



STABY

The Origin of Autumn Colours by Coevolution

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We lack an adaptive explanation for a striking phenomenon, that of bright colours displayed in autumn by the leaves of many deciduous trees. The usual explanation is that it is simply a non-adaptive secondary effect of leaf senescence. A game-theoretic model of biological signalling provides an adaptive hypothesis for autumn colours showing that they can be the result of a process of coevolution between insects and trees: if leaf colour acts as a warning indicator of the tree's vigour to autumn parasite insects, trees can gain advantage from the reduction of parasite load and insects can gain advantage from location of the most profitable hosts to lay their eggs. The results of the model are consistent with Zahavi's handicap principle. Possible explanations for the origin of the system and evidence from natural history are discussed.

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1. Introduction

The leaves of many deciduous trees change their colour in autumn before falling: it is a striking phenomenon, well known to everybody. Yet nobody has ever explained its possible adaptive meaning. We know many details about its biochemical and physiological bases, that is we know how the phenomenon occurs, but we do not know why it occurs, that is we do not know what, if any, is the adaptive advantage of coloured leaves. The phenomenon of bright colours is connected with the process of leaves senescence and abscission, but it is not the same thing. Senescence and abscission are adaptations of the tree to face a period of short daylight and low temperatures in which the cost of keeping the leaves on is bigger than the benefit due to the

photosynthesis intake (Thomas & Stoddart, 1980). Thus, we know an adaptive explanation for leaves abscission in autumn. But many deciduous trees do not show bright colours in autumn and, on the other hand, there are evergreen species that show a partial cycle of destruction and renewal (Ottander *et al.*, 1995).

The usual explanation of autumn colours of many deciduous species is that it is simply a secondary, non-adaptive, consequence of the process of senescence, in which the pigments in the leaves change their structure and we can see the colour change from green to some hue of red or yellow. This is due to the degeneration of the chloroplasts and the decomposition of the chlorophyll pigments to colourless low molecular weight products (Goodwin & Mercer, 1983). The preferential destruction of chlorophylls, that in non-senescent leaves disguise the presence of carotenoids and flavonoids, allows the red and yellow hues of these pigments to stand out (Sanger, 1971).

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However, there is a good evidence that, in addition to differential pigment decomposition, colour change is also due to synthesis of new pigments in autumn (Boyer *et al.*, 1988; Duggelin *et al.*, 1988; Chang *et al.*, 1989; Matile *et al.*, 1992). The ex-novo synthesis of these pigments in leaves that are going to fall and die in a short time cannot be seen as a secondary consequence of senescence, and requires an adaptive explanation. Merzylak & Gitelson (1995) proposed that autumn pigments might have a protective effect, preventing dangerous photooxidation processes in non-senescent leaves, but this protective effect seems useless in leaves just before abscission.

2. An Adaptive Hypothesis for Autumn Colours

Hamilton (pers. comm.) proposed an adaptive explanation for autumn colours. According to Hamilton's hypothesis, autumn colours are the result of a process of coevolution between plants and insects. The idea is that bright colours are signals revealing the strength of the tree, directed towards insects that, in autumn, lay their eggs on the tree itself. Brightly coloured trees will be favoured if the colour is a deterrent signal toward potential parasitic insects. Insects, on the other hand, will gain advantage from their capacity to recognize weaker plants, that are less able to produce chemical or physiological defences against laid eggs. Hamilton had in his mind a particular group of insects, namely aphids. In fact, aphids typically migrate on arboreous plants in autumn to lay eggs that pass the winter and they use colour vision to select host trees (Hardie, 1989). Aphids are widespread in every climatic range and they manage to live on almost every plant species of the planet. Note that aphids do not lay their eggs on the leaves. Leaves are only used as a signal and eggs are laid on the main body of the tree: therefore it is not senescing leaves that are damaged but the whole tree. The damage that aphids can produce on a host tree can be substantial, due to loss of biomass and removal of lymph, transmission of viral and fungal infections. On the other hand, individuals of a population of trees are generally highly variable in quality (Whitham, 1983; Moran & Whitham, 1990; Moller, 1995; Fritz, 1995). The reason why certain individuals are more resistant to parasite

attacks is not clear, but it is probably linked to the general health and to the availability of resources of the tree: strong trees can more easily produce chemical or physiological defence systems. Whitham (1983) shows that the survival of *Pemphigus betae* individuals on *Populus angustifolia* trees varies from 0 to 76%. Given these selective pressures on both insects and trees, the coevolution of a signalling system is advantageous for both. This hypothesis implies that the signal is costly, thus vigorous trees can afford to produce a brighter colour than weak trees, and will be less attacked by parasites. This signalling system resembles that proposed by the "handicap principle" (Zahavi, 1975, 1977; Grafen, 1990a, b).

