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Autumn tree colours as a handicap signal

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Many species of deciduous trees display striking colour changes in autumn. Here, we present a functional hypothesis: bright autumn coloration serves as an honest signal of defensive commitment against autumn colonizing insect pests. According to this hypothesis, individuals within a signalling species show variation in the expression of autumn coloration, with defensively committed trees producing a more intense display. Insects are expected to be averse to the brightest tree individuals and, hence, preferentially colonize the least defensive hosts. We predicted that tree species suffering greater insect damage would, on average, invest more in autumn-colour signalling than less troubled species. Here, we show that autumn coloration is stronger in species facing a high diversity of damaging specialist aphids. Aphids are likely to be an important group of signal receivers because they are choosy, damaging and use colour cues in host selection. In the light of further aspects of insect and tree biology, these results support the notion that bright autumn colours are expensive handicap signals revealing the defensive commitment of individual trees to autumn colonizing insect pests.

Keywords: aphid; leaf; host selection; communication; honest signal; pigment

1. INTRODUCTION

The diversity and expense of pigment synthesis in leaves about to be shed has, apart from biochemical study, attracted little academic attention. The most commonly encountered explanation of spectacular autumn colours is that they are incidental side-effects of a controlled senescence. For instance, when discussing the synthesis of new pigments in leaves about to be shed, Matile (2000) concludes that 'such biochemical extravagancies associated with leaf senescence may have evolved in the absence of selection pressure'. To our knowledge only two functional hypotheses exist in the literature. Note, however, that the fruit-flag hypothesis (colourful leaves serve to highlight fruits; Stiles 1982) is necessarily limited to fruit-bearing trees, and the ultraviolet-screen hypothesis (yellow carotenoid pigments serve to protect leaves from photo-oxidative damage prior to abscission; Merzlyak & Gittleson 1995) is more relevant to leaf construction. Importantly, while neither contradicts the signalling hypothesis, unlike the signalling hypothesis, neither can account for the striking variation in autumn coloration both within and between species of deciduous trees.

The signalling hypothesis makes predictions on two interrelated levels. On an interspecific level, tree species suffering greater insect attack should invest more in defence and defensive signalling. On an intraspecific level within signalling species, the most defensively committed individuals should produce the most intense displays, increasing the likelihood that the specialist pests driving the signal evolution will land on another individual of the same species. The inter- and intraspecific predictions are separate but interrelated, mirroring an earlier study on parasite-driven signals in birds (Hamilton & Zuk 1982). Here, we concentrate on examining interspecific trends,

to provide an empirical framework for future experimental research on individual signalling species.

2. METHODS

We investigated the signalling hypothesis by examining the association between aphid diversity and degree of autumn coloration across 262 north-temperate tree species. The data-set is available from S.P.B. on request. We focused on aphid-deciduous-tree interactions because aphids are, at present, an important and well-documented pest of trees (Blackman & Eastop 1994) and have a long proven history of association (Heie 1994). Furthermore, many aphids show a peak in migratory behaviour in autumn (Dixon 1969), just as the tree leaves are changing colour. Note, however, that the proposed signalling system is likely to hold between other plant groups and their most significant insect pests.

Aphid diversity was used as the best available comparative estimate of insect damage, leading to the prediction that trees beset by many aphid species would, on average, invest more in autumn-colour signalling than less troubled trees. Furthermore, we expected specialist (single winter host species) aphids to be most important in driving the evolution of autumn signalling because specialist pests tend to be more damaging (Coley & Barone 1996; Mackenzie 1996).

The set of 262 tree species was constructed from two field guides (Mitchell 1974; Little 1980), subject to a number of exclusions. Hybrids, clones and other cultivated species were excluded, in order to focus on naturally selected colour traits. To minimize likely false zeros in the aphid data, tree genera for which no aphid data were available were also excluded. Using strict rules based on the wording in the guides, we gave each tree species a score for the development of yellow coloration and another score for red. The scores corresponded to the following field-guide wordings relating to the degree of autumnal coloration: 0, colour change not mentioned; 1, dull (or brown-) yellow or red; 2, yellow or red; 3, bright (or striking, intense, etc.) yellow or red. A mention of brown autumn coloration scored 1 for both colour variables.

