



Linking components of complex signals to morphological part: the role of anther and corolla in the complex floral display

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Signals used in communication are frequently complex, being composed of multiple signal components that in combination improve information transfer. A variety of morphological parts are typically used to transmit components of any given complex signal. Our understanding of why a given morphological part is used to transmit a given signal component is poor. We hypothesized that the function of a given signal component is improved by its association with its morphological part and that such parts interact functionally to transmit information. In a laboratory study we characterized the function of different floral signal components transmitted by associated floral parts and the interaction of those signal components. Using *Solanum houstonii* flowers, we focused on two major floral parts, corolla and anthers, involved in signalling bumblebee, *Bombus impatiens*, visitors. We further examined how experience affected the relationship between signal component and floral part. Floral visits involve a stepwise process in which bees approach, land and acquire pollen. We found that the corolla plays the dominant role in eliciting approaches by bees, whether naïve or experienced. Landing is elicited by corolla signals and, to a lesser but additive degree, anther signals. Following experience, anther signals nearly completely dominate corolla signals in eliciting landing. The anthers convey signals mediating pollen acquisition, regardless of the bee's experience level. Our findings suggest there is selection for specific relationships between signal components and morphological parts, which in turn might drive complex signal evolution.

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Organisms frequently communicate using complex signals (i.e. displays; Hebets & Papaj, 2005; Hebets et al., 2016) composed of multiple interacting components in one or more sensory modalities (e.g. visual, olfactory, tactile; Hebets & Papaj, 2005; Herberstein, Wignall, Hebets, & Schneider, 2014; Kaczorowski, Leonard, Dornhaus, & Papaj, 2012). A variety of morphological parts may be involved in transmitting a complex signal. For instance, the complex mating display of many spider species involves multiple seismic and visual cues produced by the forelegs and the abdomen (e.g. Elias, Sivalingham, Mason, Andrade, & Kasumovic, 2010; Girard, Kasumovic, & Elias, 2011; Hebets & Uetz, 1999). Selection presumably acts to maintain the complex signal (Hebets & Papaj, 2005; Leonard, Dornhaus, & Papaj, 2011) and by extension the morphological parts responsible for sending the complex signal.

While a great deal of attention has been given to characterizing the benefits of complex signals (see Hebets et al., 2016; Leonard et al., 2011; Leonard, Dornhaus & Papaj, 2012), less is known about why particular morphological parts are used for particular signal components. A given morphological part might improve the function of its associated signal component. For instance, tadpole 'tail spots' and lycaenid butterfly 'false head' visual signals capture predator attention, and because these signals are transmitted by the tails, they direct attacks to the tail: an expendable region of the body (Sourakov, 2013; Van Buskirk, Aschwanden, Buckelmüller, Reolon & Rüttiman, 2004). Likewise, signal components that differ in their function may be segregated to some extent among physical parts that improve those different functions. For example, visual and acoustic cues associated with the upper train of peacocks attract females from a distance while the lower train provides only visual cues used in close-range courtship (Yorzinski, Patricelli, Babcock, Pearson, & Platt, 2013). The upper train is highly conspicuous relative to the lower train, and this difference in conspicuousness potentially improves each morphological part's

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signalling function. Such parts might conceivably act independently of one another or interact to some degree to improve the function of a complex signal.

Biotically pollinated plants typically communicate with their pollinators via floral displays, composed of tactile, visual, olfactory, humidity, and even electrical cues (Clarke, Whitney, Sutton, & Robert, 2013; Giger & Srinivasan, 1995; Foster et al., 2014; Muth, Papaj, & Leonard, 2016; von Arx, Goyret, Davidowitz, & Raguso, 2012; Whitney et al., 2009; Whitney, Chittka, Bruce & Glover, 2009). These cues form a complex signal that can benefit both plant and pollinator (Leonard et al., 2011, 2012). Floral cue composition commonly differs among morphologically distinct floral parts (Leonard et al., 2011, 2012; Fig 1d–f). For example, a flower's corolla often displays different colour patterns than its anthers (e.g. Fig 1). Likewise, the anthers of many plant species produce different and more kinds of odours than the corolla (Burdon, Raguso, Kessler, & Parachnowitsch, 2015; Dobson, Groth, & Bergström, 1996). Pollinators should be able to perceive and respond to such differences (e.g. Ashman, Bradburn, Cole, Blaney, & Raguso, 2005; Guerrieri, Schubert, Sandoz, & Giurfa, 2005; Muth

et al., 2016; Riffell et al., 2008). Given that the signal components of different floral parts may differ in sensory modality, do the different floral parts serve different functions for the complex floral signal? Do the signal components in different physical parts act independently, or do they interact? These questions are largely unanswered in the existing literature (but see Ashman, Swetz, & Shivitz, 2000; Connolly & Anderson, 2003; Lunau, 1992; Ushimaru et al., 2007).

