

NEWS AND COMMENTARY

Floral evolution

Spurred on by pollinators

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Columbines (genus *Aquilegia*) possess nectar spurs, backward projections of the petals within whose base nectar is secreted. Nectar spurs act as pollinator filters. Only those pollinators possessing tongues long enough to reach the base of the spur can access the nectar reward. A remarkable feature of North American *Aquilegia* is that spur length varies among species across an astonishing range, from 7.5 to 123 mm. This morphological diversity has apparently evolved incredibly rapidly. In a recent letter to *Nature*, Whittall and Hodges (2007) demonstrate that within this short period of evolution unidirectional increases in spur length have taken place. They also provide convincing evidence that these changes have been driven by shifts to pollinators with increasingly long tongues.

Their conclusions are based on a detailed analysis of a rooted phylogenetic tree of *Aquilegia*. When pollination syndrome (bee, hummingbird or hawkmoth) is mapped onto the tree, bee pollination turns out to be the ancestral state. Only two of the six possible pollinator transitions are shown to have occurred in the phylogeny: bee to hummingbird (twice) and hummingbird to hawkmoth (five times). Bee taxa have the shortest, hummingbird taxa intermediate, and hawkmoth taxa the longest spurs. To explain this pattern of evolution Whittall and Hodges develop the 'pollinator shift' hypothesis.

They propose that in some part of its range an *Aquilegia* taxon with ancestral bee pollination and a short spur receives visits not from bees, but from hummingbirds. Hummingbirds possess longer tongues than bees. Therefore, when the hummingbird is extracting nectar from the spur its body makes little contact with anthers and stigmas, leading to inefficient pollination. Plants with longer spurs are therefore at a selective advantage because, when nectar is accessed from them, the hummingbird's body comes into closer contact with anthers and stigmas, increasing the plant's reproductive fitness. Over time the spur length increases to match the length of the hummingbird's tongue.

A consequence of this evolutionary change is that bees can no longer access nectar from the long spur. The hummingbird adapted population is reproductively isolated from its bee adapted ancestor and effectively represents a new species. Reversal of the pollinator shift from hummingbird to bee pollination is highly unlikely. Shorter tongued bees will not visit plants with long spurs because they are unable to access nectar, and there will therefore be no selection for a reduction in spur length. However, pollinator shifts from hummingbird to longer tongued hawkmoths can lead to a further increase in spur length and evolution of a new hawkmoth pollinated species.

The 'pollinator shift' hypothesis accounts nicely for the observed unidirectional switches between pollinator groups and the associated increases in spur length. Further predictions of the hypothesis are that increases in spur length should not be constant over time, but should involve 'punctuated' evolution, that is sudden increases in spur length in those lineages that have switched to pollinator groups possessing a longer tongue. Finally, spur length should tend to evolve to three optima corresponding to the three different tongue lengths within bee, hummingbird and hawkmoth pollinator groups. More sophisticated analyses of the phylogenetic tree indicate that these predictions are upheld.

Despite its explanatory power the 'pollinator shift' hypothesis requires a rather implausible ecological scenario (Thomson and Wilson, 2007). Crucially, a short spurred, bee adapted *Aquilegia* population must be maintained over many generations in the absence of an effective bee pollinator. The absence of bees from the population is a necessary condition because, if present with the hummingbirds, the well-adapted bees would be responsible for most pollination and their interactions with the plant would govern the evolutionary trajectory. There would therefore be no selection for longer spurs.

An alternative hypothesis that is compatible with the data but avoids these difficulties dates back to Darwin

(1862). He argued that when plants possessing spurs interact with specialist pollinators, co-evolution should lead to a gradual increase in the length of both plant spurs and pollinator tongues. Plants possessing a slightly longer spur gain a reproductive advantage because, in probing to the bottom of the spur, pollinators increase their contact with anthers and stigmas, increasing pollination efficiency (Nilsson, 1988; Alexandersson and Johnson, 2002). Selection, in turn, acts to increase tongue length in the pollinator, since this enhances its ability to harvest nectar from the increasingly lengthy spur. Increases in spur and tongue length should occur until a limit to further increase in either spur, or more plausibly tongue length is reached. The maximum tongue length of a bee is unlikely to be significantly greater than its body size, since the tongue must fit lengthwise beneath the body in flight. Thus in an ancestral, bee pollinated *Aquilegia*, co-evolution will lead to a spur length close to the size of the bee's body.

Now suppose that a population of this bee adapted *Aquilegia* was invaded by a hummingbird with a *similar* tongue length to that of the bee, a perfectly reasonable scenario. Under these circumstances, hummingbird pollination may be as good as, or more effective than bee pollination (Castellanos *et al*, 2003). Co-evolution between *Aquilegia* and the hummingbird could therefore occur in the presence of the bee. With a more relaxed selective constraint on tongue length in hummingbirds than in bees, longer spurs would evolve until some new ceiling on tongue length were reached, imposed perhaps by maximum hummingbird beak size. Further co-evolutionary increases in spur length could subsequently take place if switching occurred to a hawkmoth with a similar tongue length to that of the hummingbird. Spurs of enormous length could ultimately evolve under co-evolution with the hawkmoth because the maximum size of a hawkmoth tongue is staggering (up to 220 mm), a fact made possible by their ability to coil the proboscis neatly beneath the head when not in use.

The predictions of the 'co-evolutionary' hypothesis elaborated above are fully compatible with the results and analyses presented by Whittall and Hodges (2007). The necessary conditions for its operation are arguably more ecologically realistic than those required by the 'pollinator shift' hypothesis. To distinguish between these two

hypotheses we will require further, complementary studies of the evolutionary changes that occur in pollinator populations when they interact with flowers that possess nectar spurs.

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