

# 9

## Why are floral signals complex? An outline of functional hypotheses

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### 9.1 Introduction

Plants produce a remarkable variety of displays to attract animals that transfer pollen. These floral displays are usually complex, broadcasting various combinations of visual, olfactory, gustatory, tactile, and thermal stimuli (Raguso 2004a). Even acoustic stimuli may be involved, as in the case of structural nectar guides used by echolocating flower-feeding bats (von Helversen and von Helversen 1999). Yet these sensorially complex advertisements likely evolved from an ancestor that primarily transmitted only chemicals, serving a defensive function (Pellmyr and Thein 1986). The subsequent amplification and elaboration of floral stimuli therefore offers an intriguing opportunity to study signal evolution. However, at present, we know surprisingly little about why floral displays consist of so many elements. This contrasts with progress in other areas: recently, researchers studying topics as diverse as sexual selection, warning displays, animal learning, and

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*Evolution of Plant–Pollinator Relationships*, ed S. Patiny. Published by Cambridge University Press. © Cambridge University Press 2012.

parent–offspring communication have explored the function of signal complexity (Rowe 1999; Candolin 2003; Hebets and Papaj 2005; Partan and Marler 2005).

Researchers studying plant–pollinator interactions, however, have not to date shown a comparable degree of interest in the topic of complex signals, as judged by an analysis of the research literature. An August 2010 search on the ISI Web of Science® database on journal articles published since 1995 returned only two on plant–pollinator topics containing the words “multimodal” and “signal-” in their titles, abstracts, or keywords (those articles being Raguso and Willis 2002; Kulahci et al. 2008). In comparison, the same search returned 59 articles on sexual selection topics.

A related search on bee learning provides further evidence that our understanding of how pollinators process and learn floral signals is based upon single sensory modalities studied in isolation. A search for articles published since 1995 that contain the words “bee” and “learning” returned 268 articles on how bees learn or process unimodal stimuli (olfactory = 142, visual = 112, tactile = 14), whereas only 12 focus on multimodal stimuli. This disparity is striking given that the great ethologist Karl von Frisch first showed that honeybees learn both colors and scents nearly a century ago (von Frisch 1914, 1919).

Not only would pollination biologists benefit from a better understanding of how pollinators interact with the complex floral signal, but such knowledge could also contribute significantly to our understanding of signal complexity in general. The study of plant–pollinator interactions integrates research from many disciplines, and thus is well-positioned to tackle fundamental questions regarding the function of signal complexity. From a proximate perspective, not only is there a wealth of information regarding the sensory and cognitive systems of pollinators (Chittka and Thomson, 2001; Giurfa, 2007), but the means by which flowers produce stimuli used by pollinators are relatively well-understood (Dudareva and Pichersky, 2006; Grotewold, 2006). Moreover, in comparison to animal signalers, plants offer opportunities for manipulative experiments that are often difficult, if not impossible, to run in other systems. For example, it is straightforward to change a display through use of artificial flowers (Makino and Sakai, 2007), through minor alteration of real flowers (Waser and Price, 1985), or through modification of individual components using both selective breeding (Odell et al. 1999) and molecular techniques (Hoballah et al. 2007). In contrast, students of animal communication may be limited to use of fewer and relatively sophisticated techniques, such as the use of robots (Taylor et al. 2008).

Although we are increasingly informed about *how* complex signals work in various plant–pollinator systems, we still know little about *why* they work as they do. We believe that a conceptual framework for the function of floral displays could stimulate research in that area. Here we present such a framework, in the form of testable hypotheses addressing the function of floral signal complexity. First, we describe hypotheses that propose benefits both to the sender (plant) and the receiver

(pollinator). We highlight new research that points towards the role of uncertainty reduction in floral trait evolution. Later, we consider instances in which the benefit of multicomponent signaling accrues mainly to the plant, including situations in which the interests of plant and pollinator are in explicit conflict.

