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The distraction hypothesis depends on relatively cheap extrafloral nectaries

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ABSTRACT

Extrafloral nectaries may have evolved because they distract insects from flowers. For this to have occurred, extrafloral nectaries must be cheaper than flowers. This requirement stands in addition to the requirement that extrafloral nectaries must reduce the rate of insect visits to flowers. In the model examined here, the cost of each extrafloral nectary divided by the cost of each flower must be less than the proportion of reproduction threatened by insect visits.

Keywords: extrafloral nectaries, Kerner hypothesis.

INTRODUCTION

Wagner and Kay (2002) reintroduce us to the Kerner hypothesis of extrafloral nectaries. That hypothesis claims that extrafloral nectaries distract exploiters from real flowers, thus improving pollination. The distraction hypothesis has at least one necessary condition: having more nectaries must reduce the per-nectary visitation rate. It is this aspect of the hypothesis that Wagner and Kay so cleverly test and confirm.

For distracting extrafloral nectaries to evolve, it is surely necessary that the extrafloral nectaries dilute nectarivore visits among nectaries. But this condition is not sufficient. The evolution of distracting extrafloral nectaries also requires that they cost less than flowers. Using a simple model, I demonstrate this added condition below.

Wagner and Kay used mock extrafloral nectaries identical in morphology to their mock flowers. In some of their trials, the composition and concentration of their nectars was also identical and in no trial was the nectar of extrafloral nectaries poorer than that of flowers. Nevertheless, the authors correctly point out the importance of the relative cost of extrafloral nectaries and flowers. They suggest that if extrafloral nectaries exist to promote distraction, then natural selection might promote the evolution of extrafloral nectaries that are cheaper than flowers to produce or maintain. But if distracting extrafloral nectaries cannot be favoured by natural selection unless they are relatively cheap compared with flowers, then, rather than distraction leading to cheap extrafloral nectaries, cheap extrafloral nectaries are necessary for the evolution of distraction in the first place.

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A MODEL OF DISTRACTION

The model consists of two components. First, it describes how ant visits depress plant reproduction. Second, it sets out an allocation formula with each extrafloral nectary consuming a fraction, p, of the resources required by a real flower.

Next, the two components are put together and the combination is optimized. Ant visits are set to a constant value, v, and apportioned to flowers and extrafloral nectaries. Finally, total plant reproduction is optimized by adjusting the proportion of reproductive resources devoted to flowers.

The depression of reproduction by flower visitors

The distraction hypothesis assumes that visitors to flowers, such as ants, reduce the flowers' reproductive effectiveness. We do not know the functional form of that depression. Is it linear? Is there a threshold number of visits below which they have no effect? Is there a threshold number of visits above which further visits do not cause further damage?

For this model, I use the simplest possible functional form. I assume linearity and no thresholds. Let b_f be the reproductive contribution of a single flower and v_f be the number of ant visits to that flower. Then:

$$b_f = b - cv_f \tag{1}$$

where b is the reproductive contribution of a single flower that receives no ant visits and c, the slope, is the reduction in that value caused by each visit. To avoid upper thresholds, I assume that $v_f \leq b/c$.

Allocation

Assume that a plant has enough reproductive resources to make k flowers. Recalling that p is the cost of making an extrafloral nectary compared with that of making a single flower, we see that the plant can apportion its resources among flowers and extrafloral nectaries according to the following equation:

$$pn_e + n_f = k \tag{2}$$

where n_e is the number of extrafloral nectaries and n_f is the number of flowers. Let q be the proportion of k made into flowers. Hence, there are $n_f = qk$ flowers and $(1 - q)k/p$ extrafloral nectaries.

Building on the results demonstrated by Wagner and Kay, I set ant visits to a constant, v. Furthermore, I apportion the visits without bias among the flowers and extrafloral nectaries. Thus, each flower or extrafloral nectary receives the following number of visits:

$$v_f = v/(n_e + n_f) = pv/(k - qk + pqk) \tag{3}$$

Total plant reproduction

Total reproduction of each plant is simply $n_f b_f$. Substituting (3) in (1) yields:

$$b_f = b - \{cpv/(k - qk + pqk)\} \tag{4}$$

So:

$$n_f b_f = qkb - \{qpcv/(qp - q + 1)\} \quad (5)$$

Result

What proportion of extrafloral nectaries will maximize equation (5)? That is, at what value of q does $n_f b_f$ reach its maximum?

The derivative of equation (5) with respect to q is

$$kb - \frac{pcv}{(qp + 1 - q)^2} \quad (6)$$

We set equation (6) to zero and manipulate its terms so that we can solve for its maximum using the standard formula for quadratic equations:

$$(p - 1)^2 q^2 + 2(p - 1)q + 1 - (pcv/kb) = 0 \quad (7)$$

where q in equation (7) is $\hat{q}$, the optimal value of q given the other constants.

