite measure of all components of its display (in any modality, e.g. colour, odour). The *y*-axis represents the probability that a flower with a given signal level will be from each class of signaller. For example, a flower with a low signal level has zero probability of being rewarding but some probability of being rewardless (and some probability of being not a flower at all). By contrast, a flower with a high signal level has some probability of being rewarding and zero probability of being rewardless. Of particular interest is the region where the PDFs overlap, where a given signal level could indicate either a rewardless or a rewarding flower. A forager sets an acceptance threshold (red dashed line) above which it will visit flowers (because they are more likely to be rewarding) and below which it will reject them (because they are more likely to be rewardless). When PDFs overlap, there will be two regions of error: accepting a flower that is rewardless ('false alarm' or type I error, indicated by purple darker hatching) and rejecting a flower that is rewarding ('missed detection' or type II error, indicated by blue lighter hatching). The forager's challenge is to set an optimal acceptance threshold to minimize both errors. (Online version in colour.)

parameter, which can be conceptualized as a composite signal whose level indicates whether the flower is rewarding or rewardless. PDFs can vary in both mean and variance across plant communities, resulting in a wide variety of curve shapes, heights and degrees of overlap among PDFs. Each curve may represent several plant species; the common feature is whether they are rewarding versus rewardless.

An animal's expected response to a given signal will depend on its acceptance threshold, the signal level at which it switches from accepting to rejecting flowers [8]. Any signals above the acceptance threshold are expected to elicit visitation to the flower, whereas a forager will avoid any flowers with a signal level below the acceptance threshold (figure 2). There are four outcomes for the forager: correct detection (visiting a rewarding flower), correct rejection (not visiting a rewardless flower), false alarm (visiting a rewardless flower: type I error) and missed detection (not visiting a rewarding flower: type II error) (figure 2; terminology from [9,42]).

Foragers can respond to the presence of rewardless flowers in three ways. First, if a forager is unable to distinguish among signals of rewarding and rewardless flowers, it will visit both flower classes. Failure to distinguish can be owing to perceptual constraints [43], memory and learning constraints [44], or a lack of prior experience with that plant species [45]. A second response by foragers unable to distinguish among signals of rewarding and rewardless flowers is to abandon the portion of signal space that contains rewardless flowers, and switch to a region of signal space with higher net rewards or easier discrimination among rewarding and rewardless flowers [46]. This would be observed in the field as foragers switching to different plant species.

Third, flower foragers may be able to distinguish signals of rewarding and rewardless flowers, in which case individuals might adjust their acceptance thresholds to maximize the probability of correct detections while minimizing false alarm probability. In this case, rewardless flowers will be visited relatively less as acceptance thresholds increase. Given that flower foragers appear sensitive to the relative rates of encounter with rewarding and rewardless flowers [47], it is

likely that in nature, they do in fact adjust their acceptance thresholds. For example, bumblebees increase their preference for a rewardless flower when a new rewarding flower becomes available and the colour of this new flower resembles the rewardless one but differs from a previously blooming rewarding flower (carry-over effects: [48]). Peak shift, a preference for more easily distinguishable signals [49], might drive foragers to prefer flowers less similar to rewardless ones and therefore to shift acceptance thresholds towards the upper range of rewarding flowers' PDF. Generalization, the tendency to respond to a signal distinguishable from but similar to one that is known to be rewarding [50,51], on the other hand, could limit the degree to or rate at which flower foragers adjust acceptance thresholds and could thus promote continued visitation to rewardless flowers.

(b) Key concepts from signal detection theory and their implications for floral resource recognition

We now use the PDF framework to examine the implications for decision-making by flower foragers of the overlapping, variable signal sets in floral communities.

(i) Overlap between signals of rewarding and rewardless flowers

The overlap between the PDFs of rewarding and rewardless flowers determines whether foragers can detect the difference in signals from these two flower classes. As we show in figure 3, when overlap is higher, there is greater potential for foragers to make mistakes. The degree of overlap will not be constant: it should vary with intraspecific variation in display traits, the degree of floral trait overlap within and between plant classes (rewarding and rewardless), and, in rewarding species, the speed of reward turnover (removal and replenishment). The overlap may range from virtually none to nearly complete (in the case of floral mimicry: see §2).

