

A test of the coevolution theory of autumn colours: colour preference of *Rhopalosiphum padi* on *Prunus padus*

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According to the coevolution theory of autumn colours, the bright colours of trees evolved as a warning signal towards parasites colonizing the plant in autumn. We monitored colonization of the aphid *Rhopalosiphum padi* on individual trees of *Prunus padus* in autumn and observed a strong preference of aphids for trees with green leaves. This is the first direct observation of a key assumption of the theory, that parasites avoid bright colours. Moreover our observations, compared with previous data gathered on the same species, suggest that aphids colonizing trees with green leaves develop better in spring than aphids colonizing trees with bright autumn colours, which is consistent with the second main assumption of the coevolution theory.

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It is well known that many trees change their colour in autumn, yet the evolutionary value of autumn colours has only begun to be investigated recently (Archetti 2000, Hamilton and Brown 2001, Archetti and Brown 2004). The coevolution theory postulates that autumn colours are a warning signal towards herbivores that lay their eggs on the trees in autumn (Archetti and Brown 2004). According to the coevolution theory, bright colours may be revealing the level of defensive commitment of the plant. On an intraspecific level, therefore, individuals of signaling species will vary in expression of this signal, with defensively committed individuals producing a more intense display, which proves aversive to the monophagous pests that drive the signal evolution. Coevolution of colours and colour preference will allow well-defended plants to reduce the load of parasites and the parasites to locate the most profitable hosts for the winter.

An assumption of the theory is that some herbivore insect species migrate to their winter hosts (the trees) when there is variation in the colour of the leaves; the theory predicts that these insects prefer trees with green leaves or dull hues of autumn colours. Aphids are the main candidate for the role of autumn parasites in the coevolution theory (Archetti 2000, Hamilton and Brown 2001, Archetti and Brown 2004) because they have colour vision (Moericke 1955), many migrate to trees in autumn to lay overwintering eggs (Dixon 1998), and because they are common, widespread and able to cause substantial damage to their host trees (Dixon 1971a,b).

Few papers discussed aphid preference for colours before the birth of the coevolution theory. Furuta (1986, 1990) suggested aphid preference for green over red autumnal leaves of *Acer palmatum*. Hagen et al. (2003) demonstrated for the first time that more colourful trees

(*Betula pubescens*) in autumn suffer less insect damage the following spring, supporting the basic prediction of the coevolution theory. However they did not analyse insect preference directly in autumn.

A complete test of the coevolution theory requires studying both insect preference for different colours in autumn and their growth rate on the tree the following spring. Moreover the relationship between autumn colours and defensive commitment of the tree must be investigated. A comprehensive discussion of the assumptions, predictions and possible tests of the theory has been done by Archetti and Brown (2004). Here we test the main assumption of the theory, that aphid migration corresponds to a period when there is variation in autumn colours, and the main prediction of the theory, that parasites avoid trees with bright leaves.

Material and methods

We monitored migration of the aphid *Rhopalosiphum padi* to its winter host *Prunus padus* in Silwood Park, in southern England, in Autumn 2002. *Prunus padus* at Silwood Park is distributed in a small area surrounded by herbs and various other small plants. The trees were planted in 1992 as two year old saplings, and are distributed in a regular pattern of 10 × 4 rows, with a distance of about 2 m from one another; we excluded 10 of the trees because they were too small (less than 1 m – trees less than 1 m in height, although attractive to aphids (Leather 1981) had too few leaves available for sampling) or because too high (impossible to sample).

The leaves of *Prunus padus* change their colour from green to red and yellow with different hues starting from the centre of the leaf. The colour was measured visually, as percentage of yellow and red versus green, twice by the same observer but independently, during the same day, once before and once after the aphid count. We also measured, at the same time and with the same method, the degree of leaf retention.

Arrival of aphids was monitored by direct observation and by reference to the Rothamsted insect suction trap at Silwood Park. We then counted the number of aphids per 100 leaves on 30 individual trees.

These measures were repeated on successive days, from the beginning of aphid migration to the end of leaf fall, for a period of approximately one month (2nd, 5th, 7th, 10th, 14th, 16th, 19th and 24th October 2002). Data on eight and timing of flowering and bud burst were collected as well in the same period.

Results

Aphids began to arrive in Silwood when there was already a huge variation in colour between trees, with

some of them still completely green, a few of them almost completely red and most of them with intermediate values (Fig. 1). Therefore the timing of the signal matches exactly the timing of aphid choice. Aphids were still migrating when leaves fell completely; complete leaf fall was suddenly accelerated, at the end of October, by a storm that made the last remaining leaves fall.