Eliminating the extraneous root, I find that the solution to equation (7) is:

$$\hat{q} = \frac{1 - \sqrt{pcv/kb}}{1 - p} \quad (8)$$

From equation (8), we see that if $p = cv/kb$, then $\hat{q} = 1$, and the plant should put no resources into extrafloral nectaries. For extrafloral nectaries to evolve, it is necessary that:

$$p < cv/kb \quad (9)$$

Interpreting the result

The key ratio cv/kb has a straightforward biological meaning. Its numerator, cv, is the total reproductive cost of all ant visits in the absence of extrafloral nectaries. Its denominator, kb, is the maximum reproductive output of all flowers in the absence of extrafloral nectaries. Hence, their ratio is the proportion of reproduction threatened by ant visits.

If $cv/kb = 1$, then the plants will be exterminated by the ants. Clearly, $cv/kb < 1$. Because the evolution of extrafloral nectaries requires $p < cv/kb$, it must also require $p < 1$. Extrafloral nectaries must cost less than flowers. How much less depends on how much damage ants can do. The greater the proportion of reproduction they can destroy, the more expensive extrafloral nectaries can be.

In Fig. 1, I plot plant reproduction as a function of q assuming that $cv/kb = 0.5$. As revealed by inequality (9), when the extrafloral nectaries cost half what a flower costs, then $\hat{q}$ (i.e. the optimum q) is 1. No extrafloral nectaries evolve. For $p < 0.5$, they do.

DISCUSSION

The model I investigated concludes that extrafloral nectaries, if they exist to distract nectarivores, must each cost less than the proportion of plant reproduction that ants, doing their worst, could eliminate by their visits to flowers (inequality 9). But the model is quite

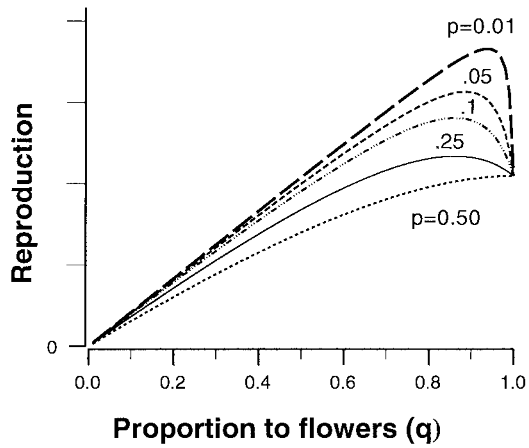

Fig. 1. Diverting some resources from flowers to extrafloral nectaries maximizes plant production if p, the cost of an extrafloral nectary, is less than cv/kb. In the example here, $cv/kb = 0.5$.

narrow and, no doubt, this ratio is model-specific. So we should not attach too much significance to the precise result.

Nevertheless, specifics of the model aside, the general conclusions appear quite robust:

- The distraction hypothesis requires that extrafloral nectaries cost less than real flowers.
- How much less depends on how much damage ant visits can do. The less potential damage, the less plants can spend on an extrafloral nectary.

The second conclusion seems so reasonable, I will not belabour it. But, to me, the first also seems obvious. Imagine a plant with extrafloral nectaries that cost the same as its flowers. What possibly could it have gained by giving up in its extrafloral nectaries whatever reproductive abilities the flowers have? Nothing at all. It can gain only if extrafloral nectaries are cheap to make, so that the expense of making them is more than compensated for by an increase in the reproductive abilities of the flowers.

By introducing the model, I wish to draw the attention of those interested in extrafloral nectaries to the importance of comparing their cost to the cost of flowers. Finding out how cheaply they can be produced may help us evaluate the distraction hypothesis.

In Fig. 1, you will observe that total plant reproduction rises as p declines. In fact, based on the model of this paper, there is no limit to this result; cheaper extrafloral nectaries are always better. But do not trust this result, for it is not robust. It depends on the assumption that the attractiveness of an extrafloral nectary is independent of its cost (equation 3). More realistically, I would expect that this attractiveness would decline as extrafloral nectaries contained smaller amounts of resources. Hence, p too should have an optimum.

Assuming the merit of the distraction hypothesis, one also wonders about the initial evolution of extrafloral nectaries. How could they have got an evolutionary start? What could the intermediates have been like?

Perhaps extrafloral nectaries gradually devolved from flowers? But the model considered here does not suggest that. It insists that extrafloral nectaries must spring up at a cost that is less than a fraction of the cost of flowers. But the model also does not allow for flower dimorphism, with some flowers fully potent and others that retain a fraction of their reproductive ability for a fraction of the cost. Such a model might show the possibility of flowers devolving into extrafloral nectaries. One wonders whether developmental plant evolutionists ever see a common origin for extrafloral nectaries and flowers?

Alternatively, one may imagine extrafloral nectaries evolving from accidental, cheap little weepy spots on plant stems. After all, the model here concludes that no amount of distraction is too little to succeed. But remember that this aspect of the model is weak. It relies on the assumption that the attractiveness of an extrafloral nectary does not depend on its cost (equation 3). Below some threshold of cost, super-cheap proto-extrafloral nectaries may not distract ants at all.

Finally, of course, one may imagine the evolution of extrafloral nectaries as the result of multiple causes, such as those discussed by Wagner and Kay. These will need to be combined into models much more complex and plastic than that of this paper.

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