Estimates of the control variables (leaf size, tree size, fruit and flower colours, climate and geographical range) were

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Table 1. Phylogenetic regressions (Grafen 1989) of autumn colour against aphid diversity.

(The columns present statistics for a range of aphid–host specificities, from extreme specialists (one winter host species) to extreme generalists (more than three genera of winter hosts). The first and second rows are *F*-values and the third row shows the corresponding degrees of freedom.)

colour	aphid diversity, categorized by winter-host specificity					
	all aphids	one species	one genus	two genera	three genera	more than three genera
redness	0.96	5.97*	0.49	2.93	1.45	0.77
yellowness	7.72**	17.28***	2.89	0.01	0.00	0.05
d.f.	1, 49	1, 40	1, 39	1, 29	1, 10	1, 33

* $p < 0.05$, ** $p < 0.01$ and *** $p < 0.001$.

obtained, where possible, from the same guides, based on simple information on geographical location, typical leaf and tree dimensions and fruit and flower colours. Fruit ($n = 135$) and flower ($n = 132$) redness were of interest in assessing the possibility of pleiotropy in leaf, fruit and flower development, and were recorded as either present or absent. Species range ($n = 117$) was recorded on a four-point scale: 0 = < 130 000 km²; 1 = 130 000–520 000 km²; 2 = 520 000–2 600 000 km²; 3 = > 2 600 000 km². Climate ($n = 117$) was quantified categorically on a three-point scale: dry, warm temperate, and cool temperate. An estimate of leaf size ($n = 135$) was obtained by multiplying leaf length by leaf width. An index of tree size ($n = 135$) was obtained by multiplying tree height by the square of the trunk diameter at waist height.

After completing colour and control scoring, we tabulated the number of autumn colonizing aphid species associated with each tree species using a recent monograph of world tree aphids (Blackman & Eastop 1994). Only aphids with winged autumnal morphs were included in the analysis. Five counts were recorded for each tree species, giving the numbers of aphid species specific to the tree at the species level, and at the levels of infesting just one, two, three, or more than three genera of trees. Aphid–tree associations recorded as very recent, when either partner has been introduced into a new area by human activity, were excluded.

The strength of association between autumnal coloration and the diversity of aphid attack was quantified using both cross-species correlation and phylogenetic regression (Grafen 1989; Grafen & Ridley 1996). Phylogenetic regression allows the incorporation of phylogenetic information into the statistical analysis of comparative datasets, in order to identify correlated character changes that occur repeatedly in evolutionary lineages. As with other correlated-divergence methods, each radiation in the phylogeny, rather than each present-day species, contributes one data point to the regression analysis (Price 1997).

A phylogenetic tree linking the 262 tree species was constructed using the taxonomic information captured in the two field guides, with branch lengths specified using Grafen's (1989) default 'figure 2' method. Phylogenetic regression was implemented using PHYLOGLM v. 1.03, running in GLIM 3.77 (Royal Statistical Society 1985).

3. RESULTS

The phylogenetically controlled analysis revealed that the degree of yellow coloration in autumn leaves was significantly correlated with the number of aphid species,

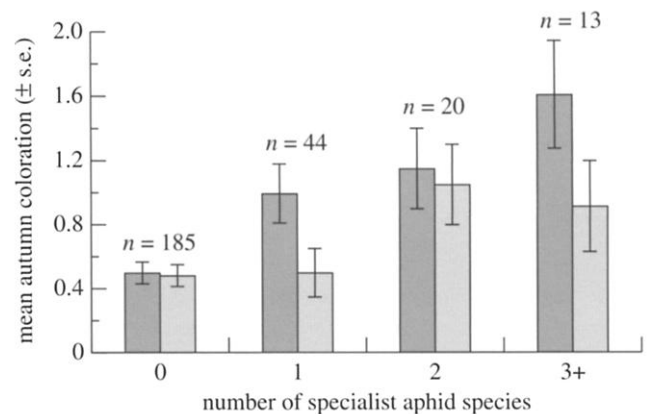


Figure 1. Autumn colour (\pm s.e.m.) as a function of specialist aphid diversity. Dark and light bars record mean yellow and red scores, respectively. For yellow, Spearman's rank correlation coefficient, $r_s = 0.30$, $n = 262$, $p < 0.005$; for red, $r_s = 0.14$, $n = 262$, $p < 0.01$.

