Animal behaviour

Fenestration: a window of opportunity for carnivorous plants

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A long-standing but controversial hypothesis assumes that carnivorous plants employ aggressive mimicry to increase their prey capture success. A possible mechanism is that pitcher plants use aggressive mimicry to deceive prey about the location of the pitcher’s exit. Specifically, species from unrelated families sport fenestration, i.e. transparent windows on the upper surfaces of pitchers which might function to mimic the exit of the pitcher. This hypothesis has not been evaluated against alternative hypotheses predicting that fenestration functions to attract insects from afar. By manipulating fenestration, we show that it does not increase the number of Drosophila flies or of two ant species entering pitchers in Sarracenia minor nor their retention time or a pitcher’s capture success. However, fenestration increased the number of Drosophila flies alighting on the pitcher compared with pitchers of the same plant without fenestration. We thus suggest that fenestration in S. minor is not an example of aggressive mimicry but rather functions in long-range attraction of prey. We highlight the need to evaluate aggressive mimicry relative to alternative concepts of plant–animal communication.

1. Introduction

Aggressive mimicry occurs if predators use deceptive communication to deceive their prey. A central element of aggressive mimicry is that prey mis-identify the predator as something benign or even attractive [1]. Aggressive mimicry has received less scientific enquiry than mimicry by prey, and it is often not clearly differentiated from sensory exploitation as alternative strategies of communication if the interests between signallers and perceivers diverge [1,2]. Sensory exploitation occurs if traits are selected that are more effective in stimulating the sensory systems of perceivers, without the implication of fooling cognitive systems associated with object identification that is at the heart of mimicry.

It has long been suggested that carnivorous plants use aggressive mimicry to deceive prey by mimicking flowers [3,4], but the current evidence for it is not strong [5,6]. However, pitcher plants may use aggressive mimicry to deceive prey as to the position of the aperture through which they could leave the pitcher [5]. Although 25% of a total of approximately 600 carnivorous plant species are pitcher plants, this hypothesis has not been evaluated against alternative hypotheses (such as prey attraction).

Pitcher plants have leaves modified into pitcher-shaped pitfall traps. They belong to three unrelated families: Cephalotraceae, Nepenthaceae and Sarraceniaceae of which the latter two often sport transparent ‘windows’ on the upper surfaces of pitchers called fenestrations (figure 1). Juniper et al. [5] hypothesized that fenestrations function to confuse insects that have flown into the pitcher; thus using mimicry of the true aperture to aid retention of prey. Implicit in this idea is the assumption that the longer a prey is retained in the pitcher, the higher the likelihood of it alighting on or falling into the fluid at the base of the pitcher. Fittingly, fenestrations are more commonly located close to the aperture but on its opposite side and not on the basal part of the pitcher (figure 1). As yet, the physiological and ecological functions of fenestrations are underexplored (but see [7]). Adaptive
communicative function appears plausible; however, aperturemimicry is not the only possible mechanism by which fenestra-
tions might influence prey capture.

Here, we tested three possible ecological functions of
fenestrations in the pitcher plant *Sarracenia minor*: attraction
to the plant from afar, attraction into the pitcher and retention
within it. Only the latter is a clear prediction of aggressive
mimicry. If fenestrations function in aggressive mimicry of
the aperture, we predicted that prey (entering the pitcher)
should be more frequently captured or retained longer in
pitchers with fenestration compared with pitchers without
fenestration. Yet, as fenestrations could also have an attractive
effect of luring prey into the trap (e.g. by increasing light levels
within the trap [7]), we tested for that effect as well. Addi-
tionally, fenestrations may exploit sensory biases of the prey
towards contrasting plants. We thus tested whether insects
alighted preferentially on pitchers with fenestration compared
with pitchers of the same plants without fenestration.

2. Material and methods

We obtained 22 *S. minor* plants from a local supplier (Gärtnerei
Carow) and used *Drosophila melanogaster* (wild-type) as well as
two ant species (*Lasius niger* and *Lasius flavus*) as prey: *Drosophila*
*melanogaster* was used because it is a suitable species to address
both short-range and long-range attraction. The two ant species
were used because ants are the most common prey species of
*Sarracenia* plants, constituting up to 97% of prey biomass [8].

To assess the effects of fenestrations, we painted these areas with
either clear varnish (Klarlack, Praktiker, seidenmatt) so that they
remained transparent in the control treatment or with green varnish
(Buntlack, Praktiker, seidenmatt) so that they became opaque and
green in the manipulative treatment (pitcher on the left). (Online version in colour.)

Figure 1. Fenestration is located close to the aperture of the pitcher trap.
The pitcher on the right is a control with fenestration covered by transparent
varnish, whereas fenestration has been covered by green varnish in the
manipulation treatment (pitcher on the left). (Online version in colour.)