## 9.2 The multicomponent nature of floral stimuli

The suite of stimuli emitted by a typical flower constitutes a complex signal. Although definitions of both terms can vary, we use “signal” and “complex” as described in Hebets and Papaj (2005). Specifically, we follow Markl’s (1983) definition of a signal as “a packet of energy or matter generated by a display or action of one organism (the signaler) that is selected for its effects in influencing the probability pattern of behavior of another organism (the receiver) via its sensory–nervous system in a fashion that is adaptive either to one or both parties.” Much of the literature relevant to complex signaling refers to “multimodal”, “bimodal”, “multiple” “multicomponent” or “composite” signals. We use “complex” as a general term including signals that are multimodal (e.g. color + scent) or generally multicomponent (e.g. color + visual pattern). Aspects of visual complexity include flower color, iridescence, color contrast, intensity contrast, photoreceptor contrast, pattern, shape, size, symmetry, and the architecture of an inflorescence (e.g. Giurfa and Lehrer 2001; Glover and Whitney 2010). Likewise, floral scents are complex blends of volatile organic compounds (Knudsen et al. 2006). Flowers may even transmit olfactory “patterns,” as scents often show a spatial gradient in concentration (Bergström et al. 1995) or vary in composition across floral structures (Dötterl and Jürgens 2005). Additional forms of olfactory complexity relevant to pollinators involve differences in the identity, abundance, and ratio of chemical components (Raguso 2008). Although less commonly studied, both the microtexture of petals (Kevan and Lane 1985) and the 3D morphology of the flower (Heinrich 1979) contribute to tactile complexity; and within the thermal modality, pollinators may perceive and discriminate among different floral temperatures (Whitney et al. 2008; Hammer et al. 2009).

## 9.3 Why are floral signals complex?

### Functional hypotheses

Producing complex displays probably entails costs for plants. Although the metabolic costs of adding a signal to a floral display are largely unknown, several traits that contribute to signal complexity are thought to incur these costs, such as flower size (Galen 1999), and to some extent, floral scent (Helsper et al. 1998; but see Grison-Pigé et al. 2001). Floral display complexity may also attract the attention of

unintended receivers, such as herbivores drawn to floral scent (Theis 2006). What benefits offset these costs to the sender and thereby drives the evolution of complex signals?

Functional hypotheses for signals generally fall into two groups: content-based and efficacy-based (Guilford and Dawkins 1991; Hebets and Papaj 2005). Content-based hypotheses refer to the “what” of a signal. The proposition that different components of a complex signal convey different “messages” is an example of a content-based hypothesis. For example, studies of avian sexual signaling (Candolin 2003) commonly test the hypothesis that different male plumage traits provide females with different kinds of information used in mate choice, e.g. age, nutrition, parasite load, immunocompetence. In contrast, efficacy-based hypotheses refer to the “how” of a signal; that is, how a message might be more effectively transmitted, detected and/or processed using multiple components. Such a function likely accounts for the transmission of both visual and vibratory signals during courtship in wolf spiders: by transmitting both signals, a male is able to maintain a similar rate of courtship success even where transmission in one modality is blocked by darkness or vibration-impeding substrates (Fig 2 in Hebets and Papaj 2005).

Any particular signal is under selection for both content and efficacy; and some explanations for signal function have elements of both content and efficacy. Thus, hypotheses from each of these perspectives are not necessarily mutually exclusive, and an emphasis on the content versus efficacy of a floral signal is ultimately a matter of individual preference. The distinction can be especially subtle when the meaning of a signal is not separable from its contribution to efficacy, as occurs when a signal conveys a quality such as “location.” Yet, even in this case, the content/efficacy framework can still help guide thinking about signal function. For example consider the hypotheses that a floral pattern (1) conveys information about the location of nectar (signal content) and (2) facilitates close-range detection because of strong color contrast (signal efficacy). Both may be true, but a researcher interested in the evolution of honest floral signaling likely finds 1 most relevant, whereas a researcher studying the overlap between floral signals and pollinator visual systems might frame an experiment around 2. Table 9.1 organizes functional hypotheses likely to be relevant to interactions between plants and their pollinators into these categories.

### 9.3.1 Content-based hypotheses

One commonly-cited hypothesis for complex signals is the **multiple messages hypothesis**, which states that different components of the complex signal convey different kinds of information (Møller and Pomiankowski 1993; Johnstone 1996). What messages might the plant convey to pollinators? One component of a floral signal may permit pollinators to distinguish it from competitors (“species

**Table 9.1** A framework of functional explanations for why floral signals consist of multiple components, adapted from reviews of animal communication by Hebets and Papaj (2005) and Rowe (1999).

### Content-based hypotheses

Multiple messages	<i>Multiple signal components convey different information</i>
Floral types	
Species identity	
Reward status	
Reward quality	
Reward type	
Location	
Location of patch within habitat	
Location of flowers within patch	
Location of reward within flower	
Redundant signals	<i>Multiple signal components improve accuracy of information</i>

### Efficacy-based hypotheses

Signal transmission	
Efficacy backup	<i>Multiple signal components facilitate transmission in variable environments</i>
Efficacy tradeoff	<i>Multiple signal components overcome transmission constraints faced by each component independently</i>
Signal detection	<i>Multiple signal components are detected more successfully or quickly</i>
Signal processing	
Parallel processing	<i>Multimodal signals processed more quickly along parallel neural pathways</i>
Perceptual variability	<i>Multiple signal components reach pollinators with varying sensory systems</i>

Table 9.1 (cont.)