When PDFs barely overlap, signals of rewarding and rewardless flowers are easy for flower foragers to discriminate (figure 3*a*). While minimal overlap should permit rewardless

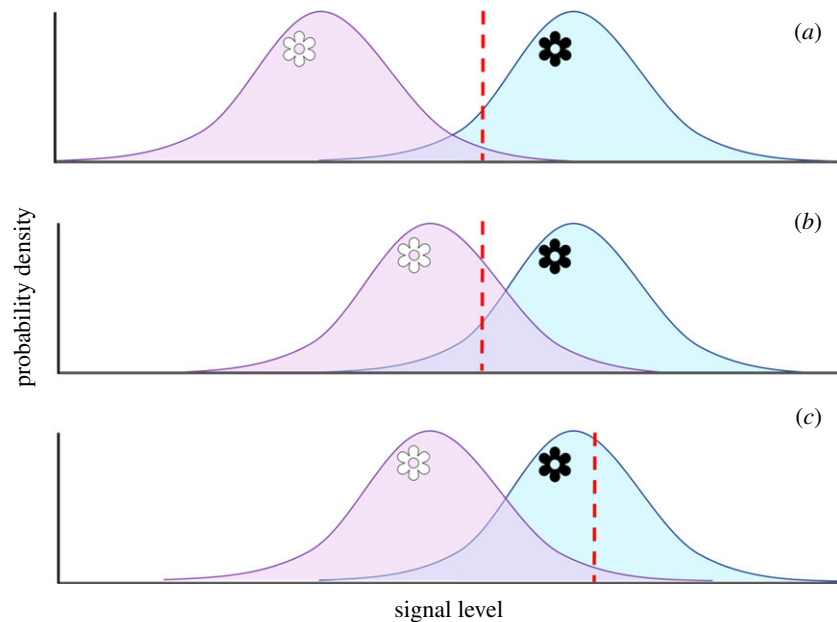


Figure 3. Variation in the degree of overlap between the PDFs (figure 2) of rewarding (black icon, blue lighter curve) and rewardless (white icon, purple darker curve) flowers. In each panel, the mean signal level of rewarding flowers is the same, but the mean signal level of rewardless flowers is different. (The variance in signal level is the same in all panels for both classes of signaller.) (a) Minimal overlap between the PDFs of rewarding and rewardless flowers, yielding relatively small regions of error (the area of the blue lighter curve below the acceptance threshold, and the area of the purple darker curve above the acceptance threshold). (b) Increased overlap: rewardless flowers' signals converge on rewarding flowers'. If the forager has the same acceptance threshold (red dashed line) as in (a), there are now larger regions of error. (c) With the same degree of overlap as in (b), the forager has raised its acceptance threshold. There is now a higher probability of missed detection (area of the blue lighter curve below the acceptance threshold), but a much lower probability of a false alarm (area of the purple darker curve above the acceptance threshold). (Online version in colour.)

flowers to be avoided, it has interesting implications for the timing of flowering by rewardless plant species that we discuss in §4. Often, however, rewardless and rewarding flowers appear similar to foraging animals. That is, PDFs overlap enough that distinguishing among rewarding and rewardless flowers will be a challenge (e.g. species 2, 6, 7 and 10 in figure 1 and figure 3b).

PDF overlap reduces the value of display traits as information about a flower's reward status [1], and therefore reduces learning opportunities for foragers. To compensate for these difficulties, foragers may adjust their acceptance thresholds (figure 3c). If discrimination is too difficult, they may also abandon this portion of signal space [52], as mentioned in §3a, and switch to a region of signal space where rewardless flowers are easier to detect. With extreme overlap, foragers have no ability to distinguish rewarding from rewardless flowers. This could occur, for example, in a plant community with many similar rewarding species and thus a wide PDF, or with plant species that produce a mixture of rewarding and rewardless flowers. With such high overlap, foragers cannot raise their acceptance thresholds to reduce the probability of false alarms, because it would lead them to reject too many rewarding flowers.

(ii) Relative frequencies of rewarding and rewardless flowers

Floral communities vary not only in the degree to which signal sets of rewarding and rewardless flowers overlap, but also in the frequency of each signaller class. As rewardless flowers become more common, the probability that a flower forager will obtain rewards from a given accepted flower decreases (electronic supplementary material, table S1). The relative

frequencies of rewarding and rewardless flowers have the potential to affect foraging decisions through several routes.