3. A Model of Insect-Tree Signalling

Consider a simple model of insect-plant interaction with discrete levels of signalling (for trees) and preference (for insects). Trees are supposed to be either strong (Q) or weak (q) in relation to their quality and either bright (S) or dull (s) in relation to the colour of their leaves in autumn. Insects cannot assess directly the quality of a tree but can only see the level of signalling. Note that quality is intended from the plant point of view, and not as a host for insect eggs. We have four possible strategies for trees: NT (never signals): regardless of quality, it never shows bright colours; AT (always signals): regardless of quality, it shows bright colours; HT (honest signal): shows bright colours if strong, dull if weak; DT (dishonest signal): shows bright colours if weak, dull if strong. We have then three possible insect strategies: DI (dull preference): lays its eggs on dull trees; BI (bright preference): lays its eggs on bright trees; II (indifferent preference) lays its eggs on either type. The strategies and their relative fitness are described in Table 1.

Given these fitness values we can look for an evolutionarily stable equilibrium (Maynard-Smith, 1982) made by a couple of strategies, one for the trees and one for the insects. It is easy to see that if the population is entirely made of HT trees then we have $W(DI) = \gamma_q$ and $W(BI) = \gamma_Q$ and the stability of DI requires $\gamma_q \geq \gamma_Q$, which is consistent with our hypothesis. Thus, DI cannot be invaded by other strategies. On the other hand, when DI is fixed in the population, the

TABLE 1
Definition of tree and insect strategies and their relative fitnesses*

Strategy	Definition	Fitness
NT (never signal tree)	$p_{qs} = p_{Qs} = 1$ $p_{qs} = p_{Qs} = 0$	$k_q \lambda_{qs} [f_{DI}(1 - \sigma_{qs}/k_s) + f_{II}(1 - \sigma_{qs}) + f_{BI}] +$ $k_Q \lambda_{Qs} [f_{DI}(1 - \sigma_{Qs}/k_s) + f_{II}(1 - \sigma_{Qs}) + f_{BI}]$
AT (always signal tree)	$p_{qs} = p_{Qs} = 0$ $p_{qs} = p_{Qs} = 1$	$k_q \lambda_{qs} [f_{BI}(1 - \sigma_{qs}/k_s) + f_{II}(1 - \sigma_{qs}) + f_{DI}] +$ $k_Q \lambda_{Qs} [f_{BI}(1 - \sigma_{Qs}/k_s) + f_{II}(1 - \sigma_{Qs}) + f_{DI}]$
HT (honest signal tree)	$p_{qs} = p_{Qs} = 1$ $p_{qs} = p_{Qs} = 0$	$k_q \lambda_{qs} [f_{DI}(1 - \sigma_{qs}/k_s) + f_{II}(1 - \sigma_{qs}) + f_{BI}] +$ $k_Q \lambda_{Qs} [f_{BI}(1 - \sigma_{Qs}/k_s) + f_{II}(1 - \sigma_{Qs}) + f_{DI}]$
DT (dishonest signal tree)	$p_{qs} = p_{Qs} = 0$ $p_{qs} = p_{Qs} = 1$	$k_q \lambda_{qs} [f_{BI}(1 - \sigma_{qs}/k_s) + f_{II}(1 - \sigma_{qs}) + f_{DI}] +$ $k_Q \lambda_{Qs} [f_{DI}(1 - \sigma_{Qs}/k_s) + f_{II}(1 - \sigma_{Qs}) + f_{BI}]$
DI (dull preference insect)	$p_s = 1, p_S = 0$	$(k_{qs} \gamma_q + k_{Qs} \gamma_Q)/k_s$
BI (bright preference insect)	$p_s = 0, p_S = 1$	$(k_{qs} \gamma_q + k_{Qs} \gamma_Q)/k_S$
II (indifferent insect)	$p_y = k_y$	$k_q \gamma_q + k_Q \gamma_Q$