Intersignal interaction hypotheses	
Attention-altering	One signal focuses pollinators' selective attention on a second signal
Context	One signal component provides a context for pollinators' response to a second component

identity”), as Wright and Schiestl (2009) have argued for the function of floral scent. Floral identity may allow pollinators to predict handling efficiency – bees may select particular species because they have learned how to extract nectar effectively (Chittka et al. 1999). Another display component could signal the presence of nectar (“reward status”). This information might be conveyed by a different chemical component (Howell and Alarcon 2007; Goyret et al. 2008) or by a visual cue (Thorp et al. 1975; Weiss 1991). Pollinators might also use a different display component to assess the value of the floral reward (“reward quality”) – as in, for example, Raine and Chittka’s (2007a) findings that bumblebees’ (*Bombus terrestris*) innate preference for the color violet corresponds with a higher rate of nectar production by violet flowers. Yet another display component could indicate the kind of reward available (“reward type”), as in the visual or olfactory stimuli associated with nectar (Raguso 2004b) or pollen (Dobson and Bergström 1999). Finally, other display components may be useful in finding a patch of flowers from a distance (Williams and Dodson 1972), a flower within a patch (Hurley et al. 2009), or a reward within a flower, as in the case of floral patterns that function as nectar guides (“location” on different spatial scales) (Waser and Price 1985).

Another content-based hypothesis is the **redundant signals hypothesis** (Hebets and Papaj 2005). The redundant signals hypothesis proposes that floral signals are complex because from the standpoint of signal production (i.e. independent of environmental transmission or receiver processing), any one signal encodes information about the sender imperfectly; producing multiple, redundant, signals, which improves the overall accuracy of the (single) message (Bradbury and Vehrencamp 1998). Redundant signals may thus function as a tactical check on signaler honesty; in mate choice, for example, females may assess multiple male ornaments because faking the production of several quality indicators is thought to be difficult (Candolin 2003).

The equivalent of this kind of “quality control” in plant–pollinator relationships is perhaps best considered in the context of rewardless mimic flowers. These flowers exploit an animal for pollination service but provide nothing in return (Renner 2006). Some rewardless orchids, for example, mimic another flower species that does offer a reward; others mimic a female insect, luring males who attempt to

mate with the flower but succeed only in picking up pollen and transferring it to the next mimic (Schiestl 2005). Transmitting additional signal components that provide pollinators with more information regarding floral identity could facilitate discrimination between rewarding flowers and unrewarding mimics, benefiting both the pollinator and the rewarding plant species. Support for such facilitation in discrimination is found in the bee learning literature. For example, Kunze and Gumbert (2001) found that *B. terrestris* learned more quickly to distinguish between two similar colors of artificial flower (one rewarding, one unrewarding) when they transmitted different scents than when they were unscented or transmitted the same scent. Additionally, in a discrimination learning test, Kulahci et al. (2008) found that *B. impatiens* showed the highest visitation rate to the rewarding flower type when flowers differed in two features (shape and scent) versus a single feature (shape only or scent only). Although these results are consistent with other explanations, one function of transmitting both a visual as well as an olfactory signal may be to provide pollinators with redundant information about floral identity.

### 9.3.2 Efficacy-based hypotheses

Efficacy-based hypotheses for complex signals propose that multiple components allow a plant's message to be more effectively transmitted through the environment and/or more effectively detected or processed by the pollinator.

All signals tend to degrade as they propagate through the environment (Bradbury and Vehrencamp 1998). Transmission-based hypotheses propose that multicomponent signals reduce the effects of environmental degradation of information produced by the sender. One such hypothesis, the **efficacy backup hypothesis**, states that flowers emit multiple stimuli so that under any given set of environmental conditions, at least one will convey information (cf. "robustness" in Ay et al. 2007). For example, flowers may produce both scent and visual stimuli so as to ensure that at least one kind of stimulus is useful, regardless of environmental conditions (Kaczorowski et al. unpublished data). On windy days, when scent is less localizable, visual components may be more useful; on overcast days or in deep shade, when visual stimuli are difficult to discern, scent may function more effectively. Although this explanation for multimodal signals seems highly intuitive, we know of no evidence even in a controlled semi-field situation to support this hypothesis.

The **efficacy tradeoff hypothesis** proposes that different components of the complex floral display solve different challenges in signal efficacy related to transmission or detection. Perhaps no single component can maximize efficacy on all counts, regardless of environmental variability. For example, scent may be more detectable at a distance than visual cues, while a visual cue may better allow a flower to be localized precisely once the pollinator is in the vicinity of the plant.

