

Forget-me-not: Complex floral displays, inter-signal interactions, and pollinator cognition

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Abstract Flowers are multisensory displays used by plants to influence the behavior of pollinators. Although we know a great deal about how individual signal components are produced by plants and detected or learned by pollinators, very few experiments directly address the function of floral signal complexity, i.e. how the multicomponent nature of these signals benefits plant or pollinator. Yet, experimental psychology suggests that increasing complexity can enhance subjects' ability to detect, learn and remember stimuli, and the plant's reproductive success depends upon ensuring that pollinators learn their signals and so transport pollen to other similar (conspecific) flowers. Here we explore functional hypotheses for why plants invest in complex floral displays, focusing on hypotheses in which floral signals interact to promote pollinator learning and memory. Specifically, we discuss how an attention-altering or context-providing function of one signal may promote acquisition or recall of a second signal. Although we focus on communication between plants and pollinators, these process-based hypotheses should apply to any situation where a sender benefits from enhancing a receiver's acquisition or recall of information [*Current Zoology* 57 (2): 215–224, 2011].

Keywords Multimodal signal, Learning, Attention, Bee, Context, Flower

1 Introduction

What benefit does a multi-component display offer senders or receivers, when a simpler one might be less costly to produce? Over the past decade, interest in this question has steadily grown among researchers studying communication in a wide variety of different contexts (rev. in Candolin, 2003; Hebets and Papaj, 2005; Partan and Marler, 2005). As a result, researchers now have relevant models of optimal signal design and decision-making (e.g., Ay et al., 2007; Bro-Jørgensen, 2010; Fawcett and Johnstone, 2003; Hutchinson and Gigerenzer, 2005) as well as a literature that defines (and continually refines) empirically testable hypotheses for signal complexity. However, the vast majority of this work involves animal signalers, as evidenced by an ISI Web of Science® search for journal articles containing both the words “multimodal” and “signal-” in their titles, abstracts, or keywords (Fig. 1). Plants, perhaps the most familiar complex signalers, have not received the same functional scrutiny (rev. Leonard et al., in press). Yet, angiosperm flowers are a quintessential example of how the evolution of a complex signal is directed by the behavior of other species. A typical flower is a multi-sensory billboard (Raguso, 2004), which uses a dazzling variety of stimuli to attract and reward animal visitors that transfer the plant's male gametes (pollen) to

and from conspecific flowers. Even a casual visual comparison of the flowers produced by animal- vs. wind-pollinated plants (Fig. 2) underscores how this

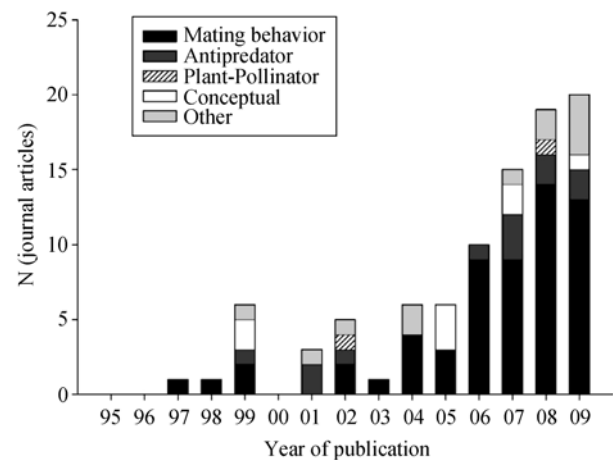


Fig. 1 Results of an August 2010 search on the ISI Web of Science® article database for journal articles since 1995 on animal behavior topics that contain the words “multimodal” and “signal-”

Papers were assigned to one of five categories: mating behavior (female mate choice, intrasexual competition); interactions between predators and prey; experiments involving pollinator species' response to floral signals; literature reviews, conceptual frameworks or theoretical models. Papers categorized as “other” involved studies of intraspecific communication that did not easily fall into one of the other categories.