As rewarding flowers decrease in relative frequency, opportunities to learn the signals of rewarding versus rewardless flowers should also decrease [53], similar to the effect of increasing PDF overlap. In this situation, then, floral visitors are likely to shift their foraging to flowers with a signal set that does not heavily overlap with rewardless flowers [18], or to adjust their acceptance thresholds to accept fewer rewardless flowers [1]. While this hypothesis has not directly been tested in complex flower communities, it is consistent with experimental [18] and observational [54] studies showing that pollinators prefer a flower colour that is more frequently rewarding.

When rewardless flowers are sufficiently rare, foragers will have little opportunity to learn their signals. This should promote continued visitation to rewardless flowers, as there may be little incentive for foragers to learn to discriminate rewardless from rewarding flowers. Consistent with this hypothesis, Smithson & Gigord [18] found continued visitation to a floral morph that was only occasionally rewardless.

Behavioural responses to the relative frequencies of rewarding and rewardless flowers—as well as to the degree of signal set overlap—are highly context-dependent. In the electronic supplementary material, table S1, we show how the probabilities that a forager succeeds or fails to feed from a flower it visits change with both the relative frequency of rewarding flowers and the probabilities of correct detection and false alarm. While the probability of successfully feeding declines as rewarding flowers become less frequent, this decline is slower when the probability of correct detection is lower (owing to increasing PDF overlap or low acceptance threshold, as discussed in §3b(i)). In general, forager responses to diminishing reward acquisition within a patch (which may be owing

to diminishing frequencies of rewarding flowers) vary with factors such as the magnitude of the change [55], the nature of the change (e.g. nectar concentration versus volume; [56]) and even forager species (e.g. bumblebees versus honeybees; [55]).

(iii) Costs and benefits of acceptance and rejection

Floral resource recognition results in both benefits and costs to flower foragers, not only from visiting flowers (i.e. correct detection and false alarm), but also from *not* visiting them, given the opportunity (i.e. correct rejection and missed detection). Benefits for foragers exist mainly in the form of rewards received upon making a correct detection. However, benefits may also include learning opportunities from correct rejections that reduce assessment costs of subsequent visits to rewardless flowers. While correlational studies indicate learning benefits [57], the magnitude of such benefits relative to other foraging costs and benefits, and the conditions under which foragers receive learning benefits, remain unknown.

Visiting empty flowers and assessing a flower's reward status impose energy and time costs, including those associated with (i) assessment, (ii) lost opportunities, and (iii) increased morbidity risk. Assessment costs arise from attending to a flower's signals of reward status, and also from probing a flower to determine whether it is rewarding. While the latter may require more time or energy, the former requires investment in learning and memory. Opportunity costs arise as foragers waste time at rewardless flowers, thereby decreasing the proportion of time available for other functions, such as finding mates or building nests. As rewarding flowers decrease in relative frequency, foragers should become less likely to receive a benefit (reward) from a given flower, and more likely to incur both assessment and opportunity costs. Morbidity costs include increased wing wear, and the risk of exposure to predators, parasites and disease transmission [58–60]. Again, when visiting more flowers in an attempt to find rewards, costs to the forager are higher.

These costs are influenced by flower properties. Initial assessment costs are higher when signals have a smaller active space—the range in which a forager can detect a flower's signal—that requires closer physical proximity to make that assessment. Costs will also be higher for sets of flowers that are less well learned, such as plant species that have recently opened or that are rare. Costs of probing vary with flower morphology. Flowers with deep corollas or nectar spurs require a longer handling time for many foragers to determine reward status [61].

Which types of costs a forager incurs also depends on the types of errors it tends to make. Both types of errors—false alarms and missed detections—inflict assessment costs as a forager decides whether or not to attempt to feed at a flower based on its signals. False alarms additionally inflict opportunity costs and a larger assessment cost because of attempting to feed from a flower after the initial assessment. Thus, the costs of false alarms are likely to have a stronger impact on acceptance threshold placement than will costs of missed detections in the context of floral resource recognition. However, if the costs of learning new reward-signal correlations are high, flower foragers may be unable to sufficiently adjust acceptance thresholds to maximize foraging efficiency. Determining the specific impacts of each of these costs on floral visitors' foraging success is an area in which more empirical data would be valuable.