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A recent study by Streinzer et al. (2009) supports such a scenario for the display of the sexually deceptive orchid *Ophrys heldreichii*. *O. heldreichii* transmits an olfactory signal that mimics the scent of female solitary bees and is detected by males at long distances (Kullenberg and Bergström 1976). However, the flower also has a conspicuously colored perianth. By comparing the responses of male long-horned bees (*Tetralonia berlandi*) at different distances from intact flowers versus flowers with the perianth removed, Streinzer et al. 1990 showed that presence of the color signal reduced search time when the bee was within 30 cm of the flower; and at this close range, disruption of the olfactory signal (increasing wind speed) had no effect on the bees' ability to locate the flower. At greater distances, however, removal of the perianth did not affect searching behavior, but search time slowed with increasing wind speed. Ultimately, the range at which signals in each modality operate may depend greatly upon pollinator ecology and sensory physiology (Giurfa et al. 1996; Spaethe et al. 2001; Balkenius et al. 2006) as well as plant species, as some flowers transmit more scent than others, and some are less visually detectable than others.

The environment not only degrades a signal but is also a source of competing signals and stimuli that can obscure a floral display. **Detection-based hypotheses** for floral complexity propose that multicomponent signals facilitate detection of the signal against this background noise. In this case, the benefit of signal complexity relates to the enhanced efficacy of detection by the sensory system of the pollinators, rather than enhanced transmission through the environment. Within the visual modality, floral size, color, and brightness are all likely to influence detectability (Chittka and Spaethe 2007) and thus a combination of these may convey additional benefits. Adding a signal in a different sensory modality can also increase detectability: human-based psychophysical research suggests that multimodal stimuli are detected both more quickly and successfully than unimodal stimuli (Stein and Meredith 1993; Rowe 1999). The benefit of increased detection is perhaps self-explanatory; additionally, even small increases in speed of detection may contribute to a higher nectar collection rate (Burns 2005), a factor that can directly affect reproductive success in species that make countless foraging decisions daily, such as bumblebees (Heinrich 1979; Pelletier and McNeil 2003).

Once a signal has been successfully transmitted and detected, it is processed by the receiver's nervous system. Could complex floral signals be processed more effectively than simple signals? The **parallel processing hypothesis** proposes that a complex signal, whose components are processed in parallel, conveys information more effectively than a signal that attempts to transmit the same amount of information in a single channel (modality or component). Parallel processing refers to the capacity of a modularized nervous system to process multiple streams of information more or less simultaneously, rather than sequentially. If complex



stimuli are processed along parallel neural pathways, then use of multiple components may allow receivers to process a greater amount of information without sacrificing processing speed (Hebets and Papaj 2005). Even within one sensory modality, aspects of signals may be processed along parallel circuits, as is the case for visual processing of movement and color in mammals (Livingstone and Hubel 1988) and olfactory processing in many insect species (Galizia and Rossler 2010). Of course, information in different modalities may be processed at different speeds: humans for example, process an auditory stimulus 40–60 ms more quickly than a visual stimulus (Stein and Meredith 1993). A test of this hypothesis would thus require studying in more detail the decision times of receivers in response to multi-component and single-component signals. If all components of a signal have to be processed in order to make a correct decision, then total decision time when components are processed in parallel should be similar to the slowest of the individual components (Thomas 1996; Kulahci et al. 2008). Alternatively, when components are processed in series, total decision time would approximate the sum of the decision times for each component or modality separately. On the other hand, if processing only one component of the complex signal is sufficient to make a correct decision, then total decision time under parallel processing should approximate that of the component that can be processed fastest, whereas under serial processing decision time would be determined by which component is analyzed first (and thus not necessarily the fastest component).

Finally, complex floral displays might be a response to **perceptual variability** among receivers (Hebets and Papaj 2005). It is well-established that pollinators show variability in sensory acuity both within and across species. For example, bumblebees of different sizes (Spaethe and Chittka 2003; Spaethe et al. 2007) and *M. sexta* reared on different quality larval diets (Goyret et al. 2009) show different sensitivities to visual and olfactory floral stimuli. Production of a multi-component signal might thus allow a flower to attract a wider range of pollinators. A recent experiment suggests that this function could apply as well across species: Muchhala et al. (2008) found that even though bats transfer the most pollen to the flowers of the tropical shrub *Aphelandra acanthus*, its flowers transmit a sweet scent attractive to hawkmoths, and also remain open during the day, attracting (visually-oriented) hummingbirds with a bright yellow color. In this case, the ability to attract hummingbirds as well as bats may reflect the value of pollen quality as well as quantity: 73 % of pollen transferred by bats was heterospecific, compared to only 6 % of the pollen brought by hummingbirds (Muchhala et al. 2008).