* p_{xy} is the probability that a tree of quality x (q or Q) shows a colour of level y (s or S); p_y is the probability for an insect to lay its eggs on a tree of colour y ; k_x is the frequency of trees of quality x ; λ_{xy} is the survival rate of an xy tree during its growth; the quantity in square brackets is the survival rate of the tree during the attack of the parasites; f_i is the frequency of insect strategy i and σ_{xy} is a measure of the damage caused by insects on xy trees, thus $(1 - \sigma_{xy})$, $(1 - \sigma_{xy}/k_s)$, $(1 - \sigma_{xy}/k_S)$, are the probabilities that an xy tree survives the attack of insects adopting, respectively, strategies II, DI, BI (in our hypothesis $\sigma_{qy} > \sigma_{Qy}$); k_{xy} is the frequency of xy trees; γ_x is the probability that an insect survives on an x tree (in our hypothesis $\gamma_q > \gamma_Q$).

conditions of stability for HT, respectively against invasion of NT, AT, DT, are

$$\lambda_{QS} \geq \lambda_{Qs}(1 - \sigma_{Qs}/k_q), \tag{1a}$$

$$\lambda_{qs}(1 - \sigma_{qs}/k_q) \geq \lambda_{qS}, \tag{1b}$$

$$k_q [\lambda_{qs}(1 - \sigma_{qs}/k_q) - \lambda_{qS}] \geq k_Q [\lambda_{Qs}(1 - \sigma_{Qs}/k_q) - \lambda_{QS}]. \tag{1c}$$

Equation (1c) can be incorporated into the first two conditions, that can be rewritten in the form

$$(\lambda_{Qs} - \lambda_{QS})/\lambda_{Qs} \leq \sigma_{Qs}/k_q, \tag{2a}$$

$$(\lambda_{qs} - \lambda_{qS})/\lambda_{qs} \geq \sigma_{qs}/k_q. \tag{2b}$$

The terms on the left are a measure of the cost for the production of the y colour by an x tree. Equations (2a) and (2b) are the conditions under which (HT,DI) is a couple of ESS. These conditions state that the cost for the production and maintenance of the signal has to be less than the cost due to parasite attack, for strong trees, while for weak trees the cost of the signal is larger. This

means that only for high-quality trees a bright, costly, signal is worth it. Moreover, given eqns (2a) and (2b), and since $\sigma_{qs} > \sigma_{Qs}$ we must also have that the cost of the signal is greater for weak than for strong trees. These are exactly the conditions for a signalling system based on the handicap principle.

The presence of the parameter k_q in eqns (2a) and (2b) points out that the existence of a signalling system depends on the environmental conditions acting on the trees' strength. For example, it is possible that eqn (2a) is not found in excessively poor environments (large k_q , NT prevails over HT) or eqn (2b) is not found in excessively rich environments (small k_q , AT prevails over HT). This can account for the fact that autumn colours are not universally widespread among deciduous trees, although this can also be explained by genetical or physiological causes.

It is easy to see that when the population is entirely made of NT or AT trees instead we have a series of indifferent equilibria, that is $W(DI) = W(BI) = W(II)$, in fact the insect cannot operate any choice. When the population of trees is entirely made of DT, then the best insect strategy is BI, but when the population of insects is entirely

made of BI the plant strategy DT is not stable. When the insect population is fixed on II instead, then NT strategy for trees is an ESS, provided that $\lambda_{xs} > \lambda_{xS}$, that is, if the signal is costly.

