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Reply

How to investigate a putative signal? Stick to the right method when assessing the response of a receiver

The evolution of autumn leaf coloration moved into the focus of ecologists after the seminal publication by Hamilton & Brown (2001). In that article, Hamilton & Brown proposed the coevolutionary hypothesis, suggesting that red and yellow leaves in autumn evolved as warning signals to repel herbivorous insects, particularly aphids. Despite strong interest in the topic, experimental studies supporting this hypothesis are lacking. In a recent article, we describe the first experiment reporting that autumnal leaf colour does *not* influence host selection in aphids (Schaefer & Rolshausen 2007). Instead, we found a strong positive correlation between aphid numbers and fruit production in a cohort of same-aged mountain ash (*Sorbus aucuparia*) trees.

In our experiment, we used artificial green or red leaf colours and caught aphids with glue. Döring & Hardie (2007) question the use of glue, because aphids will not necessarily remain where they first land. Instead, aphids will gather additional cues before settling on a plant or rejecting it. According to Döring & Hardie (2007), post-landing decisions might counterbalance host choices made during flight, which remains unaccounted for in our experiment. Obviously, post-landing decisions are important, but this comment is confused about the stage at which aphids might react to a warning signal.

When searching for suitable hosts, aphids face a hierarchy of decisions: (i) on which individual to land (decision among plant individuals), (ii) where to sample a plant (decision within plant individuals), and (iii) whether or not to vacate the plant after sampling. Importantly, the coevolutionary hypothesis makes predictions about aphid behaviour only at the first level, the decision among plant individuals. This is because the general adaptive significance of warning signals (here leaf colour) is that they ensure mutual avoidance of well-defended prey (individual trees) and predators (aphids). Thus, both the partners would benefit from a warning signal, because it enables aphids to select suitable hosts among other plants more efficiently, and well-defended plants to reduce infection risks caused by sampling (see Ng & Perry 2004). To test the coevolutionary hypothesis, it is therefore crucial to establish whether leaf colour functions as a visual signal that reduces initial landing rate *before* post-landing decisions can occur. Instead of using glue, Döring & Hardie (2007) advocate observations of aphid behaviour, but studies relying on observations have so far failed to establish whether leaf colour reduces initial landing rates (Ougham *et al.* 2005); mainly because the first contact of aphids with a plant cannot be assessed with reliability. In contrast, glue captures aphids at the first contact with a plant. It is thus a more reliable method for studying aphid behaviour in response to a putative warning signal when compared with simple observations.

The use of glue is further essential for advancing our current understanding of the evolution of autumn colours, because it allows us to distinguish the coevolutionary hypothesis from related hypotheses concerning post-landing decisions. For example, the defence indication hypothesis posits that leaf colour is linked to the production of defensive compounds via a common biosynthetic pathway (Schaefer & Rolshausen 2006). In this scenario, leaf colour did not evolve to repel aphids, but aphids react to pleiotropic effects of pigment production. Consequently, even though leaf colour does not function as a warning signal, fewer aphids might be *observed* on strongly coloured plants, because they vacate these plants after probing. It is thus necessary to measure the first contact with a plant in order to differentiate between alternative hypotheses on plant–herbivore interactions.

In their reply, Döring & Hardie (2007) imply that the detrimental effects of aphids are limited to reproductive individuals. However, aphids are the most common vectors of plant viruses and often transmit infections by probing tissue (Ng & Perry 2004). Indeed, aphids that do not reproduce and colonize a host are often primarily responsible for virus spread (Edwards 1963). Thus, warning signals should generally deter aphids from landing and are not necessarily limited to colonizing aphids. Moreover, if the selective pressures exerted by aphids are strong enough to generally translate into the evolution of autumnal leaf coloration in plants, aphids' avoidance of strongly coloured plants is expected to be relatively invariant. Finally, reproductive plants are characterized by high levels of circulating nutrients. Therefore, our result that aphids land preferentially on plants with a high reproduction rate holds even if aphids feed on the plant without reproducing.

In our study site, mountain ash individuals were growing in a vegetation belt. We found no evidence for an edge effect explaining fruit set and aphid numbers independently. We therefore maintain that resource allocation conflicts explain why aphids attend to reproductive investment in plants.

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The accompanying comment can be viewed at http://dx.doi.org/10.1098/rsbl.2006.0592

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