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Fig. 2 Animal-pollinated wild flowers of the Sonoran desert display a variety of visual and tactile stimuli

A. *Lupinus sparsiflorus*. B. *Streptanthus carinatus*. C. *Salvia columbariae*. D. *Encelia farinosa*. E. *Penstemon parryi*. F. *Mentzelia jonesii*. In contrast, wind-pollinated plants present simpler flowers that lack bright colors and patterns. G. *Cyperus* sp. H. *Pennisetum* sp. I. *Avena* sp.

communicative function has shaped multiple floral traits: wind-pollinated flowers, even those derived from animal-pollinated ancestors, generally produce smaller flowers that are usually unscented, unpatterned, and drab in color (Ackerman, 2000; Culley et al., 2002).

Apart from the familiar visual and olfactory signals, animal-pollinated flowers transmit stimuli that are tactile (e.g., petal microtexture: Kevan and Lane, 1985; 3-D architecture: Heinrich, 1979), gustatory (e.g., Kessler et al., 2008), thermal (rev. Raguso, 2004) and acoustic (i.e., structural nectar guides used by bats: von Helversen and von Helversen, 1999). Considerable signal complexity exists within each of these sensory modalities as well: visual signals vary in aspects such as color, brightness, contrast, size, pattern, iridescence, and symmetry (e.g. Waser and Chittka, 1998). Similarly, scents vary in composition, ratio, and abundance (rev. Raguso, 2008); flowers even present olfactory patterns, as scents are often produced along a gradient or vary in type across different flower regions (rev. Effmert et al., 2006).

Until recently, most research on the connection between plant signals and pollinator behavior has focused on single sensory modalities (rev. Leonard et al., in press). Indeed, pollinators' ability to associate floral stimuli with rewards has contributed to several now-classic studies on learning and memory (von Frisch, 1914-1915; reviews in Giurfa, 2007; Papaj and Lewis, 1993). Among bees, for example, much is known re-

garding visual processing of color, symmetry, and pattern (rev. Giurfa and Lehrer, 1999); similarly, classical conditioning of the proboscis extension reflex (PER) has allowed researchers to explore olfactory discrimination and processing pathways in great detail (rev. Chittka and Raine, 2006; Smith et al., 2006; Galizia and Menzel, 2000). From the standpoint of floral signal production, sensory modalities are most commonly researched separately (e.g. Dudareva and Pichersky, 2006; Grotewold, 2006).

Researchers who study pollinator behavior are increasingly interested in multicomponent floral signals, but often focus on how individual components are learned, rather than the benefit of complexity per se. For example, when forced to prioritize among previously rewarded stimuli, honeybees select scent over color and color over shape (Gould, 1993). Yet, rather than being perceived separately, visual and olfactory signals often interact to attract pollinators, as occurs during nectar foraging in the hawkmoth *Manduca sexta*. The moth is more likely to approach a visual signal than an odor source (Raguso and Willis, 2002, 2005), but both signals are necessary to elicit the full sequence of nectar feeding (Goyret et al., 2007). This inter-signal interaction can itself depend upon the timing and order of signal exposure: *M. sexta* use an odor plume to orient towards a visual target, but a brief exposure to odor also enhances their responsiveness to the visual signal (Goyret et al., 2007).

Thus, we know a great deal about how floral signals are produced, as well as how pollinators detect and learn these signals. We also know that components of the floral signal may be costly, both metabolically (rev. Galen, 1999) as well as ecologically (e.g., floral scent can attract herbivores: Theis, 2006). What, then, is the function of floral signal complexity? Here we develop hypotheses regarding the potential fitness benefit of a complex signal to both plants and pollinators. We focus on hypotheses that involve the potential for signal complexity to facilitate pollinator learning and memory, although other types of explanations are also possible. Indeed, in a forthcoming review (Leonard et al., in press), we consider functional hypotheses that do not depend on learning, such as the possibility that signals function as "backups" that allow the pollinator to locate the plant under variable environmental conditions (e.g. scent facilitates location on cloudy days; color facilitates location in windy conditions), or allow the plant to attract different species of pollinators with disparate sensory physiologies.