regardless of host specificity (table 1). Repeating the analysis for specialist aphids alone, the positive association with yellowness was strengthened, and an independent significant correlation with redness emerged in both the raw (cross-species) and the phylogenetically controlled analyses (table 1 and figure 1).

The analyses of both the raw and the phylogenetically controlled data show statistical significance, hence the evidence for a non-chance relationship between strength of autumn coloration and diversity of specialist aphids can be regarded as secure. Strong autumn coloration is over-represented in tree species that are hosts to specific aphids (i.e. aphids that are their most particular enemies). Note that the correlation between aphid diversity and autumn redness strengthens when phylogenetic control is imposed, suggesting numerous convergences to autumnal redness accompanied by an aversion to red on the part of the appropriate aphids. That yellow autumn colours might need to have re-evolved on fewer occasions fits with the relative ease of manifesting yellowish pigments. These are mainly derivatives of β -carotene and related compounds, which are universal accessories of photosynthesis.

To investigate the potential for a causal relationship between aphid diversity and autumn coloration, the above analyses were repeated for specific aphids while

Table 2. Phylogenetic regressions (Grafen 1989) of autumn colour against specialist aphid diversity, given a range of controls.

(The columns present phylogenetic regressions of autumn colour on specific aphid diversity, given different controls. The first and second rows are F -values and the third row shows the corresponding degrees of freedom.)

colour	no control	leaf size	tree size	climate	geographical range	autumnal redness	autumnal yellowness	fruit redness	flower redness
red	5.97*	7.47*	6.91*	0.51	2.22	—	5.62*	5.90*	5.53*
yellow	17.28***	11.40**	8.36**	9.91**	12.97**	17.96***	—	8.94**	9.34**
d.f.	1, 40	1, 36	1, 37	1, 28	1, 27	1, 43	1, 42	1, 24	1, 25

* $p < 0.05$, ** $p < 0.01$ and *** $p < 0.001$.

controlling for a number of relevant and potentially confounding variables (climate, geographical range, leaf size, tree size, fruit colour and flower colour; table 2). In all cases, the significant correlation between yellowness and specific aphid diversity remained, regardless of the control used. The climate and geographical-range controls resulted in the redness correlation losing significance; however, further tests indicated that the loss of significance in these two cases was a consequence of a reduced data-set (geographical information was available for only 117 species) rather than an effect of the controls. Leaf yellowness was found to be positively and significantly correlated with both range size (phylogenetic regression, $F_{1,18} = 7.39$, $p < 0.05$) and tree size (phylogenetic regression, $F_{1,22} = 11.44$, $p < 0.01$). These results may reflect a bias in field knowledge: big, widespread trees will generally be better described. None of the remaining variables showed any significant relationship with either the redness or the yellowness of autumnal leaves. Overall, the use of varied controls strengthens the argument that the specific-aphid–autumn-colour link is causal.

4. BIOLOGICAL CONTEXT

In addition to the association between parasite burden and elaboration of autumn colour, several aspects of aphid and tree biology make the case for autumn signalling more compelling.

(a) Autumn coloration is expensive

An essential component of a handicap signal is cost (Zahavi 1975; Grafen 1990). If the signal is not costly then a weak signaller could pretend to be strong and thus undermine signal reliability. A number of potential honesty-ensuring costs are associated with leaf-pigment signalling.