The effects of the costs and benefits of acceptance and rejection on floral resource recognition will also interact with the degree of overlap and relative frequencies of rewarding and rewardless flowers. Little empirical or theoretical research has addressed this phenomenon, but we can make several logical predictions that highlight the importance of learning and assessment in guiding foraging decisions.

- (i) Higher overlap of the PDFs of rewarding and rewardless flowers will lead to higher assessment costs, because in this circumstance, it will be more difficult to distinguish between the two classes of flowers. Consistent with this prediction, bumblebee pollinators take longer to first land on a flower [62] and more slowly learn to avoid rewardless flowers [63] when rewarding and rewardless flowers are similar colours.
- (ii) As PDFs increasingly overlap or rewardless flowers become rare, signals provide less information about rewards and thus the benefits from learning will decrease.
- (iii) When PDFs overlap greatly or when rewarding flowers are rare, the relative value of rewarding flowers increases. Thus, costs of missed detection can be more important than costs of false alarm under such extreme circumstances.
- (iv) The effect on a forager of its foraging decisions is the difference between the costs and the benefits of those decisions. As a consequence, even very high costs may be worth bearing if the concomitant benefits are large. For example, there may be a positive net effect of foraging from a deep tubular flower if the likely reward is a large volume of nectar, even if it requires high assessment costs and a long handling time in order to gain it.

(c) Signal detection in complex plant communities

We now consider how the floral community patterns described in §2 might affect floral resource recognition.

(i) Floral resource heterogeneity

Floral resource heterogeneity presents three challenges faced by foragers that, to our knowledge, have not been addressed by signal detection theory.

- (i) Adjusting thresholds to match current conditions can be constrained when floral resources are highly heterogeneous. This is because PDF overlap and the associated probabilities of correct detection and false alarm rapidly vary. Constraints may be imposed by flower foragers' cognitive processes, their general foraging strategies, or the costs they accrue while foraging. For example, when floral displays are highly heterogeneous, carry-over effects (a preference for signals similar to known rewarding ones) may keep visitors foraging on flowers that resemble rewarding ones [45], as mentioned in §3a. Additionally, foragers' attempts to adjust acceptance thresholds in response to frequent changes in PDF overlap could inflict high learning costs, or require extra assessment to make adaptive choices [64]. These learning and assessment costs could prevent flower foragers from adjusting acceptance thresholds. Further, certain flower foragers are known to be risk-sensitive and thus to reduce visitation to flower

morphs with high variance in nectar availability (e.g. [15,65]).

- (ii) Flower foragers (and foragers in general) often rely heavily on recent past information to guide foraging decisions [66–68], but they may be unable to do so if plant communities are too dynamic. The rates of change in PDF overlap and relative frequencies of rewarding and rewardless flowers alter the value of such past information. In theory, floral reward heterogeneity increases the need to assess individually every flower that a forager encounters. This will increase overall foraging costs, which may be offset by the benefits of gaining more accurate information to guide foraging decisions. Recent research shows that flower foragers assess flowers for longer when the reward status of a given flower morph varies in fairly simple laboratory conditions [64,69]. How this applies to field conditions remains an open question. Plant communities are more dynamic than laboratory settings can feasibly be. Further, in the field, animals seem to exhibit higher behavioural constancy, with less information collection, than under laboratory conditions [70].
- (iii) Display traits vary in their correlation with reward status, and in how that correlation changes over time. This variation may favour foragers that are better learners. Some display traits change slowly or not at all with changes in reward status (e.g. petal colour), whereas others are directly correlated with a flower's current reward status (e.g. electrostatic fields induced by nectar, hydrocarbon footprints of recent flower visitors). The former is particularly true for the majority of plant species that do not intrinsically signal individual flowers' reward status (but see [71]). The latter signals may require longer assessment or assessment at closer range and thus bear higher assessment costs (electric fields decay rapidly with distance [1] and hydrocarbon footprints have low volatility [72]). However, signals that track a flower's current reward status could serve to reduce PDF overlap of rewarding and rewardless states.