### 9.3.3 Intersignal interactions

Often, the function of one signal may include altering the receiver's response to another signal (Hebets and Papaj 2005). For example, Kunze and Gumbert (2001) also reported that bumblebees learned to distinguish between two similar colors of

flower more quickly when the flowers transmitted the same scent than when they were both unscented. Thus, beyond transmitting information about floral identity, the mere presence of floral scent affected the bees' response to visual stimuli. Such intersignal interactions can be understood within either an efficacy framework (e.g. one signal enhances the detection or processing of another), or a content framework (e.g. the meaning of one signal depends upon the presence of a second signal).

One efficacy-based hypothesis that involves an intersignal interaction relates directly to a cognitive process known as selective attention (Smith 1996; Dukas 2002). The **attention-altering hypothesis** proposes that one component facilitates detection of a second component by directing a receiver's attention selectively to that component. As with any explanation based on attention, this hypothesis implies that there are constraints on the pollinator's sensitivity to particular stimuli; in the absence of such constraints, the pollinator would always be in a state of maximal sensitivity to all floral stimuli at once. For example, a floral scent may focus a pollinator's attention on visual floral stimuli specifically, such as color or shape, or trigger a search image associated with a particular flower type (Goulson 2000). A testable prediction of this hypothesis is that when a floral scent is detected, a pollinator trades sensitivity to visually based predatory stimuli off against sensitivity to visually based floral stimuli. Or, one could test this prediction in nocturnally foraging moths, asking whether floral scent affects the ability to detect the ultrasound of insectivorous echolocating bats (Skals et al. 2003).

Some evidence that complex signals are better at capturing the attention of pollinators comes from the literature on flower constancy. Flower constancy refers to the tendency of a pollinator to visit one floral type even when other equally rewarding flower types are available. One explanation for flower constancy involves a constraint on the capacity of pollinators' working memory to contain multiple flower types (Chittka et al. 1999). Working memory (information stored for a short duration), and attention (information processed moment-to-moment) are inexorably linked (Dukas 2002). In support of the connection between limited working memory and constancy, field observations show that bees are more likely to be constant (choose a similar flower type) within a few seconds of leaving the preceding flower (Chittka et al. 1997), a timespan during which the last-visited flower type would be stored in working memory. Interestingly, bees show increased constancy as floral signal complexity increases (Gegear 2005; Gegear and Lavery 2005), a finding that would be consistent with a complex floral signal occupying more of the bees' working memory capacity than a relatively simpler signal.

A second, content-based, form of interaction is the **context hypothesis** (Hebets and Papaj 2005), which specifies that one component of a display provides the context in which the pollinator interprets another signal. Research in experimental psychology has shown that, in addition to learning to associate a stimulus with reward, subjects also learn "background" stimuli that provide context; subsequent

removal of these cues can impair performance (Shettleworth 1998; Skow and Jakob 2005). For example, all pollinators encounter or learn stimuli in situations other than foraging – when locating and selecting host plants (e.g. Weiss and Papaj 2003; Goyret et al. 2008), home sites (Fauria et al. 2002), or mates. It is possible that one component of a floral display helps pollinators to distinguish between different contexts, triggering them to interpret and learn other floral signals. For example, bumblebees land more frequently on artificial flowers that transmit scent (Leonard et al. in press), and Giurfa et al. (1995) found that flower-naïve honeybees would not land on unscented artificial flowers. These findings suggest that scent may provide a foraging context, priming pollinators to learn or recall floral stimuli (Raguso and Willis 2002; Goyret et al. 2007). A test of this hypothesis might include comparing the performance of individuals trained to learn colors in two contexts, for example, at the colony entrance versus at feeders (as in Worden et al. 2005) when a scent is present in one context versus when both are unscented.

Beyond helping pollinators to identify stimuli as belonging to a “foraging” context, floral stimuli may provide a context for learning and remembering other stimuli associated with floral identity. Psychological research suggests that forgetting may be caused in part by changes in background stimuli (i.e. the “context-change account of forgetting”, Bouton et al. 1999); in an ecological setting, the background stimuli experienced by pollinators will vary substantially across time and space. If one component of the floral display (e.g. scent) was transmitted relatively constantly and consistently across different environments, then this component might facilitate recall of a second signal (e.g. color) by recreating the context in which that signal was first learned.