The carotenoid yellows of many autumn displays follow the selective resorption of chlorophyll (Sanger 1971). The highly selective resorption of leaf pigments leads to a significant and avoidable loss of energy; for instance in *Acer platanoides* no more than 50% of carotenoids are recovered before leaf fall, whereas around 95% of chlorophylls are resorbed (Merzlyak & Gittleson 1995). The cost to the tree is compounded by the loss of the lipids in which the carotenoids are suspended. A further cost of autumn signalling may be incurred due to the loss of primary production following an early cessation of photosynthesis.

In addition to differential pigment decomposition, colour change also results from the synthesis of new

compounds. A number of fluorescent compounds and optical brighteners have been recorded only in autumn leaves (Duggelin *et al.* 1988; Matile *et al.* 1992). The case against a simple economy is even stronger for the anthocyanin reds and purples because they are manufactured in often massive quantities in autumn leaves (Boyer *et al.* 1988; Ji *et al.* 1992), suggesting a major energetic cost to red autumnal colour.

The range of potential costs associated with the synthesis and loss of pigments indicates that there is the potential for handicap signalling in autumn trees. The variability in autumn colours within species (see §4c) may indeed honestly reflect the variation in defensive commitment among trees. The expense, waste and scattered phylogenetic distribution of autumn displays suggest that autumn colours are adaptive. The following three points show that their most probable function is to serve as conspicuous signals: in short, they are 'pick on someone else' signals to specialist autumn-flying insects.

(b) Aphids are damaging

An expensive signalling strategy will only evolve if the recipients' behaviour is economically important to the signaller. Aphid damage is often high: if *Drepanosiphum* aphids were eliminated from sycamore trees, it has been estimated that wood deposition would increase 2.8-fold (Dixon 1971a). Infested saplings of lime and oak often weigh less at the end of a year than they did at the start (Dixon 1971b). Even fleeting contact with aphids can cause serious damage through the transmission of viruses (Harris & Maramorosch 1977); hence, signalled deterrents that act before the insect samples the plant (antixenosis) carry an important benefit over deterrents (e.g. toxins) that act at the point of sampling (antibiosis).

The aphid record back to the Carboniferous (Heie 1994) suggests that damage has occurred throughout the entire history of the angiosperms, the most autumn-coloured group. Maples (*Acer*) are particularly troubled by specific aphids, as this quote from Blackman & Eastop (1994) reveals: 'There are several aphid genera which are virtually specific to *Acer*, and within these genera there is a high degree of monophagy, although a few species are able to colonize several *Acer* species.' We note that maples are well known across north-temperate regions for their brilliant autumn colours.

(c) Aphids are discriminating

Individuals within a plant population commonly show extensive variation in quality as hosts for their insect

pests (Whitam 1983; Moran & Whitam 1990; Fritz 1995). For example, tree-specific survivorship of autumn migrants of *Pemphigus betae* colonizing *Populus angustifolia* varies from 0 to 76% (Whitam 1983).

In the face of such high fitness differentials between hosts, colonizing insects will experience a strong selection pressure to develop mechanisms of adaptive discrimination between good- and poor-quality hosts. When herbivores are selecting existing tissues, direct assessment of a critical fitness determinant, say leaf size, is generally possible. In the case of autumn-ovipositing insects, the situation is more complex due to the time lag between host selection in autumn and host exploitation by progeny the following spring. Adaptive discrimination is constrained by the availability of host features detectable at colonization and correlated with host quality at the time of exploitation. Despite these constraints, autumn migrants of *P. betae* colonizing cottonwood trees show preferential colonization of more favourable hosts (Moran & Whitam 1990).

The potential role of autumn coloration in the discriminatory process of autumn migrants is supported by the existence of considerable variation in both the timing and the degree of colour change among individuals of colourful tree species at a single site (Furuta 1986, 1990). Autumn migrants of *Periphyllus californiensis* colonizing *Acer palmatum* in Japan were recorded to colonize yellow-orange *A. palmatum* individuals preferentially, leaving the most intensely red individuals almost aphid free (Furuta 1986, 1990). Note that the few aphid individuals colonizing the reddest trees suffered reduced fitness as measured by the fecundity of their progeny in spring (Furuta 1990).

