

BRIEF COMMUNICATION

**PHYLOGENETIC EVIDENCE FOR A FLOWER SIZE AND
NUMBER TRADE-OFF¹**

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The size and number of flowers displayed together on an inflorescence (floral display) influences pollinator attraction and pollen transfer and receipt, and is integral to plant reproductive success and fitness. Life history theory predicts that the evolution of floral display is constrained by trade-offs between the size and number of flowers and inflorescences. Indeed, a trade-off between flower size and flower number is a key assumption of models of inflorescence architecture and the evolution of floral display. Surprisingly, however, empirical evidence for the trade-off is limited. In particular, there is a lack of phylogenetic evidence for a trade-off between flower size and number. Analyses of phylogenetic independent contrasts (PICs) of 251 angiosperm species spanning 63 families yielded a significant negative correlation between flower size and flower number. At smaller phylogenetic scales, analyses of individual genera did not always find evidence of a trade-off, a result consistent with previous studies that have examined the trade-off for a single species or genus. Ours is the first study to support an angiosperm-wide trade-off between flower size and number and supports the theory that life history constraints have influenced the evolution of floral display.

Key words: floral display; flower number; flower size; inflorescence size; life history trade-offs; phylogenetic independent contrasts.

Floral display is fundamental to plant fitness. Two important aspects of floral display, flower size and flower number, have demonstrable effects on pollinator visitation rate and total seed production (Bell, 1985). From this one might predict that selection should act to increase both traits. However, resources are finite and result in life history trade-offs (Roff, 2002). Resource allocation in plants is predicted to proceed hierarchically (Venable, 1996; Weiss et al., 2005), divided first between vegetative and reproductive functions, then within them. Because the pool allocated to floral function is thus limited, there should be a trade-off between flower size and

number (Worley and Barrett, 2000; Caruso, 2004). This idea is pervasive in theoretical models of floral display evolution (Cohen and Dukas, 1990; Sakai, 1993, 1995, 2000; Harder and Barrett, 1995; Schoen and Ashman, 1995; Sato, 2002).

In spite of the compelling theoretical basis for its existence, evidence for a trade-off between flower size and display size has been elusive (reviewed by Worley and Barrett, 2000; Ashman and Majetic, 2006; Caruso, 2006). While some empirical studies have shown a negative correlation between flower size and number (Carroll and Delph, 1996; Meagher, 1999; Delph et al., 2002, 2004; Caruso, 2004), others have found no such relationship (Worley and Barrett, 2000, 2001; Ashman and Majetic, 2006). In a species-level comparative study that did not control for phylogeny, Worley et al. (2000) found evidence for a trade-off between flower size and number among 45 species in the genus *Narcissus*. Yet the traits were positively correlated when the pattern was examined among populations of a single species, *N. dubius*, suggesting an effect of taxonomic scale on the ability to detect trade-offs.

One common explanation for the deficiency of evidence for the trade-off is that flower size and number are complex traits; each is influenced by a multitude of ecological and life history features. For example, a predominantly self-fertilizing mating system can lead to selection for smaller flowers (Wyatt, 1984; Lyons and Antonovics, 1991; Goodwillie, 1999; Goodwillie and Ness, 2005), change in pollination mode is associated with shifts in flower size and number (Proctor et al., 1996; Weller et al., 2005), and male plants of sexually dimorphic species tend to have larger displays with a greater number of smaller flowers than female plants (Delph et al., 2002, 2004). Selection on fruit size, seed size, and phenology can also influence the relationship (Primack, 1987). Annual plants may exhibit a more pronounced trade-off between flower size and flower number than perennials because their opportunity for trade-offs

¹ Manuscript received 6 April 2007; revision accepted 18 October 2007.

The authors thank R. Bertin for generously providing access to his extensive database of dichogamous species and their traits. A. Worley kindly provided the *Narcissus* flower size and number data from the analysis published in Worley et al. (2000). A. Brach helped procure the *Clematis* data set. S. Kembel and N. Kraft assisted with configuring Phylocom software. They thank D. Ackerly, K. Bolmgren, C. Caruso, S. Otto, A. Randle, and D. Roff for their insightful comments and suggestions on earlier versions of the manuscript. This paper is the product of discussions and ideas that emerged from The Paradox of Mixed Mating Systems working group at the National Science Foundation's National Evolutionary Synthesis Center (NESCent), NSF #EF-0423641. They thank the members of the working group for their contributions to the development of this study. R.D.S. was supported by a Natural Sciences and Engineering Research Council of Canada (NSERC) postdoctoral fellowship, and S.K. was supported by NSF grant DEB-0324764.