## 9.4 Uncertainty reduction and the complex floral signal

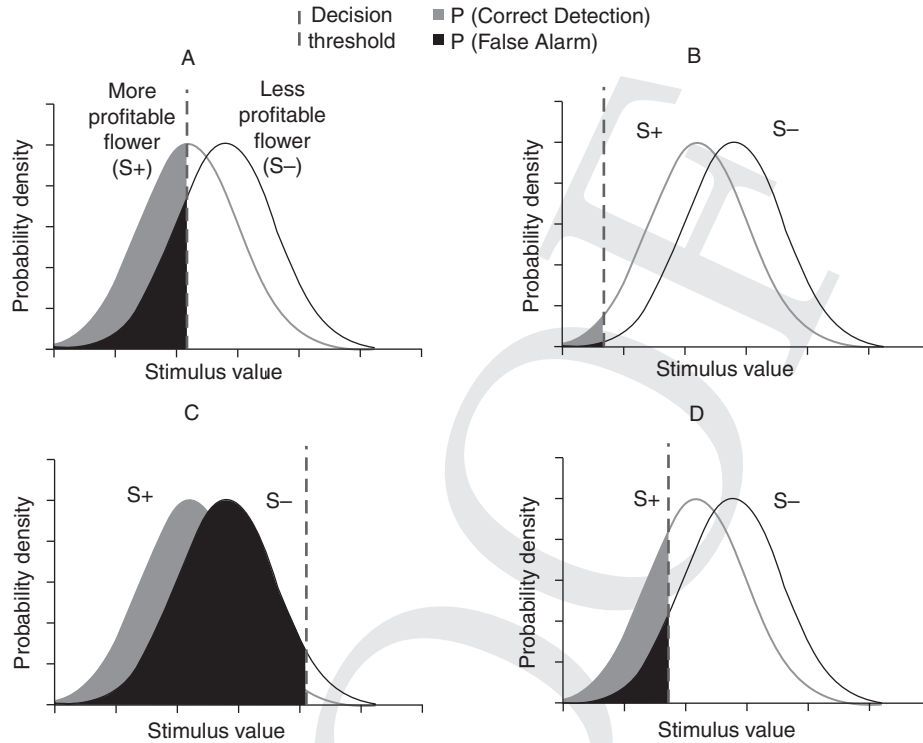
A number of the hypotheses in our framework suggest that the floral signal is an uncertain one from the pollinator’s perspective. Pollinators searching for floral rewards may experience uncertainty at several levels, such as in locating a flower against a background of distracting stimuli (Goulson 2000) or in distinguishing among flowers of similar species. For example, in their survey of flowers visited by bumblebees (*B. terrestris*) in Würzburg (Germany), Raine and Chittka (2007b) report an average nectar collection rate (microliters/24 hours) of 2120 for *Salvia pratensis* and 520 for *S. verticillata*. A bee might therefore benefit by selectively visiting the more profitable species, *S. pratensis*. However, flowers of these two species present rather similar visual and tactile stimuli: both transmit strongly in bee UV–blue color space (Raine and Chittka 2007b), both are bilaterally symmetrical flowers with landing platforms, and both are arranged on vertical inflorescences. After gaining

experience with the two species, what happens when a bee enters a new patch and locates a vertical inflorescence of UV–blue, bilaterally symmetrical flowers?

In a general sense, the answer depends upon the bee's level of uncertainty in discriminating between the two floral types, as well as the costs and benefits of landing on each. Uncertainty can be influenced by several factors: for example, the degree of signal overlap between the two flower types, environmental stimuli that obscure transmission of the floral signal, and internal "noise" in the bee's sensory processing system. Signal Detection Theory (SDT) (Green and Swets 1966; Wiley 2006) provides a framework for predicting pollinators' behavior in the face of this signal uncertainty. SDT can also be invoked to help explain why floral displays are complex signals.

A first assumption is that, from the perspective of the pollinator, uncertainty in any form is likely to be costly. It may cause pollinators to take longer to make decisions; for example, bees take longer to make landing decisions as the difficulty of a discrimination task increases (Chittka et al. 2009). In addition to time costs, there may be costs associated with errors in choice. These may be errors both of commission (e.g. "false alarm": visiting an unprofitable flower type) and omission ("missed detection": failing to land on a profitable flower type). In an SDT framework, we can model two similar flower types as transmitting overlapping distributions of stimuli along some perceptual axis, and assume that pollinators use a threshold-based rule to decide which stimuli to land upon (Fig 9.1a). In that case, the probability of false alarm and correct detection ( $=1 - p[\text{missed detection}]$ ) are related: a pollinator may be conservative, landing on few flowers and thus experiencing a low rate of false alarms but low rate of correct detections (Fig 9.1b); alternatively, a "cavalier" pollinator might land on almost all stimuli encountered, yielding a high rate of correct detections but also a high rate of false alarms (Fig 9.1c). Both false alarms and missed detections are not only potentially costly to the pollinator but may be costly to the plant as well. In general, any factor that causes pollinators to be less likely to locate, contact, and transport pollen to conspecific plants represents a potential loss of the plant's reproductive success.