(d) *Aphids use colour in host selection*

For a number of well-studied aphids, yellow-green light has been shown to be the most attractive (Prokopy & Owens 1983; Hardie 1989), though for the great majority of species the precise preferences are unknown. Interestingly for the present hypothesis, however, it has been shown for three species of yellow-seeking aphids that an undiluted hue of the most attractive wavelength attracts fewer aphids than the same hue diluted with white (Moericke 1969). We suggest that this preference for impure yellow will result in avoidance of trees showing maximal signalling in favour of others managing to produce only impure tints. We argue that the important cue is relative intensity: individual hosts are competing to produce the most intense colour and so avoid colonization. An analogy can be made with the handicap-signalling theory of stotting in gazelles, in which gazelles perform energetic stotting displays to dissuade cheetahs from giving chase (Fitzgibbon & Fanshaw 1988). While a cheetah may select a metaphorically 'off-colour' gazelle, aphids may literally prefer off-colour trees.

Among aphids with known visual sensitivities, reflected red light is thought to be at or just beyond the perception of the majority (Prokopy & Owens 1983). However, a number of studies suggest that reds can play an important role in aphid antixenosis (Ellis & Hardman 1988; Singh & Ellis 1993; Ellis *et al.* 1995). Our hypothesis predicts that specialist aphids of red autumnal trees will have red-sensitive vision and show increasing aversion to increasing red coloration.

5. DISCUSSION

The diversity of autumnal coloration has been remarked upon many times in comparisons of trees both across (e.g. Ji *et al.* 1992; Matile 2000) and within (e.g. Furuta 1986, 1990; Matile 2000) species. Simple observation easily reinforces this claim. Here, we suggest that this diversity of coloration reflects, in part, a signalling interaction between certain tree species and their most aggressive pests. The comparative data on autumn coloration and aphid diversity point to a suggestive pattern of association. Evidently, direct experimental investigations are now required to test these ideas on characteristically bright tree species and their autumnal pests.

The use of comparative data to investigate the signalling hypothesis is complicated by a lack of comparative data on the damage sustained by specific tree species as a result of autumnal infestation with aphids. Ideally, we would present data on an 'impact factor' of aphids on each individual host species, but, as is often the case in comparative studies, the limits of the available data force the adoption of alternative measures. As a result of this limitation, we used instead the diversity of aphids per tree species as an indicator of the insect damage sustained per tree species. Interestingly, the diversity of specialist aphids emerged as the key correlate with autumn coloration, which, when viewed in conjunction with the signalling hypothesis, reinforces the independent suggestion that specialist pests tend to be more damaging to their plant hosts (Coley & Barone 1996; Mackenzie 1996).

From an experimental perspective, the major outstanding prediction of the handicap-signalling hypothesis is the intraspecific association between signal intensity and insect attack, within a signalling species. The importance of relative signal intensity in intraspecific host selection needs to be investigated both in observational field studies and in simple choice experiments, focusing on colourful tree species and their specialist autumn colonizing pests.

The causes of within-species variation in signal intensity are likely to be diverse, though we have focused primarily on the degree of defensive commitment. Note that defensive commitment is not necessarily correlated with plant resource holding or vigour; indeed the inverse may even be true (Mutikainen *et al.* 2000). Experimental investigations on tree clones raised under differing resource conditions could offer important insights into the relationships between resource holding, defensive expenditure and autumnal coloration.

Broadening the perspective on insect pests beyond aphids is likely to be most fruitful for the red-signalling trees. That the colour-signalling system may have evolved against many insects in addition to aphids is suggested by the weaker, yet still positive, correlation found for red.

In summary, we suggest that tree species suffering increased insect damage are more likely to evolve signals of defensive commitment perceptible to their insect pests. Autumn coloration is suggested to be a handicap signal of such commitment: the intensity of coloration honestly indicates defensive commitment through the costs of pigment synthesis, resource loss and primary-production loss. Aphids are likely to be an important group of receivers because they are choosy, damaging and have colour-sensitive vision.

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