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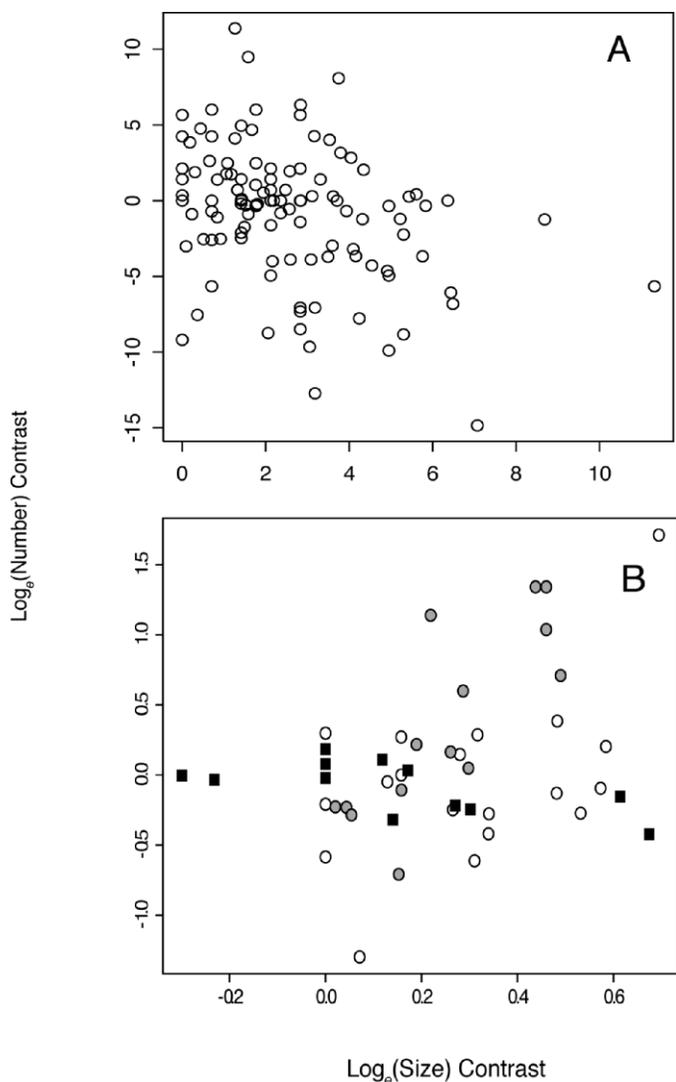


Fig. 1. Phylogenetic independent contrasts (PICs) of the difference in $\log(\text{flower diameter})$ (in mm) and $\log(\text{flower number})$ for (A) species in the across-angiosperm analysis with branch lengths ($N = 116$) and (B) species in *Clematis* (squares, $N = 12$), *Collinsia* (closed circles, $N = 18$), and *Narcissus* (open circles, $N = 19$). In both analyses, flower number was scored as the average reported number of open flowers per inflorescence.

involving future reproductive success is more limited (Morgan, 1998; Sato and Yahara, 1999). Additionally, geitonogamy and pollen discounting increase with flower number and thereby influence optimal display size (Barrett et al., 1994). Finally, selection on life history that modifies overall allocation to reproductive vs. somatic growth can yield positive relationships between floral display traits and obscure underlying trade-offs between flower size and number (Worley et al., 2003).

Closely related species should be more alike in their ecology and life history because of common descent, and failing to control for phylogenetic relatedness can mask existing patterns of association between traits (Harvey, 1996). In spite of this, no previous study of flower size and number has controlled for phylogeny, possibly explaining why so few studies have detected a trade-off. Here we address whether flower size and number are negatively correlated using phylogenetic indepen-

dent contrasts (PICs). To maximize our statistical power, we collected data from 251 angiosperm species, representing 63 families. We also explored the scale-dependence of such analyses by conducting separate PIC analyses among taxa within the genera *Clematis*, *Collinsia*, and *Narcissus*.