We found a negative correlation between the percentage of red–yellow leaves and the number of aphids, as predicted by the hypothesis (Fig. 2). This correlation is significant for the mean values of the period, both for gynoparae (autumn migrants; $R = -0.859$, $p < 0.0001$) and oviparae (born from the gynoparae on the leaves;

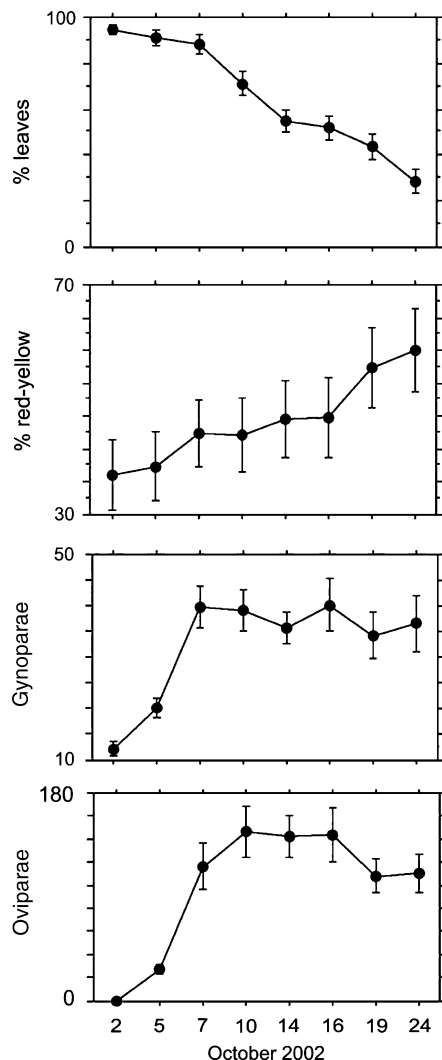
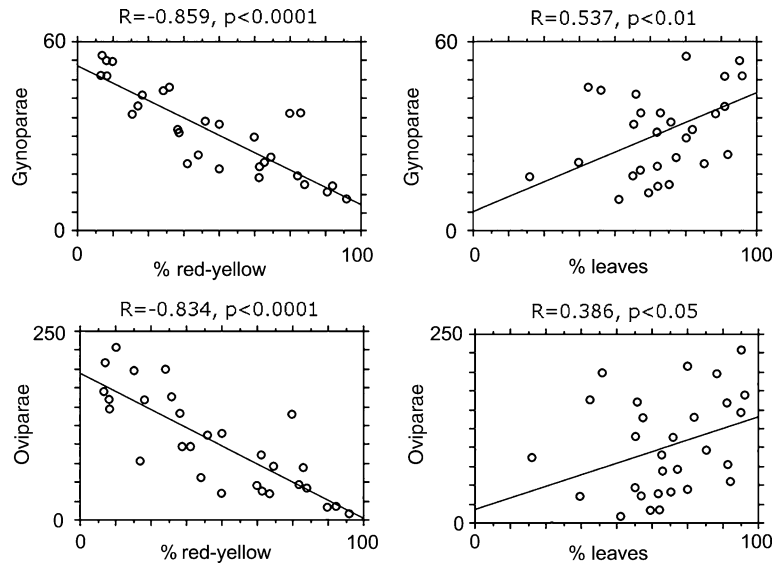


Fig. 1. Mean values of degree of leaf retention (% leaves on the tree), degree of red and yellow (% red and yellow leaves), number of gynoparae per tree (on 100 leaves) and number of oviparae per tree (on 100 leaves) on successive days of October 2002. Bars show the standard error.

Fig. 2. Correlations between the mean (of the eight days of the observations) number of aphids (number of oviparae or gynoparae per 100 leaves) and the mean degree of red–yellow or of leaf retention per tree.



$R = -0.834$, $p < 0.0001$), and for each day when the data were collected. There was also a significant correlation between the mean value of the degree of leaf retention and the mean number of aphids (Fig. 2; $R = 0.537$, $p < 0.01$ for gynoparae; $R = 0.386$, $p < 0.05$ for oviparae), as Moran and Witham (1990) had also previously observed. The correlation between colour and number of aphids still holds even when correcting for the degree of leaf retention (oviparae: $R = -0.814$, $p < 0.001$; gynoparae: $R = -0.796$, $p < 0.001$). No significant correlations were found between colour or number of aphids and tree height, the number of flowers produced or the timing of bud burst in the spring.

We also tried to measure the growth rate of aphids in spring but this was not possible as there were very few aphids surviving after the winter and at the end of the spring only one tree had a population of aphids (as revealed by the formation of galls).