4. Origin of Leaf Colour

So far, we have only dealt with stability of the signalling system, stating that a stable equilibrium can exist, made of the two strategies HT and DI, under conditions (2a) and (2b). This means that a signalling system is possible between trees showing bright colours in case they are strong and insects "trusting" the signal and choosing dull trees. This does not prove in any way that this equilibrium can be actually reached from the initial conditions of the system, that is, we have to explain the origin of the coevolutionary process. We can imagine that the ancestral conditions were: absence of preference in insects and absence of colour in trees (equilibrium NT,II). It is very difficult that at the same time two mutations occur, one in the population of insects (for preference towards dull colours) and the other in that of trees (for extra pigments production in autumn); one must have followed the other in a coevolutionary process. Actually, may be it is not necessary to begin with no preference since, after all, insects must tell a tree from a non-tree, and this might impose a preference based also on colour. On the other hand, a preference cannot evolve if there is nothing to choose, and when the populations of trees is fixed on NT we can imagine the population of insects to be II. The following discussion is useful in any case to understand how a transition from (NT,II) to (HT,DI) is possible, (NT,II) being the original condition or not.

We can easily see that HT cannot invade NT in this case; in fact both HT and NT pay the cost for the presence of parasites, but HT is penalized by the cost of the signal. HT cannot even invade (NT,BI) because in this case parasites will always choose HT, which pays a cost for the signal too. HT could invade (NT,DI) but in this case we have to explain how the population changes from (NT,II) to (NT,DI), that is how the preference for a colour in the insects rises before the existence of the colour itself. When the population is entirely made of NT trees, then $W(DI) = W(BI) = W(II)$ and we have a series of indifferent, neutrally

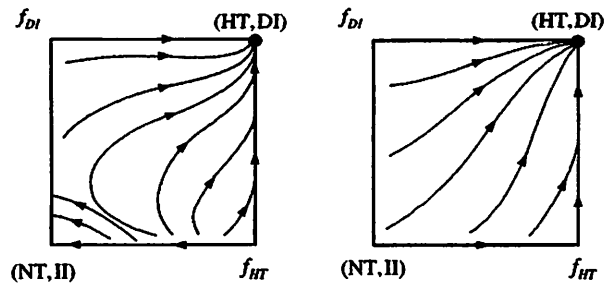


FIG. 1. Evolutionary dynamics of the origin of autumn colours. The computer simulation confirms that the proposed signalling system can evolve. The vertical and the horizontal axes, respectively, represent the frequency of DI and HT strategies. The left vertical axes denote a series of indifferent equilibria. The lines with arrows represent trajectories of the dynamics. Left: origin without colour contrast. The area on the bottom left corresponds to frequencies for which the population cannot be invaded by HT ($k_q = 0.5$, $\sigma_Q = 0.4$, $\sigma_a = 0.5$, $\gamma_a = 1$, $\gamma_Q = 0.6$, $\lambda_{qs} = 0.9$, $\lambda_{qS} = 0.3$, $\lambda_{Qs} = 1$, $\lambda_{QS} = 0.9$, $\epsilon = 0$). Right: origin with colour contrast effect ($\epsilon = 0.3$).

stable, equilibria. In fact, there is no signal and no possibility to choose. The (NT,DI) intermediate equilibrium can be reached through a series of neutrally stable equilibria by genetic drift. For HT to invade the population it is not necessary, however, that DI completely replace II but it is enough that the frequency of DI increases over a certain threshold (Fig. 1). Another possible explanation is that of a pleiotropic effect: the insect preference for a certain hue could have been initially a collateral effect of another gene or group of genes favoured by natural selection in another contest.

Another evolutionary path is possible: the stable equilibrium (HT,DI) can be reached through the intermediate (HT,II), that is, colour rises before preference, if the colour has another selective advantage apart from acting as a signal. This selective advantage can result from the effect of the colour contrast between leaf and insect: green insects (most aphids, for example) will be more conspicuous on yellow-red leaves than on green leaves, and therefore will have a smaller survival rate on the first, due to predators that can more easily locate them. This will reduce, as a consequence, the damage to the tree with bright yellow-red leaves. Thus, the disadvantage for HT due to the cost of the colour can be counterbalanced by the advantage that insects are, partly, more easily detectable by predators.