Recently, researchers interested in SDT and floral signal evolution have utilized a classical psychophysical "peak shift" approach (Hanson 1959; Shettleworth 1998) to explore how uncertainty in distinguishing between flowers that differ in reward value affects where a pollinator should optimally locate its decision threshold. In these experiments, the optimal decision threshold minimizes the probability of false alarms while maximizing the probability of correct detections. In a peak shift experiment, subjects gain experience with two similar stimuli that differ in reward value. One stimulus, the "S+" provides a reward; the other stimulus, "S–" is unrewarding or punishing. During a test phase, subjects' responses are measured across a wide range of stimulus values. Rather than responding most strongly to the S+ value, subjects' strongest ("peak") response to test stimuli



**Fig 9.1** Pollinators discriminating between similar flowers that differ in reward value (S+ versus S-) face a classic signal detection problem. (A) When flower types transmit overlapping distributions of stimuli, pollinators may use a decision threshold to decide which stimuli to land upon. Regardless of where the decision threshold is located, pollinators will face a probability of making a false alarm (landing on S-, the less profitable flower) as well as a probability of correct detection (landing on S+, the more profitable flower,  $=1 - p[\text{missed detection}]$ ). (B) A pollinator might use a conservative decision threshold, not landing on most stimuli that it encounters. In this case, false alarms are reduced but correct detections are reduced as well. (C) A cavalier pollinator might land upon almost all stimuli it encounters, ensuring a high probability of correct detection, but a high probability of false alarms as well. (D) When false alarms are costly, relative to missed detections, a slightly conservative decision threshold minimizes false alarms while maximizing correct detections. This threshold is not located at the most common value of the rewarding flower (as in A) but is shifted in a direction away from the S-.

is often observed to be a novel stimulus value that is shifted in a direction away from the S- value. Lynn et al. (2005) used SDT to develop a functional account of the peak shift phenomenon: given uncertainty in distinguishing between S+ and S-, subjects' observed preference for a novel stimulus value (that is more distinct from S- than S+) can be interpreted as a strategy adopted to reduce the risk of false alarm (incorrectly responding to S-) (Fig 9.1d).

These expectations have relevance for plant–pollinator interactions: Lynn et al. (2005) showed that bumblebees (*B. impatiens*) trained to discriminate between a rewarding S+ and punishing S– that are similar colors of artificial flowers show peak shift when offered a wide array of floral colors. Moreover, the degree of the shift varied in relation to the nature of the relative costs of false alarms and missed detections. Wright et al. (2009) similarly demonstrated that honeybees show peak shift in response to olfactory stimuli (S+ and S– were two scents presented as blends in two ratios). In both these experiments, rather than responding most strongly to a floral signal they had learned was rewarding, bees instead preferred a novel stimulus value that was more different than S–. In ecological terms, this bias suggests that bees who experience uncertainty in discriminating between two similar floral signals associated with different payoffs (e.g. *S. pratensis* versus *S. verticillata*, or a model and its Batesian mimic) become conservative in their decision-making, seeking out not the average (or most common) signal value of the model (S+) but other, rarer values of the floral signal, in order to minimize the chances of visiting the less profitable flower. Of course, these rarer signal values may not even be the same species as S+; if not, then pollen transported from the model species is wasted.

In both Lynn et al. (2005) and Wright et al. (2009), the stimuli that bees encountered differed in only a single aspect (color or blend ratio). One way to explore whether more complex floral signals function to reduce pollinators' uncertainty would be to compare the magnitude of bees' peak shift in response to one stimulus type (e.g. color) when another stimulus (e.g. odor) is added to the floral signal. To this end, Leonard et al. (in press) performed a peak shift experiment on two groups of bumblebees. For one group, floral stimuli differed only in color; for another group, floral stimuli differed in both color and scent. While bees trained and tested on floral stimuli that differed in color showed a color preference shift away from the S– color, bees trained and tested on stimuli that differed in both color and scent did not. Bees thus behaved as though more certain about the color of the rewarding flower type when in the presence of floral scent. Intriguingly, bees showed this enhanced ability to identify the color of S+ without showing evidence that they learned the identity of the odor associated with it. These findings suggest an intersignal interaction, whereby bees acquire better information about color in the presence of floral scent. While the process underlying this intersignal interaction has yet to be determined, it is so far consistent with either the attention-altering or the context hypothesis.