Despite these challenges, flower foragers are relatively successful at predominantly visiting rewarding flowers (e.g. [73,74]). They may accomplish this in part by avoiding flowers in portions of signal space with too many rewardless flowers at any given point in time or space [18,54]; this would result in foragers seeking flowers with signals that more reliably indicate rewards, e.g. by switching to a different species or searching in a new patch. Further, some plant community changes are predictable and foragers can learn these patterns. In particular, flower foragers readily learn the time of day at which a given plant species offers a specific reward (e.g. nectar versus pollen), and adjust their foraging accordingly [75,76]. Another intriguing possibility is that foragers adjust which specific components (e.g. flower colour, floral scent or hydrocarbon footprints) of a flower's signal they use to assess reward status. While such adjustments are largely unexplored in a realistic community context, multimodal signals (e.g. flower colour and scent together) have been shown to help foragers distinguish between rewarding and rewardless artificial flowers under highly controlled conditions ([77,78], but see [79]).

Floral resource heterogeneity also presents a challenge to studying forager decision-making. Different individual foragers will have recently experienced different degrees of PDF overlap, different relative frequencies of rewarding or rewardless flowers, and costs as well as benefits of decision-making. This individual variation in experience has the effect of increasing population-level variation in forager behaviour, as different individuals set different acceptance thresholds based on recent encounters [1]. Thus, individuals are likely to show different responses in experiments unless their entire history of experience with flowers is controlled, and variation in their responses may not be interpretable unless this experience is known. While this condition is straightforward to meet with captive-raised individuals in highly controlled environments—the usual context in which responses are tested—fully understanding how foragers make decisions under natural floral resource heterogeneity will also require experimentation with wild foragers and in community settings.

(ii) Floral trait overlap

Owing to overlap in floral display traits in plant communities, rewardless flowers may often be similar not just to one rewarding species or set of species with similar displays. Rather, there may be two (or more) classes of rewarding species, each with a separate PDF. The rewardless species' signals may overlap with the signal sets of both classes of rewarding flowers. As a simple example, imagine a floral community in which flowers of some rewarding species are dark blue and other rewarding species are white, and flowers of rewardless species are pale blue. We illustrate in figure 4 how such overlap means that both tails of the rewardless species' PDF can overlap with the PDFs of the two rewarding classes, giving rise to two separate regions of acceptance.

The presence of multiple classes of signal, including in a floral community, may reduce the ability to detect any one signal [9]. Indeed, bees are less able to distinguish a rewarding colour when they learn it in the presence of even one unrewarding flower, compared to when they learn the rewarding flower with no other colours present [80]. More generally, when rewardless species' signals overlap with more than one signal set of rewarding species, the implications for foragers' learning and decision-making are unclear. On the one hand, the strong tendency of some foragers to generalize a learned rewarding signal to similar signals [50] could increase visitation to rewardless species because more of their signal set is similar to one of the rewarding signal sets. On the other hand, foragers' preference for signals that they can discriminate more easily (peak shift) could promote visitation only to rewarding flowers that are least similar to the rewardless species. Whether foragers exhibit simultaneous peak shift to two separate signal sets is unknown, and would be an interesting avenue for future research.

4. Implications of floral resource recognition for plants

We have largely considered the problem of signal detection in flowering plant communities from an animal perspective, focusing on foragers visiting flowers to seek valuable resources (rewards). However, it is critical to consider that plants both benefit and are harmed by the behaviour of these foragers.