HT can invade (NT,II) if $\lambda_{QS}(1 - \sigma_{QS}) \geq \lambda_{QS}(1 - \sigma_{QS})$, and this is not possible if $\sigma_{QS} = \sigma_{QS}$, but with the colour contrast effect we have $\sigma_{QS} < \sigma_{QS}$; in particular, we can write $\sigma_{QS} = \sigma_{QS} - \varepsilon$, where ε ($0 < \varepsilon < \sigma_{xy}$) is a measure of the colour contrast. If $\varepsilon = 0$ there is no colour contrast. If $\varepsilon = \sigma_{QS}$ then $\sigma_{QS} = 0$ and the condition for invasion becomes $\lambda_{QS} \geq \lambda_{QS}(1 - \sigma_{QS})$. This condition is similar to eqn (1a) but more restrictive, and moreover it is difficult that $\varepsilon = \sigma_{QS}$ and more likely we will have $\varepsilon < \sigma_{QS}$, thus the condition will be even more restrictive. Anyway, with the colour contrast effect the evolution of the system from the origin is possible (Fig. 1). It is easy to see that now (HT,II) can be invaded by DI. Note that the system will evolve to (HT,DI) by means of the signalling process, and the colour contrast is no more necessary when the process has started. The colour contrast has no effect on the stability of (HT,DI).

5. Aphid Preference and Tree Vigour

According to Hamilton's hypothesis, pigments synthesized in autumn leaves are a demonstration of the tree's vigour to potential parasite insects that lay their eggs on the tree. So far no field data exist that support this hypothesis, however indirect evidence exists.

Brown (1996) analysed 265 deciduous tree species and proved that the species with coloured leaves in autumn are mostly those with parasite aphids. Moran & Whitham (1990) show that migrants of the aphid *Pemphigus betae* in autumn choose the most profitable trees according to some features: extension of the foliage surface and delay of abscission. They did not test for leaf colour. Preference for a certain colour is not straightforward, even if *Aphis fabae* displays a positive response to monochromatic light in the blue–yellow range, with a peak response in the green range (Hardie, 1989). It is important to notice that, according to the hypothesis, insects are attracted or repelled not by a certain colour *per se* but by relative intensity of the colour: each tree in the population is in competition with others to produce the brightest colour and thus avoid insect attack. Therefore, the duller colour can still be seen as a red or yellow hue, but it will attract insects according to its relative intensity,

that is, compared to that of the neighbours. It is possible that over a certain amount of coloured pigments, the brightness of the leaves cannot increase substantially, and the competition is on the duration of the colour: strong trees will be able to give up photosynthesis first and to withstand longer the costs of the autumn colour. An indirect evidence of this fact is that aphids prefer trees that hold their leaves on for long (Moran & Whitham, 1990).

According to our hypothesis, autumn colours are costly. In this respect, they cannot be defined as aposematic colours. Aposematic colours (Poulton, 1890) are adaptations to increase the probability that a predator recognizes a certain species: they do not necessarily reveal the quality of the bearer, and other species can evolve a colour that resembles that of a toxic species even if they are not dangerous. In this case, there can be "dishonest" signallers as far as their number in the population becomes so high that the signal loses its warning value. In the case of autumn colours instead, the honesty of the signal depends on the fact that signalling is costly.

This cost is due to many causes: the reduction of photosynthesis, and hence of the primary productivity (Stiles, 1982); the ex-novo synthesis of pigments (Britton, 1983) and the loss of these pigments, that are only partially reabsorbed before abscission (Merzylak & Gitelson, 1995). Because of the existence of these potential costs, the intensity of the colour should strongly depend on the tree health. The relationship between vigour and autumn colour, however, is still to be tested: this could be done comparing the colour of clones of the same tree grown in different health conditions.

6. Conclusion

According to the hypothesis of coevolution, autumn colours are warning signals directed to parasitic insects. If the production of the colour is costly, and hence if only strong trees can afford the cost of the colour, then this signalling system is an instance of Zahavi's handicap principle. The model shows that the stability of the system depends also on environmental conditions affecting plant vigour: the system collapses if the environment is too poor or too rich. These results go

beyond the demonstration of the verbal argument put forward by W.D. Hamilton and provide a handle for stringent empirical test of the theory.

This paper is dedicated to Bill Hamilton who allowed me to work on his original idea when I was a visiting student at the Department of Zoology of Oxford University. I wish to thank Carlo Matessi for extensive discussion and advices on the model.

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