

## Commentary

# What you smell is more important than what you see? Natural selection on floral scent

The notion that floral traits are under phenotypic selection is widely recognized in evolutionary ecology, and myriad studies have documented strong selection on traits such as flower number, flower size, color, and shape (reviewed in Parachnowitsch & Kessler, 2010). Indeed, some of the most striking examples of presumed phenotypic selection come from floral morphological traits, such as the nectar spurs of Madagascar Star Orchids pollinated by hawkmoths with impressively long tongues (reviewed in Whittall & Hodges, 2007). However, despite the often overpowering smell of many flowers, few studies have measured phenotypic selection on floral scent. Scent traits are notoriously difficult to measure and analyze compared with many other floral traits, in part due to the technical skills needed to collect and analyze scent, and in part because 'scent' is a very complex trait. Moreover, measuring phenotypic selection on floral traits, including scent, often involves hundreds of plant replicates, requiring a heavy investment in plant chemistry. Thus, the work presented by Parachnowitsch *et al.* in this issue of *New Phytologist* (pp. 667–675) provides a significant step forward in our understanding of phenotypic selection on floral traits by showing that floral scent can be under stronger selection than more traditionally measured floral morphological traits, such as floral size and color.

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Using plants from three natural populations of *Penstemon digitalis* in a common garden, Parachnowitsch *et al.* characterized scent variation and measured phenotypic selection on floral morphological traits and scent. The authors found population-level variation in scent composition but not overall emission, and positive selection on number of flowers, daily display, inflorescence height, and floral scent, but not flower size or color. The most exciting result of the paper is the finding that there was

greater selection for scent traits than either flower size or color, which are much more frequently examined in studies of floral evolution. *Penstemon digitalis* is not strongly scented to the human nose; thus, the findings of this study suggest that variation in even weakly scented flowers to humans may have strong impacts on plant fitness. We are aware of few studies that have measured phenotypic selection on floral scent (but see Schiestl *et al.*, 2011). Hopefully this seminal work by Parachnowitsch *et al.* will inspire others to make similar investigations with other model systems in pollination biology.

The other big contribution of this paper is the authors' inroads into how scent is analyzed. Floral bouquets can easily be comprised of 40+ compounds (Knudsen *et al.*, 2006), with large variation in not only amounts but also presence of individual compounds, making statistical analysis challenging. A larger issue is that, from a biological viewpoint, the whole may be more than the sum of the parts; 'scent' is typically thought to be perceived as one trait by the perceiver. The same compounds can elicit different behaviors from different perceivers, or from the same perceiver in different contexts, and the ratios of compounds can change how animals respond to scent (reviewed in Raguso, 2008). Animals may learn mixtures based on a subset of key components, while other components do not affect responses (Reinhard *et al.*, 2010), and the response to mixtures can be fundamentally different from the response to the individual components that comprise the mixture (Riffell *et al.*, 2009). While it might be ideal to analyze each scent component individually, the large number of compounds combined with typically modest sample sizes often means there is very little power to test effects. Therefore, researchers studying scent typically take one or more of several approaches: analyze total scent emissions and/or total scent emissions in fragrance categories (e.g. monoterpenes, sesquiterpenes); analyze scent diversity (the total number of compounds, regardless of relative quantities); or use principal components analysis to define a small number of component 'traits' for analysis, each comprised of different ratios of component compounds. Each of these approaches has the advantage of simplifying a very complex data set, but has the risk of missing the most biologically important responses if these occur in relatively minor compounds. Parachnowitsch *et al.* used the approach of first measuring total selection on each compound via selection differentials (which include direct selection and selection via trait correlations). Then, for scent compounds that showed significant selection differentials, they included those scent compounds in a multivariate model to measure selection gradients (direct selection only, controlling for other traits in the model). While one could quibble about the pros and cons of their data reduction scheme, their approach uses a logical framework and provides selection gradients on individual compounds, which provide for more ease of comparison to other studies focusing on

morphological traits. We envision that continued advances will be made in how best to analyze these complex scent-based traits.

Scent has conventionally been viewed as a trait that is highly variable based on environmental conditions, such as sunlight, temperature, and soil moisture (reviewed in Reinhard & Srinivasan, 2009). How much of that variability can be ascribed to genetic variation has remained minimally explored. Thus, one additional strength of Parachnowitsch *et al.*'s study is that they measured plant traits in a common garden. Plants were transplanted just before flowering, and so the authors cannot rule out the importance of environmental variation throughout plant growth that could affect scent expression. Nonetheless, their finding that scent composition differed among populations in the common garden suggests that there may be genetic variation in scent bouquets, complementing other examples describing 'sweet' and 'skunky' morphs of *Polemonium viscosum* (Galen *et al.*, 1987) and differences in female and hermaphrodite scent in strawberry (Ashman *et al.*, 2005). More convincing evidence that scent variation has a genetic component would come from plants produced in a breeding design, or using replicate clones grown from cuttings in a common garden. However, the finding that scent composition may be genetically based is a necessary first step in discussing the potential for scent to evolve in response to natural selection. Hopefully, this starting point will inspire others to examine the genetic basis of floral scent and even quantify heritability in future work.

This paper makes a great step forward by demonstrating natural selection on floral scent traits. However, for those interested in phenotypic selection on floral scent, there is still significant work to do. Parachnowitsch *et al.* rightly comment that they do not know the agents of selection on floral scent in their study. *Penstemon digitalis* flowers are visited by bumble bees, hummingbirds, and small bodied bees, and it is unknown how the abundance, ratios, or behaviors of these pollinators vary as a function of floral scent, and how these visitors link variation in floral scent to plant fitness. Moreover, although the agent of selection is presumably pollinators, many different interactions, both mutualist and antagonist, use floral traits as cues. It is now widely recognized that floral morphological traits may represent an adaptive compromise between plant interactions with mutualist pollinators and antagonists such as herbivores, seed predators, and nectar robbers (reviewed in Strauss & Irwin, 2004). The degree to which floral scent represents a similar adaptive compromise remains unknown, although the adaptive significance of specific scent compounds is just starting to be explored in a multi-species context (Kessler *et al.*, 2008; Galen *et al.*, 2011; Theis & Adler, 2012). As some of these authors themselves point out in another paper (Parachnowitsch & Kessler, 2010), demonstrating that pollinators are the agent of selection on traits requires manipulating pollination (via supplemental hand pollination to remove pollinator choice) and measuring patterns of selection in the presence and absence of pollinator choice. Moreover, more nuanced approaches, such as observations of pollinator and other floral visitor foraging rates and behaviors, may help link variation in scent to plant fitness through the use of path analysis, although the level of replication required can be staggering. Also, direct manipula-

tion of key scent compounds and measurements of plant–insect and plant–pollinator interactions may provide additional ecological and evolutionary insight (Galen *et al.*, 2011; Theis & Adler, 2012). Parachnowitsch *et al.* make a significant step forward by identifying specific floral compounds that are experiencing natural selection. The next step should be identifying the agents of selection using observations and experiments, to determine whether pollinators are indeed driving the selection patterns found here.

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