First, we review the evidence that plants and pollinators benefit from pollinator learning; next we describe three testable hypotheses (attention-triggering, attention-consuming, context) that explain how signals might interact to facilitate pollinators' learning to identify a rewarding flower type. Importantly, our linking of signal complexity and receiver cognition has relevance for interactions other than those between plants and pollinators— we suggest that these hypotheses apply to any situation where senders benefit from facilitating a receiver's ability to learn or remember a signal. Such cognitive enhancement might function in complex signaling during anti-predator displays (Rowe and Guilford, 1992), mate recognition (e.g., Roberts et al., 2010) and establishment of territories (Stamps and Krishnan, 2001).

2 Fitness Benefits of Pollinator Learning

Learning about floral stimuli has fitness consequences for both plants and pollinators. From the plant's perspective, a well-learned signal should increase the rate at which the pollinator will transport its pollen to a conspecific flower (Chittka et al., 1999). If learning promotes selective foraging, then plants may also benefit from receiving less heterospecific pollen, which can interfere with reproduction (rev. Lewis, 1993). From the pollinator's perspective, the ability to accurately identify profitable flowers should promote foraging efficiency. Not only do plant species differ greatly in the value of nectar rewards (e.g., Raine and Chittka, 2007), but many pollinators are also at risk of deception by Batesian mimics that offer no reward yet take time and energy to visit (rev. Renner, 2006; Schiestl, 2005). Learning about flowers can also involve a temporal component (Gould, 1987; Zhang et al., 2006), as the nectar availability of a particular species often changes over the course of a day or a season (Heinrich, 1979). Spatial memory can also be involved, as pollinators may learn the location of a rewarding patch of flowers and return repeatedly to it (e.g., Healy and Hurly, 2001).

A recent experiment by Raine and Chittka (2008) demonstrates the fitness benefits of pollinator learning: first, the researchers established that 12 different bumble bee *Bombus terrestris* colonies differed in how quickly foragers learned to discriminate between two colors of artificial flowers in a laboratory setting. Next, the authors allowed these colonies to forage freely outdoors on local plant species, while measuring each colony's nectar collection rate. In bumble bees, nectar collection rate contributes directly to colony-level repro-

ductive success, i.e. the number of queens and males produced (Burns, 2005; Pelletier and McNeil, 2003). The authors found that colonies whose foragers learned the laboratory-based color discrimination task more quickly also showed a higher nectar collection rate in the field— in fact, the fastest- and slowest-learning colonies' nectar collection rates differed by 40%. While this evidence is so far correlative, it is consistent with an enhanced ability to learn or discriminate among flower types translating into increased reproductive success.

3 Floral Strategies to Facilitate Pollinator Learning

What strategies might plants use to ensure pollinators learn and remember them? One option might be to increase the quality or quantity of reward, as pollinators generally show faster learning and longer retention of floral stimuli associated with higher reward values (e.g., Buchanan and Bitterman, 1988). Potential constraints on increased reward value include the cost of nectar production (Pyke, 1991), as well as the observation that pollinators may not transport pollen as far after experiencing a high value reward (Chittka et al., 1997; Dukas and Real, 1993). Another possibility might be to increase the distinctiveness of one signal, relative to co-flowering species, as pollinators are better at discriminating between more distinct floral stimuli (color: Dyer and Chittka, 2004; scent: Guerrieri et al., 2005). Or, a plant might facilitate learning by amplifying a single signal component (e.g. increasing size, brightness, or scent concentration), enhancing learning or memory by increasing its signal value against background noise (rev. Shettleworth, 1998).

Alternatively, or in addition, a plant might facilitate pollinator learning by producing a more complex floral display. For example, bumble bees *B. terrestris* learn to discriminate between rewarding vs. unrewarding artificial flowers more quickly when they differ in both color and scent (Kunze and Gumbert, 2001) rather than only color or only scent; bees are also more accurate when flower types differ in both color and shape (Dyer and Chittka, 2004) rather than color alone. Likewise, research on compound conditioning shows that after honeybees learn to respond to two signals (e.g., color and scent) separately, they respond more strongly to both combined than to either alone (Couvillon and Bitterman, 1980). In a recent study, Kulaheci et al. (2008) found that complex floral signals increase foraging efficiency. The authors compared the decision-making of bumble bees *B. impatiens* foraging on artificial flowers differing ei-

ther in a single component (either scent only or shape only) or in two components (both scent and shape). During training sessions, bees learned that one flower type offered a reward (sucrose), and the alternative type was unrewarding (water). In a test phase, relative to bees offered flowers differing in a single aspect, bees whose flowers differed in both shape and scent demonstrated a higher visitation rate to the rewarding flower type.