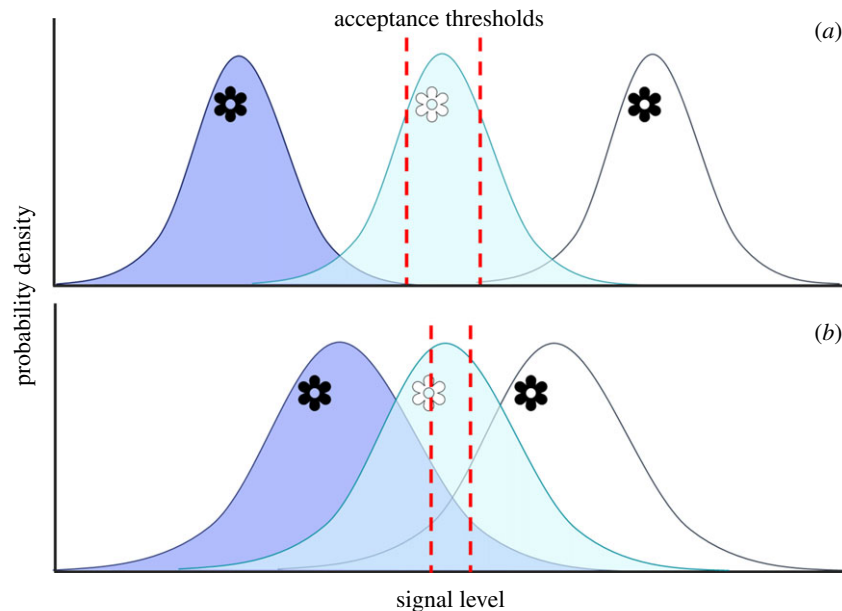


Figure 4. In many floral communities, there will be more than one distinct signal set indicating rewarding flowers (black icon; two signal sets shown here, by the dark blue grey and white curves), and the signal set of rewardless flowers (white icon, light blue grey curve) may overlap with both of them. Curves are PDFs, as explained in figure 2. (a) The forager must set two acceptance thresholds (red dashed lines). It will visit a flower whose signal level falls in either of the regions of acceptance, and avoid a flower whose signal level is in the ‘window of rejection’ between the two red lines. (b) When there is more overlap between the PDFs, the regions of error are greater, and the optimal acceptance window is narrower. (Online version in colour.)

The patterns of floral reward production and display that we have discussed have been selected in the context of attracting attention from the subset of those foragers that transfer pollen effectively and, potentially, reducing attention from the subset that does not. A full treatment of the plant perspective on floral signal production and detection is beyond the scope of this paper, as is a synthesis of the animal and plant perspectives. We leave these as critical research goals for the future, but highlight here several important considerations related to selection on floral reward and display traits in noisy environments.

The broad patterns that we highlight as characteristic of many floral communities—floral reward heterogeneity and floral trait overlap—restrict the degree to which the flower displays that plants have evolved can in fact signal meaningful information to foragers, and thus the ability of foragers to use this information to inform foraging decisions. This holds several implications for plant fitness and the degree to which rewardlessness can become or remain part of a viable reproductive strategy for plants.

There are at least two major ways in which floral reward recognition should influence plant fitness consequences associated with the rewardless reproductive strategy. First, forager preferences for a given signal should decrease as the proportion of empty flowers expressing that signal increases (§3b(ii)). Accordingly, mating success of rewardless species may be negatively frequency dependent, decreasing when rewarding species are relatively abundant in the community. Negative frequency dependence holds at least three implications for the mating success and selection of constitutively rewardless species. (i) Selection may favour rewardless plants that flower earlier or later than do rewarding plants in the same community (e.g. [81]), thereby reducing competition with rewarding species. Alternatively, when the flowering times of rewardless species highly overlap with abundant rewarding species, the cost of missed detection may be low. In such a case, pollinators could afford to be choosy (resulting in negative frequency-

dependent effects on mating success). Consequently, rewardless species may (ii) become or remain rare, or (iii) experience selection to produce relatively small floral displays, which would reduce the overall presence of rewardless flowers in the landscape (and thus opportunities to learn to avoid them) somewhat independently of population density. On the other hand, rewarding flower scarcity across an entire plant community (owing to high forager abundance and thus depletion of rewards or low availability of resources such as water or nitrogen that plants need to make rewards) may drive foragers to lower their acceptance thresholds, relaxing negative frequency-dependent effects on rewardless species.

Thus, rewardless species may be especially vulnerable to demographic stochasticity, unless they evolve phenological separation from rewarding species. In addition, climate change-induced shifts in seasonal patterns are known to reshape flowering phenology, resulting in changes to co-flowering patterns in plant communities [82]. One effect of such changes may be a widening of the flowering season [82,83]. This may bring species with peripheral phenological niches (those that are limited to blooming at the extremes of a community flowering season) into increased phenological overlap with other species. For early or late-blooming rewardless species, increased phenological overlap may dramatically increase competition with rewarding species for pollinators. Further, the degree to which selection could subsequently reduce phenological overlap may be limited by harsh weather events at seasonal extremes (e.g. [83,84]).