Several basic steps are required for pollination, which involves the transmission of pollen to the pollinator and typically involves the acquisition of a floral reward by the pollinator. Plants must initially provide signal components that attract pollinators to the flowers (Fig 1a). Following pollinator attraction, signal components that orient the pollinator on the flower come into effect (Fig 1b). For instance, many flowering plant species display so-called nectar guides on their corollas that direct pollinators to nectaries, which hold the nectar reward (Leonard & Papaj, 2011; Penny, 1983). Finally, signal components that facilitate pollen transfer to the pollinator come into effect (Fig 1c). For plant species that offer pollen as a floral reward to their pollinators (Kevan & Baker, 1983;

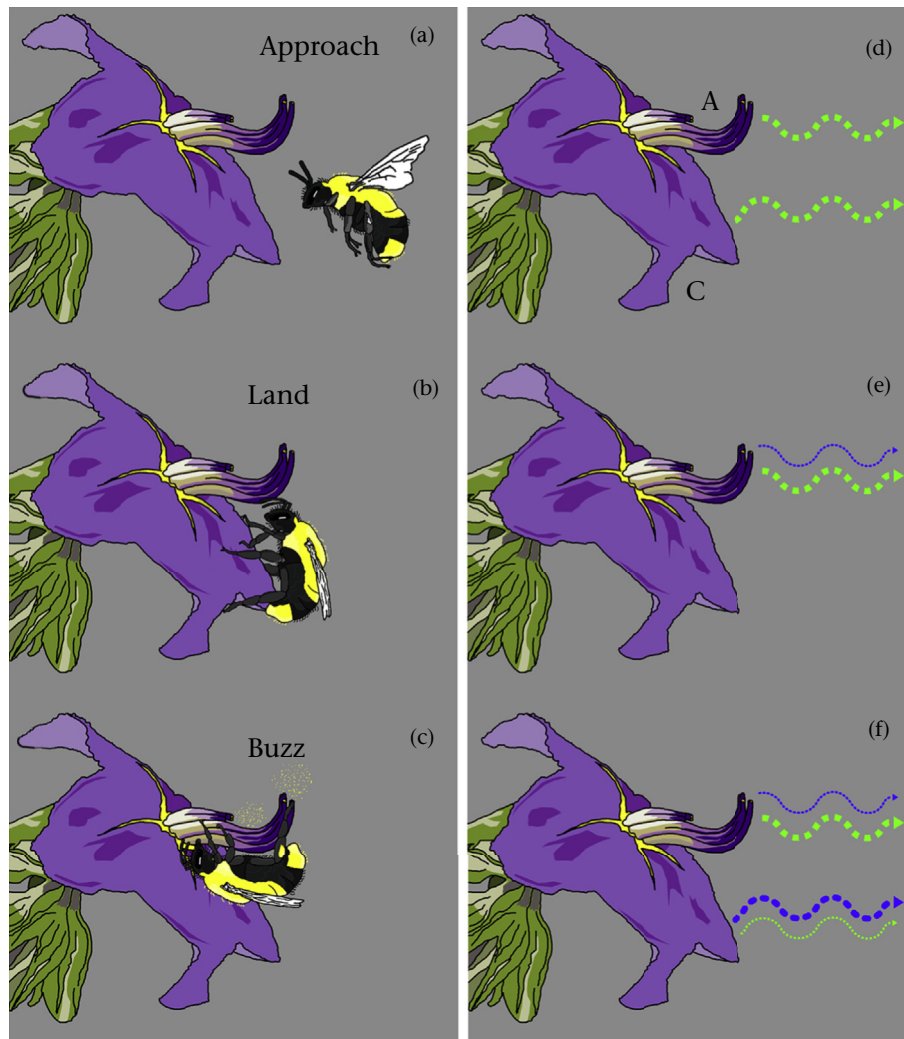


Figure 1. The basic steps involved in the transfer of pollen to the bee from flowers that offer pollen as the sole reward, such as those of *Solanum houstonii*. (a) Attraction is followed by (b) landing, which is followed by (c) physical contact with the anthers and then pollen extraction (via buzzing). The complex floral signal might be transmitted by (d) multiple floral parts (such as the anthers, A, and the corolla, C), (e) multiple signal components from a single floral part, or even (f) multiple signal components each from a separate floral part. Likewise, each basic step involved in the transfer of pollen might involve different combinations and weighting of floral parts and their signal components. Separate signal components are indicated by differently coloured lines; line thickness indicates weighting.

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