4 Independence vs. Interaction: How do Complex Signals Promote Learning?

There are two basic ways in which complex signals might promote learning and memory. First, signals may act independently to facilitate learning. For example, scent and color may be two independent means by which a pollinator discriminates between floral types. If both signals independently convey information about floral identity (e.g., a rewarding flower type transmits Color A + Scent A, and an unrewarding flower type transmits Color B + Scent B), then pollinators may make more accurate choices when they can sample both of these components rather than a single component (e.g., only Color A vs. Color B). The additional component simply provides more information about floral identity. This explanation resembles the “redundant signals” hypothesis (Hebets and Papaj, 2005), but with special emphasis on learning and memory. A test of this hypothesis would involve showing that pollinators learn both the color and scent of rewarding vs. unrewarding flower types, and show a pattern of responses to colors and scents that suggests they have learned the two as a combination (e.g., after training to flower types in example above, Color A + Scent A is preferred to Color A + Scent B or Color B + Scent A).

Secondly, facilitation of learning may involve inter-signal interactions, whereby one signal component facilitates the receiver’s learning of other component (s) (Hebets and Papaj, 2005). For example, research by Rowe and Guilford (1996) has shown that chicks *Gallus gallus domesticus* learn an aversion to aposematically colored food better when discrimination training occurs in the presence of pyrazine, a common chemical component of insect warning signals. This effect of pyrazine on learning is only observed when the unpalatable food is aposematically colored. Pyrazine may thus focus the chicks’ attention on particular colors, or provide a context for learning specific food-palatability associations

(Hebets and Papaj, 2005).

A recent experiment suggests that such inter-signal interactions may be key to understanding complex floral signal function. We found that bumble bees that learn to discriminate rewarding and unrewarding colors in the presence of floral scent behave as though more certain about the distinction between the colors than do bees that learn in the absence of scent (Leonard et al., 2011). Using a psychophysical “peak shift” approach, we first trained bees to visit artificial flowers of a particular hue (green, rewarding with sucrose) and to avoid flowers of a slightly different hue (blue-green, punishing with saltwater); in a test phase, we recorded how often bees landed upon a wide range of floral hues (ranging in regular increments from yellow-green to blue, and including both training hues). When flowers were unscented, bees did not land most frequently on the green hue rewarded during training, but instead preferred to land on a novel hue (a yellowish-green) that was even more distinct from the blue-green hue associated with punishment. This shift in peak preference away from the rewarding color suggests that bees were uncertain about the difference between rewarding and punishing colors, even after training. They were consequently conservative in their landing responses, so as to minimize the possibility of mistakenly landing on the green-blue hue.

Interestingly, when we repeated the experiment using scented artificial flowers and new subjects, bees showed a peak landing preference for the exact green hue rewarded during training, indicating they were more certain about the difference between rewarding and unrewarding colors, and thus perceived less risk of mistakenly landing on the green-blue hue associated with punishment. Intriguingly, abolishing peak shift did not involve bees having learned the identity of the scent associated with the rewarding hue, because in this experiment they did not do so to a significant degree. In this case, the floral scent served mainly to facilitate color learning (see also Kunze and Gumbert, 2001); this finding is the first, to our knowledge, to show that a signal in one modality (scent) allows a pollinator to gain better information about a signal in a second modality (color).