The second major influence of floral reward recognition is that avoidance by flower foragers of signals associated with rewardless flowers should increase as the cost–benefit ratio of visiting such flowers increases (§3c(iii)). Accordingly, selection should favour rewardless plants with floral traits that allow short handling times and easy access to reproductive parts, hence reducing visitation costs. However, there may be circumstances under which the cost of missed detections generally outweighs the cost of false alarms. Under such conditions

(for example, when rewards are rare or difficult to find), selection against complex flowers may be relaxed. It is worth noting that long handling times and complex floral architecture are not uncommon among brood-site mimicking or sexually deceptive rewardless species, which often employ traps (e.g. [85,86]) and which advertise currencies more closely tied to fitness than food.

5. Conclusion

Floral communities are noisy. With this noisiness come limitations for flower foragers, and opportunities for rewardless plants. Floral reward heterogeneity and floral trait overlap limit how effectively foragers can use floral signals to inform their foraging decisions. This limitation provides an opportunity for rewardless species to avoid detection and sanction, and to secure pollination services from foragers. Signal detection theory tells us that the relative costs of missed opportunities (missed detection) versus wasted effort (false alarm) should influence where foragers set their optimal acceptance thresholds, while the degree of floral display trait overlap will affect the magnitude of these costs, and floral resource heterogeneity will affect the accuracy of acceptance thresholds. Together, the effects of these factors on forager behaviour will determine how successfully rewardless species elicit visitation by flower foragers, and hence determine the viability of rewardlessness as a floral strategy. Thus, the foraging efficiency of flower visitors and the mating success of rewardless plants are subject to the vagaries and complexities of community context.

Several longstanding questions remain, and more emerge from our own consideration of this topic. We conclude by highlighting the following unresolved issues, from both the forager's and the plant's perspectives, relevant to the noisy environment in which flower foraging takes place that we consider especially pertinent and exciting.

(a) Forager perspective

1. Foragers' behavioural responses to floral rewards, as well as the cognitive and learning processes underlying them, have mainly been studied with rewarding and rewardless flowers that are (i) easy to distinguish or (ii) identical. We have pointed out here, however, that the problem foragers face in nature is considerably more complex than this. Therefore, experiments in which foragers are faced with rewarding and rewardless flowers that resemble each other rather closely in one or more display traits (colour, odour, etc.) or signal modalities (visual, olfactory, etc.) will provide valuable insights into the mechanisms underlying choice, as well as their consequences. Experiments comparing multiple flower-foraging species will also facilitate an understanding of how cognitive capacities and processes impact foragers' functioning as pollinators.
2. Although nectar is the most common floral reward, there are in fact other resources that foragers seek within flowers, including pollen, oils and even edible 'reward' petals, as well as nest material (resin) and mate-attracting volatiles [87]. Further, some flower-foraging species are searching for more than one of these resources, sometimes at the same time and from the same set of flowers. This is another level of complexity in the plant/pollinator landscape that deserves attention. Do foragers have different acceptance

thresholds for different floral resources? If so, when an individual is collecting two different types of resources on a foraging bout, does it employ two different acceptance thresholds at the same time? This might be quite advantageous, if it were feasible. In particular, foragers seeking pollen (the primary source of protein and lipids for bees) might readily accept nectarless flowers, as pollen-specializing honeybees accept lower quality nectar than nectar-specializing individuals [88]. When that forager is seeking nectar, however, a nectarless flower should probably be avoided if possible. Perhaps surprisingly, the degree to which foragers can learn and manage signal-reward associations for multiple rewards simultaneously may depend upon which reward a forager is searching for at the time of the encounter [89].

3. Nectar-feeding foragers access food in different ways. In flowers with tubular corollas, it is common to see two distinct foraging strategies (both of which may be expressed by an individual forager): foragers may feed 'legitimately' through the flower's opening, or 'rob' through a hole that they or another forager chew through the corolla near the nectary [2]. As legitimate visitors' and nectar-robbers' floral handling strategies are so different, we can predict that they will have different criteria for assessing the value of a flower, and thus different floral assessment costs. Do robbing foragers therefore have different acceptance thresholds than do legitimate visitors?
4. The signal detection theory literature in behavioural ecology has primarily dealt with situations in which there is one class of desirable signallers and one class of undesirable signallers. Viewing floral reward recognition through the lens of signal detection theory highlights a more complex scenario in which there may be multiple classes of signaller (figure 4). Future theoretical and empirical work could investigate how this affects acceptance thresholds, and uncover other contexts in which multiple signaller classes may be present.