Discussion

We observed that an aphid species (*Rhopalosiphum padi*) began to migrate to its winter host (*Prunus padus*) when some of the trees were almost completely red, some of them completely green and most of them variable in colour, and colonization went on until leaf fall. The timing of the signal with intraspecific variation of colour, at least in this case, is extraordinarily exact, as assumed by the coevolution theory.

More importantly, a strong preference of aphids for trees with green leaves was observed. This is in agreement with the observations of Hagen et al. (2003) and is also the first direct evidence of colour preference (for green) in autumn. Therefore our observations support the coevolution theory.

It is possible that other species have other preferences. Wilkinson et al. (2002) state that yellow is normally an attractive colour to aphids, but it will be necessary to investigate preference for colours in autumn in many more species. On the other hand it has been shown that among aphids that are attracted to yellow, individuals have a preference for the most diluted shade (Moericke 1969). The fact that yellow is attractive to aphids (but direct evidence for this in autumn is lacking) would not be inconsistent with the coevolution theory (Archetti and Brown 2004). A preference for dull yellow will result in avoidance of trees displaying the strongest yellows (or red) in favour of others displaying only impure tints. The important cue is therefore relative intensity – individual hosts are competing to produce the most intense colour and thus avoid colonisation (Archetti and Brown 2004). It would be interesting to study how aphids react to different colours (red or yellow) but unfortunately this is not easy in *Prunus padus* because single leaves have different intermediate hues of both colours.

Is it possible that aphids choose their host tree by means of the degree of leaf retention and correlation with colour is just a casual relationship? According to our data, and also previous data (Leather 1981, Moran and Witham 1990), preference for trees that retain their leaves for longer is a possibility. However, as we showed, this does not rule out a role for colours. Indeed the correlation for colours was stronger than the correlation for the degree of leaf retention, and it is possible that the correlation for the degree of leaf retention is a side-effect of the preference for green leaves.

It should also be noted that *Rhopalosiphum padi* makes its decision to start producing sexual morphs based on July temperatures (i.e. well before its migration period begins, Ward et al. 1984) in order to ensure that the oviparae have enough time to mate and lay eggs

before leaf fall – they should thus seek out those trees that retain their leaves longer, i.e. trees with green or yellow leaves.

We did not manage to measure the growth rate of aphids in spring because of the very low number of individuals that survived winter. The abundance of aphids of this species is known to be very low in southern England compared to its main area of distribution (Scotland) and while the number of insects in autumn was great enough to have significant results, the winter mortality was so high that very few trees ended up with any aphids at all in spring and just one of them had galls at the end of the spring. Therefore it has not been possible to test whether the growth rate of the aphids is higher on trees that were green in autumn.

Previous data (Leather 1986) on the growth rate of the same aphid species on the same tree, however, show that the growth rate of *Rhopalosiphum padi* on *Prunus padus* in Scotland is lower on trees that had experienced the lower load of aphids in autumn. Colour had not been measured in that case, but if the same correlation of colour with abundance of insects exists in that case too, then this means that aphids grow better on trees with dull leaves (because these are the ones with the greatest number of aphids). Certainly, the trees that the aphids preferred in the autumn and on which they performed better in the spring were those that retained their leaves for longest (Leather 1990). This would be an indirect confirmation of the second part of the hypothesis. However we must still be cautious on this point; to be sure it would be necessary to measure directly the link between tree condition and the degree of defensive commitment.

A direct link between autumn colouration and tree condition has been recently reported by Hagen et al. (2004): they explored the relationship between autumn colouration and level of fluctuating asymmetry in leaves (indicator of the tree's quality) in *Betula pubescens* and found that bright autumn birches are in better condition and therefore, they suggest, should be better at fighting off herbivores.

In principle one might argue that tree colour is due only to random environmental factors and that aphids seek for the most nutritional trees irrespective of colour preference, with green being preferred only because green leaves have more nutrients. Bright colours, however, are expected to allow a better protection against photo-oxidation (Merzylak and Gitelson 1995, Hoch et al. 2001, Schaefer and Wilkinson 2004) and, as a consequence, to recover more nutrients from falling leaves; therefore if aphids look for the best nutritional capacity they should prefer yellow (Holopainen and Peltonen, 2002), not green (which is exactly the opposite of what our data show).

We have shown that aphids avoid bright colours in autumn, and we suggest that this is consistent with the coevolution (signalling) theory. The theory is clearly open to further direct observation and certainly before rejecting it or accepting it more data are needed from many more species.

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