Several recent reviews highlight the importance of understanding inter-signal interactions. However, since their perspectives are either somewhat more phenomenological or strategic (e.g., Partan and Marler, 2005; Candolin, 2003; see also Leonard and Hedrick, 2010), we follow the structure of Hebets and Papaj (2005), in which hypotheses are grouped according to whether

they adopt an “efficacy-based” or “content-based” perspective on signal complexity (Guilford and Dawkins, 1991). Efficacy-based hypotheses address whether multiple components influence the transmission, detection, or processing (the “how”) of a signal. In contrast, content-based hypotheses address whether multiple components influence the meaning (the “what”) of a signal. An inter-signal interaction hypothesis can thus either be efficacy-based (one signal enhances the detection or processing of another) or content-based (the meaning of one signal depends upon the presence of a second signal). Since every signal is under selection for both efficacy and content, explanations from each of these perspectives are not mutually exclusive. For each of our three hypotheses (Table 1), we consider how the inter-signal interaction might facilitate both learning (acquisition of new information) as well as memory (recall of previously acquired information).

5 How Might Inter-Signal Interactions Facilitate Learning or Memory?

5.1 Attention-altering

At any one moment, pollinators detect more stimuli than their nervous system can process—floral signals are inevitably set amidst a background of not only noise but also of stimuli transmitted by predators, potential mates, conspecifics, host plants, and the physical environment. Pollinators also have potential access to a vast reserve of information stored in long-term memory (rev. Chittka et al., 1999). However, working memory, defined by Dukas (2002) as “information stored in an activated state for some short duration” guides decision-making, and is limited in its capacity. Attentional mechanisms determine what kinds of information, either newly acquired from the external environment or imported from long-term memory, gain control of working memory (rev. Knudsen, 2007). We suggest two efficacy-based hypotheses which explain how signal complexity might alter the attention of receivers, thereby allowing information about the signaler access to working memory.

The first possibility is that one component of the floral signal increases the attention paid to a second component. We term this the “**attention triggering**” hypothesis, which we have adapted from the “alerting” hypothesis of Hebets and Papaj (2005). In this scenario, detection of one component brings a different component of the complex display into working memory. This process might enhance recall or learning in situations where receivers encounter one component before the rest of the complex display.

It is well-established that long-term memory links information in different sensory modalities. In humans, for example, temporal lobe neurons that function in individual recognition respond to stimuli that are both visual (a picture of the person, or their written name) and auditory (hearing the person’s name spoken) (Quiroga et al., 2009). Are components of floral signals similarly linked in long-term memory, such that a component in one modality activates pollinators’ memory of a component in a different modality? In fact, studies on honeybees by Reinhard et al. (2004a, b) and Srinivasan et al. (1998) show that scent triggers recall of colors associated with flowers. In these experiments, bees were first trained to visit feeding stations that presented different colors and scents. In Reinhard et al. (2004a), one feeder presented yellow + rose scent, and the other presented blue + lemon scent. In a test phase, the feeders were unscented, but colors remained. When scent previously associated with one of the feeders (e.g., rose) was injected into the hive, foragers preferentially visited the feeder that had the appropriate (e.g., yellow) color. These findings show that bees link visual and olfactory information from food sources, and suggest that one function of scent may be to transfer visual stimuli associated with a particular flower from long-term into working memory. We propose that such a process might benefit the plant by alerting the pollinator that flowers of a given color are nearby, even if they cannot be seen immediately. Floral scent may thus keep the bee focused on searching for a particular visual signal, rather than on competing floral stimuli.

Table 1 Functional explanations for why multi-component signals might enhance receivers’ learning or recall of information about the signaler

Inter-signal interaction hypotheses	
Attention-triggering	<i>One signal component increases attention paid to a second component</i>
Attention-consuming	<i>Production of multiple components focuses receiver’s attention on display</i>
Context	<i>One signal component provides a context for receiver’s response to a second component</i>

Adapted from reviews of animal communication by Hebets and Papaj (2005) and Rowe (1999).