## 9.5 Sender–receiver conflict: a third axis of explanation for multicomponent floral signals

Uncertainty reduction hypotheses generally assume that the complexity of a signal is mutually beneficial to sender and receiver. However, this is not always the



case. In reality, plant-pollinator interactions are distributed along a continuum from mutualism to exploitation (Bronstein, 1994). In the gray area between the two extremes, we may find that different components of the signal have different patterns of joint fitness consequences for pollinator and plant. For example, flowers often transmit stimuli that attract pollinators in other contexts, as reviewed recently by Schaefer and Ruxton (2010) and Schiestl et al. (2010). Such sensory exploitation is thought to be the case with floral scent. Many components of floral scent also play a role in within- (pollinator) species communication (e.g. benzaldehyde, geraniol, linalool), and Schiestl (2010) has argued that this duality in function is not coincidence but, in many cases, a plant's exploitation of a pre-existing pollinator sensory bias for a chemical compound. Along a similar vein, Biesmeijer et al. (2005) have suggested that several characteristics of floral patterns (dark central spots, radiating lines) exploit a visual preference that evolved in the context of locating an entrance to a nest or burrow. These hypotheses suggest that plants may benefit by adding a signal that pollinators already find attractive; such a signal could improve the detectability of the flower, but potentially reduce pollinator fitness if attraction to the signal is strong enough to allow the plant to limit rewards.

Yet another example of potential sender-receiver conflict was put forward recently by Kessler and colleagues for the *Nicotiana*-hawkmoth interactions. Kessler et al. (2008) used transgenic *Nicotiana* plants to show that one component of the floral signal (benzyl acetone) served as an attractant for hawkmoth pollinators. This component is presumably of benefit both to hawkmoths, which receive a nectar reward, and to *Nicotiana*, which obtains pollination services. However, another chemical component of the floral signal, nicotine contained in the nectar, acts as a repellent. In field assays, flowers of transgenic plants lacking this component experienced a higher visitation rate than those of control plants. The authors argue that the repellent effect of nicotine thereby enhances plant fitness by promoting outcrossing. At the same time, the repellent probably reduces pollinator fitness by reducing the rate at which nectar is collected. Thus, one floral component (benzyl acetone) may be mutualistic, while the other (nicotine) is exploitative. This example implies that the complexity of the floral signal can effectively be a consequence of the complexity of the evolutionary game played between plant and pollinator. We thus propose that, in addition to content and efficacy, a third "manipulation" perspective on signal complexity that considers the sometimes-coincident, sometimes-conflicting interests of plant and pollinator.

## 9.6 Conclusions

Floral signals act in concert to influence pollinator behavior, yet pollinators' responses to these signals are usually studied in isolation. Without more research on complex, multimodal signaling by flowers, our understanding of floral evolution

is incomplete: in many cases the function of one signal cannot be fully understood independently from another signal. Moreover, the study of floral complexity offers a new perspective on both the maintenance of pollination mutualisms and the relationship between signal complexity and receiver uncertainty. With the goal of spurring new research, we end this review with some open questions for plant–pollinator researchers intrigued by the complexity of floral displays to consider.

**What are the production costs of floral complexity?** Most research to date focuses on the benefits of floral signal complexity in terms of pollinator learning and decision-making. Yet floral displays are costly to produce and possible costs of complexity have not been quantified. Although Bradbury and Verhrencamp (1998) provide a framework describing the costs associated with signal production in different sensory modalities by animals, we know of no equivalent review covering plant signalers. Such an overview could provide interesting points of comparison. For example, what are the relative costs of a simple versus complex display, or of increasing the complexity of a display relative to changing the quality or quantity of reward? How can we measure the cost of adding a component/modality, relative to increasing signal strength in the same modality?

**What advantages do multimodal signals offer plants in terms of dynamic signaling?** Signals are not static entities, but vary over time and space. Among animal signalers, signal components of different modalities vary at different scales (Bradbury and Verhrencamp 1998), for example, a visual signal is generally modulated more rapidly than a chemical signal. But do these modality-specific expectations hold true for complex floral signals? In flowers, at least, both visual and olfactory signals can be changed quite rapidly (Weiss 1991; Knudsen et al. 2006). Moreover, could the use of a multimodal signal allow plants to adjust their signaling depending on environmental conditions, such as producing more scent under low light levels? Recent research suggests this kind of functional flexibility in animal signalers (Cheroske et al. 2009), but to our knowledge this possibility has not been directly explored in plants, although data exist regarding environmental influences on signal production (Jakobson and Olsen 1994). Given the recent interest in plants' induced responses to herbivory (Kessler et al. 2010), the potential for multimodal signals to modulate pollinator attraction seem to us to be a wide-open area of research.

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