MATERIALS AND METHODS

We used data on average flower size and number from a database of >4000 seed plant species compiled by R. Bertin and C. M. Newman for the study of ecological correlates of dichogamy (results published in Bertin and Newman, 1993). The database contains all data relevant to reproductive ecology and mating systems of flowering plants and was last updated from the scientific literature in January, 2001 by R. Bertin and C. M. Newman.

Flower size was measured as average corolla diameter. When a range of sizes was reported, we used the midpoint value. In cosexual, gynodioecious, and androdioecious species, measurements are from hermaphrodite flowers. In monoecious and dioecious species, measurements are from female flowers.

Flower number was scored as the average reported number of open flowers per inflorescence. One could argue that total flower number, rather than daily display size, is the most appropriate measure of overall investment in flower number. Unfortunately, data on total number of flowers are not available for most of the species in our study. Not surprisingly, however, daily flower number and total flower number are often correlated. Harder and Cruzan (1990) found a significant correlation between daily inflorescence size and total flower number in 14 of 17 species studied. In addition, Worley and Barrett (2001) concluded that daily and total flower number are controlled by the same genes in *Eichhornia paniculata*, supporting our use of the daily number as a surrogate for total flower number. Hereafter, we use "display size" to distinguish our measurement of flower number from total flower number. We log transformed flower size and number to fit the assumption of normality (Kolmogorov-Smirnov test, $P > 0.9$).

Bertin's database yielded flower size and display size data for 251 species spanning 63 families. A phylogenetic tree of relationships between the 251 species was created based on the family-level consensus tree of Davies et al. (2004) using the program PHYLOMATIC (Webb and Donoghue, 2005), with subsequent adjustments to accommodate differences in family concepts between the Angiosperm Phylogeny Group (2003) and PHYLOMATIC.

In addition to the angiosperm wide data set, we acquired data on flower size, display size, and phylogenetic relationships for 13 species in the genus *Clematis* (Ranunculaceae), 23 species of *Collinsia* (Plantaginaceae), and 25 species of *Narcissus* (Amaryllidaceae). Only four species (*C. sparsiflora*, *N. poeticus*, *N. pseudonarcissus*, and *N. tazetta*) also occurred in the larger data set. Flower size and display size for *Clematis* species were from Wang and Bartholomew (2001). Phylogenetic relationships in *Clematis* were based on Miikeda et al. (2006). Flower size and display size for *Collinsia* species were determined using the Jepson Manual (Hickman, 1993), Calflora (2006), and unpublished data collected by S. Kalisz. Phylogenetic relationships in *Collinsia* were obtained from Armbruster et al. (2002). To assure consistency with the Worley et al. (2000) analysis, we obtained flower size and display size for *Narcissus* from A. Worley. The original references for their data are cited in Worley et al. (2000). We used the phylogeny from Graham and Barrett (2004) for the independent contrast analysis of *Narcissus* taxa, which contains 25 of the original 45 taxa cited in Worley et al. (2000).

We used Phylocom, version 3.40 (Webb et al., 2006), to perform phylogenetically independent contrasts (PICs; Felsenstein, 1985) to estimate the correlation between flower size and display size. We did the analyses first with all branches scaled to unit length, an assumption that has been shown to be robust to Type I error when accurate branch length information is unattainable or there is high uncertainty in branch length estimates (Ackerly, 2000). For the angiosperm data set, we also ran the PIC analysis using branch lengths based on the approximate clade ages estimated by Davies et al. (2004). Statistical analyses were performed in the R language, version 2.4.1 (R Development Core Team, 2006).

RESULTS

The Bertin data set yielded 116 phylogenetically independent contrasts (Fig. 1A). The correlation coefficient between

contrasts of flower size and display size is significant and negative using both unit branch lengths ($r = -0.250$, $df = 115$, $P < 0.001$) and temporal branch lengths ($r = -0.188$, $df = 115$, $P < 0.01$).