Beyond recall, the attention-triggering hypothesis could apply to learning as well. For example, might one component of a floral display bias a pollinator towards acquiring information about a second component? Although this hypothesis is for the most part unexplored, the literature on social learning may provide a relevant background for future experiments. In many species, information transmitted by conspecifics influences foraging behavior (rev. Galef and Giraldeau, 2001; Leadbeater and Chittka, 2007). Among social species of pollinators, floral scent brought back to the nest alerts foragers to specific foraging opportunities (e.g., Johnson and Wenner, 1966). For example, Molet et al. (2008) found that bumble bees *B. terrestris* exposed to a scent in the colony air, in the colony's honey pots, or brought back by a returning forager were more likely to land upon artificial flowers transmitting the same scent vs. a different scent. An olfactory signal transmitted socially in the colony might prime bees to learn other features of the flower (e.g., color) when they encounter it in the field. Indeed, attentional processes are thought to generally involve "salience filters" (Knudsen, 2007) which selectively promote representation of stimuli of learned biological relevance into working memory. Does pre-exposure to a flower's scent inside the colony increase the biological relevance of the flower's other signals, facilitating their import to working memory? This testable prediction that a socially-acquired component of a complex signal increases the salience of other components seems plausible, but to our knowledge has not been evaluated.

The effect of a complex signal on attention might also depend upon signal components being held together in working memory. According to this "**attention-consuming**" hypothesis, a more complex floral signal is able to out-compete other stimuli for access to working memory. Competitive selection is a basic attentional process, through which stronger signals are given priority access to working memory (rev. Knudsen, 2007); by transmitting multiple stimuli, a flower may increase its overall signal strength and thereby exclude other stimuli from working memory. In contrast to the attention-triggering hypothesis, this explanation requires that receivers trade off attention to a complex signal against attention to other stimuli. Therefore this hypothesis presumes that complex signals are learned more readily and that once learned, inhibit learning of other complex signals; such a process may benefit plants more than pollinators. An experiment testing this hypothesis might consider whether, relative to a simpler

signal, a more complex floral signal decreases bees' detection of stimuli associated with other flower types or predators.

Experiments on the phenomenon of flower constancy provide evidence for the attention-consuming hypothesis. Flower constancy refers to the tendency of pollinators to selectively visit one flower type, passing over other, equally rewarding, flowers (rev. Chittka et al., 1999). From the plant's perspective, constancy likely increases pollen transport to conspecifics; from the pollinator's perspective, constancy is usually interpreted as evidence of sensory or cognitive constraints that results in less-than-optimal behavior. For example, Gegear and Laverty (2001) have proposed the "trait variability" hypothesis, which explains constancy as a consequence of the limited capacity of pollinators' working memory to process different combinations of multiple floral traits. In support of this hypothesis, Gegear (2005) and Gegear and Laverty (2005) found that bumble bees *B. impatiens* were more constant when foraging on flowers that varied in more than one aspect. In fact, field observations suggest that bees are more likely to show constancy when they encounter a similar type within a few seconds of leaving a flower—that is, during the phase of information processing that includes working memory (Chittka et al., 1997). Thus, signal complexity may be a strategy that plants use to monopolize the working memory of pollinators.

In theory, a complex signal that focuses attention might enhance either the acquisition or recall of information. Interestingly, research on human subjects has shown that attention may have a stronger influence on the acquisition, or encoding process. When learning a task, research has shown (e.g., Baddelay et al., 1984; Craik et al., 1996) that subjects who divide attention across two tasks show reduced accuracy, relative to subjects that are able to focus on learning a single task; divided attention does not disrupt recall to the same extent, but does slow it down. An experiment exploring the attention-consuming properties of a floral signal might profitably consider whether the effect is most important during learning vs. recall.

5.2 Context

According to the content-based **context hypothesis**, one component of a display provides a context that facilitates learning or recall of a second component. An example from a non-learning perspective illustrates how one component of a display can provide context: Hughes' (1996) study of the open-claw visual signal produced by male and female snapping shrimp found