(b) Plant perspective

5. The noisy floral landscape that foragers face is in part the result of proximate, uncontrolled variation (e.g. microhabitat differences in water availability that constrain reward production, unequal rates of depletion across the course of the day). However, it is also the outcome of floral trait evolution (e.g. favouring species-specific patterns of reward production and presentation). There is a critical need to explore how the signal detection capabilities of different classes of foragers (including floral enemies: robbers, herbivores and seed predators) have selected for key floral traits. In particular, as we have stressed, only a subset of flower foragers confer the mutualistic benefit of pollen transfer. Different classes of visitors may differ to some extent in their signal detection abilities, e.g. owing to species-specific cognitive capacity, and in their acceptance thresholds, e.g. owing to other available foraging options and thus the cost of missed detections. Might floral traits have evolved that, tapping into these distinct thresholds, differentially attract the beneficial subset of foragers? Many floral traits have not only evolved to attract certain pollinator subsets but to deter others [90], so this is not unreasonable.
6. Small population sizes and restriction to peripheral phenological niches may be challenges that rewardless plants

face as a result of negative frequency-dependent mating success resulting from co-occurrence with abundant rewarding species. As a result, rewardless species may be disproportionately sensitive to extinction relative to rewarding species. In this sense, rewardlessness may, at least in some cases, represent an evolutionary trap. Comparative work is needed to determine whether this is indeed the case. The great phylogenetic diversity and the strong representation of both rewarding and rewardless species in the Orchidaceae and Bignoniaceae may make these lineages especially useful for testing this hypothesis.

(c) Forager–plant integrative perspective

- Flowers may use multiple modalities simultaneously to signal reward status. It is possible that such multimodality makes it easier for flower foragers to detect rewardless flowers, if such flowers tend to overlap with rewarding flowers in only one modality. This raises questions from both the plant's and the forager's perspectives. To what degree do the flowers of rewardless and rewarding flowers differ across multiple display traits? The evidence presented in §2 suggests that separate display traits are often genetically linked. This would limit the degree to which selection can favour a rewarding plant that differs from rewardless species through multimodal signalling. Further, how do flower foragers respond to multiple signals of reward status? While flower foragers can use multimodal signals to improve foraging accuracy (e.g. [91]), they may only use information from one modality [79].
- Rewardlessness has evolved many times in the angiosperms [6]. It should be very informative to revisit its phylogenetic distribution in the light of the signal detection analysis we have presented here. One might explore, for example, the diversity of the floral landscapes in which rewardless species are found, how many other species in their communities share their flower traits; and what sensory modalities are primarily used by the

floral visitors that consistently make mistakes and visit those flowers repeatedly.

As long as floral communities remain noisy—with floral reward heterogeneity and high floral trait overlap—flower foragers will continue to make mistakes and visit rewardless flowers. However, whether rewardlessness will be a viable plant reproductive strategy for a given plant species should depend on the extent to which this noise interferes with foragers' ability to recognize floral signal and use this information to optimize their foraging strategies for floral rewards. Ultimately, signal detection theory should provide insight into when rewardlessness will and will not evolve and persist.

Data accessibility. This article has no additional data.

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Endnotes

¹We acknowledge the distinction between signals and cues—namely, whether a trait represents an adaptation which modifies another organism's behaviour [1]—but do not consider it further in this article. For brevity, and following the convention in the signal detection theory literature, we use the term 'signal' for both. This is justifiable in this article because our focus is on how animals distinguish meaningful information from background noise, regardless of whether that information is carried in a signal or a cue.

²Note that we refer to animals that seek rewards at flowers as 'flower foragers' rather than as 'pollinators'. The term 'pollinator' implies that foraging confers a benefit of pollen transfer to the visited plant, which cannot be assumed without detailed study in the field [2]. Regardless, our discussion of signal detection pertains to all flower-foraging animals, regardless of the effects of their behaviours on plants. Selection, however, can be expected to have acted on signal production primarily to enhance visitation by the set of visitors that do in fact confer benefits to plants (i.e. those that consistently pollinate by their actions). We return to this point in §4.

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