Results of PIC analyses within genera were variable. The correlation between flower size and display size for *Clematis* data set supports a trade-off (Fig. 1B: $r = -0.441$, $df = 11$, $P < 0.01$). However, flower size and display size in the *Collinsia* data set were positively correlated (Fig. 1B: $r = +0.329$, $df = 17$, $P < 0.001$). Finally, we found no significant correlation between flower size and display size (Fig. 1B: $r = 0.131$, $df = 18$, $P = 0.387$) in *Narcissus*. Without correcting for phylogeny, flower size and display size were negatively correlated in *Narcissus* ($r = -0.479$, $df = 24$, $P = 0.015$), a result consistent with Worley et al. (2000). Because of the constraints of the existing phylogeny, our sample size for the PICs analysis for the genus *Narcissus* was smaller than the one reported by Worley et al. (2000), which may have contributed to our failure to detect the trade-off.

DISCUSSION

Across angiosperms, we find a negative correlation between corolla diameter and the number of flowers displayed in an inflorescence, suggesting that lineages are limited in their ability to simultaneously increase allocation to both flower size and display size. This result is somewhat surprising, given the sources of potential error associated with our measures of floral resource allocation, especially those associated with plant size and longevity. The significant correlation indicates that there is sufficient variance in the proportional allocation of resources to flower size and number, as measured by corolla diameter and number of open flowers per inflorescence, for a phylogenetic signature of a trade-off to be evident. This result emerged despite the magnitude of expected variation across angiosperms in total resource allocation to floral display.

Although this trade-off is one of the most common assumptions in plant reproductive ecology, numerous previous studies have been unable to demonstrate that such a trade-off exists (e.g., Worley and Barrett, 2000, 2001; Ashman and Majetic, 2006). Our analysis differs from previous efforts in emphasizing phenotypic correlation in a phylogenetic context and at a macroevolutionary scale. Although negative correlations can result from other processes (for example, direct selection for particular combinations of characters), the large-scale analysis supports the hypothesis of a trade-off between flower size and number.

In contrast to our angiosperm-wide result, our analyses of *Collinsia* and *Narcissus* agree with most prior studies and failed to detect a trade-off between flower size and number (reviewed by Worley et al., 2000; Ashman and Majetic, 2006). It is noteworthy that empirical investigations of life history traits in a wide range of taxa have revealed several instances that appear to contradict trade-offs predicted by theory, particularly in cases where the data represent a single species or genus (reviewed by Reznick and Tessier, 2000; Roff, 2000). What could account for the apparent effect of phylogenetic scale in the detection of these empirical patterns?

One possible explanation is that relative variances of proportional resource allocation and total resource availability are clade-specific and differ markedly between genera. Resource-partitioning models (James, 1974; van Noordwijk

and de Jong, 1986; de Jong and van Noordwijk, 1992) show how the detection of a trade-off depends on the variance in proportional allocation relative to the variance in total availability of resources. Specifically, if variance in proportional allocation is small relative to variance in total availability, positive correlations between traits are expected in spite of the underlying trade-off. For *Collinsia*, our results suggest that variance in proportional allocation to flower size vs. number is small relative to variance in total allocation to reproduction, resulting in an apparent positive correlation between flower size and number. In *Clematis*, the converse may be true, allowing the trade-off to be detected. We currently lack the data to explicitly test these hypotheses but view the general prediction of idiosyncratic variance ratios of proportional allocation to total availability of resources at small phylogenetic scales as worthy of further investigation.

Other factors likely to be important in understanding floral display trade-offs include potential correlations with fruit and seed size (Primack, 1987). Whether selection on flower size is driven by pollinator attraction, by correlated selection on seed and/or fruit size via selection for dispersal and seedling establishment, or by both, has significant implications for resource allocation and the shape of the size–number trade-off. Observed correlations between seed, fruit, and flower size (Primack, 1987) bear investigation in this context.

One caveat of our study, which uses phenotypic correlation between traits rather than genetic correlations, is our inability to establish a causal basis for the observed relationship. Although phenotypic correlations between morphological traits are generally consistent with genetic correlations, they must be interpreted with caution and cannot be used to determine whether the trade-off arises from the joint additive action of genes (Partridge and Harvey, 1985; Roff, 2002). Moreover, correlations of PICs are not strictly translatable as either phenotypic or genotypic correlations. Nevertheless, future studies that seek to uncover a genetic correlation between flower size and flower number should keep in mind that variance in resource status among individuals can mask trade-offs.

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