that males alter their responses to an open claw depending upon the presence of male or female chemical signals. In this system, the chemical signal provides a context for males to interpret the meaning of the open claw. From a learning perspective, the presence of one signal component may help receivers to distinguish between similar stimuli encountered in different situations. Often, floral visual signals resemble stimuli relevant to pollinators in non-foraging contexts. For example, in some species of hummingbirds, the color red is associated with male plumage as well as with commonly-visited flowers (e.g., Kodric-Brown and Brown, 1978); similarly, both floral patterns and entrances to bee colonies are often dissected shapes with dark centers (Biesmeijer et al., 2005). Chemically, many flowers transmit compounds also used in intraspecific communication: geraniol is both a component of floral scent and is also found in the Nasonov pheromone that honeybees use to mark flowers and colony locations (Schiestl, 2010). Recent articles argue that these floral signal components attract pollinators by exploiting pre-existing sensory biases (Schaefer and Ruxton, 2010; Schiestl et al., 2010). However, the role of individual learning in this evolutionary scenario has not been explored: in the face of this perceptual overlap, adding an additional distinctive component to the floral display might help pollinators to differentiate between contexts. Why might such learning benefit the plant? Research has shown that, at least regarding relatively simple floral stimuli, what a pollinator learns in one context can interfere with learning in a different context (Fauria et al., 2002; Worden et al., 2005). Recall of information can also be confused across contexts: Weiss and Papaj (2003) have shown that color information learned in one context (nectar foraging) can be confused with information learned in a different context (oviposition). Moreover, except for cases where successful pollination requires pseudocopulation (flower resembles a female) or pseudoantagonism (flower resembles a territorial intruder, rev. in Jersáková et al., 2006), the plant presumably benefits from pollinators' ability to recognize it as a food source—adding a signal component might be one way to promote this distinction.

A signal component that provides context can also facilitate recall of learned information. Research in experimental psychology has demonstrated that subjects learn not only the stimulus associated with a reward, but also a suite of “background” stimuli (rev. Shettleworth, 1998). When this context is changed, performance usually declines. For example, Skow and Jakob (2005)

trained jumping spiders to avoid aposematically colored milkweed bugs in arenas decorated in either a complex or simple manner; when subjects were later presented with the same prey type, those whose arenas were changed showed less avoidance than subjects re-tested in the same arena type. More generally, Bouton et al. (1999) have proposed the “context-change” account of forgetting: according to this model, performance in a learned task declines over time (without reinforcement) because of inevitable changes in the background stimuli. Pollinators, for example, almost certainly experience fluctuations in background stimuli over time or space. Perhaps by transmitting a relatively stable, constant, component, a plant increases the continuity of the background, enhancing recall of other floral traits.

A test of the context hypothesis might involve training a pollinator to respond to two different signal components (e.g., colors) in two separate contexts (e.g. nest entrance vs. foraging) and determining whether addition of another floral signal component (e.g. scent) reduces confusion between contexts, or enhances recall of color information associated with each task.

6 Conclusion

Studying the interactions between plants and their pollinators offers an opportunity to explore how receiver psychology has shaped signal design in an ecological context. Although we have focused on communication specifically between plants and pollinators, the hypotheses we have described should apply generally to any interaction where a sender benefits from facilitating the receiver's acquisition or recall of information. Indeed, work on multimodal aposematic signaling (e.g., Rowe and Guilford, 1992) has many points of comparison with our discussion of how complex floral signals enhance learning. We also note that though the majority of research on complex signaling concerns female mate choice, the relationship between courtship signal complexity and female learning is almost completely unexplored. Yet we can imagine many scenarios in which males would benefit by producing a signal that facilitated female learning or memory. A recent study by Akre and Ryan (2010) on the acoustic signals of male túngara frogs emphasizes this point: male calls that are more complex (3 chucks vs. 1 chuck) appear to be stored for longer in females' working memory, enhancing females' ability to localize a call after a short period of silence.

Only a small number of experiments have so far considered functional explanations for floral signal com-

plexity, yet we see few obstacles to this intriguing direction of research. After all, plants offer opportunities for manipulative experiments that are often difficult to accomplish with animal signalers. For example, while increasingly sophisticated experiments on animal signalers involve the use of robots, adding or removing a signal component from a floral display often requires simple manipulation of the floral phenotype, or use of artificial flower models. Moreover, the rich literature on insect learning provides a wide range of techniques and protocols useful in designing tests of the functional hypotheses we outline in this paper. Such research should yield insights into perhaps the best-known, but least studied, exchange of complex signals in the natural world.

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