To test for the effect of fenestration on luring prey from the lip
of the pitcher (where nectar is naturally produced) into the traps,
we let 200 *D. melanogaster* crawl singly from an Eppendorf tube
onto the lip of the aperture of a pitcher (i.e. 100 per treatment
onto five successively per individual pitcher). The animals had
no access to food for approx. 30 h and were anaesthetized with
CO₂ at least 24 h before the experiment and put singly into an
Eppendorf tube at room temperature. A 24 h recovery time after
anaesthetization is recommended for behavioural experiments
[9]. They were not manipulated in any other way nor immobilized.
We repeated the experiment with 40 ants of both *L. niger* and
*L. flavus* which were not anaesthetized. All insects were uncon-
strained; thus, they could move in any direction from the lip
including flying away from it (*D. melanogaster* only). We compared
the number of flies and ants entering the trap and the latency (up to
15 min) to do so between treatments. To test for the effect of reten-
tion, we compared between treatments the time that individuals of
each species spent inside the pitcher, and the survival rate of indi-
viduals that had entered the trap. We tested for these effects with
separate linear mixed models for latency, retention time and survi-
vial as dependent variables and treatment (clear or green varnish)
as a fixed effect and plant individual as a random effect. We pooled
both ant species when analysing their survival, given that we
found no difference between the two species. Analyses were
done with the package lme4 in R.

To test for the effect of fenestration on attracting potential
prey to the plant, we positioned 22 *S. minor* plants, each with
one control pitcher and one manipulated one, singly into a
cage (30 × 30 × 18 cm) that held 50–90 *Drosophila* individuals.
We then compared the number of *Drosophila* individuals alight-
ing on each pitcher within 5 min with a paired *t*-test. This test
was only conducted with *D. melanogaster*. Capture success was
high in our experiments. Hairs on the inside of the pitchers
were curved downwards. We hypothesized that they hindered
prey from leaving the pitcher. To test that function, we cut a
hole into the pitcher (below the fenestration) and positioned
singly 15 *L. niger* and 15 *D. melanogaster* within an Eppendorf
tube on that hole. Using Binomial tests, we analysed whether they
preferentially moved downwards.

3. Results

A total of 141 *Drosophila* individuals (70% of those tested)
entered the pitcher from the lip (mean latency 2.03 min ±
0.28 s.e.m.). There were no effects of treatment or plant individ-
ual on either the latency or the number of flies entering
the pitcher (GLMM, all effects *p* > 0.2). The retention time of
flies within the pitcher (3.39 min ± 0.32) did not depend on
treatment or plant individual (GLMM, both effects *p* > 0.5).
A total of 78 (55% of flies that had entered the pitcher) were
captured by the plants. Again, there was no effect of treatment
or plant individual upon survival of prey (GLMM, both effects
*p* > 0.5). Likewise, fenestration had no effect on *L. niger* and
*L. flavus* ants. A total of 42 ants entered the pitchers. They
had no preference for pitchers with fenestration nor did they
stay longer in those pitchers (GLMM, all effects *p* > 0.3). A
total of 20 ants were caught by the plants, but there was no
effect of treatment or plant individual upon survival of ants
(GLMM, both effects *p* > 0.6). Hairs curved downward
inside the pitcher apparently impeded upward movement of
prey. Once inside the pitcher, both *L. niger* and *D. melanogaster*
moved significantly more often downwards than expected by
chance (Binomial-test both *p* < 0.01).

We found evidence that fenestrations function to attract
prey towards the plants. Control pitchers attracted
significantly more flies than manipulated ones (paired Wilcoxon test, $V = 118$, $p = 0.047$; figure 2).

4. Discussion

In contrast to the prediction of aggressive mimicry, fenestrations did not increase the retention time of $D$. melanogaster and ants within pitchers nor did they lure them from the lip into the trap. We therefore conclude that fenestrations in $S$. minor do not function to confuse prey inside the pitcher about its exit location. Fenestration also did not lure more prey into the pitcher by increasing light levels inside of it. Instead, the main function of fenestrations in $S$. minor may be to attract potential prey from afar; in our experiment, more $Drosophila$ flies landed upon pitchers with fenestration compared with those without fenestration.

The attractive function of fenestrations is plausible given that well-studied insects like bees and bumblebees show biases, sometimes innate, towards contrasting floral displays [10]. Whether the typical prey of pitcher plants exhibits such biases is unknown. An alternative explanation appears unlikely, i.e. that prey are attracted to fenestrations because they are associated with higher nectar rewards or with more attractive volatiles. First, in our experiments we used a within-individual comparison that minimizes difference in scent and nutritional rewards. Second, our manipulation changed only a small part of the natural surface of pitchers in each treatment.

Our experiments help to tease apart aggressive mimicry from other forms of (aggressive) communication in plant carnivory. Our experiments suggest that fenestrations can also influence attractiveness and/or conspicuousness of pitchers in a way that can enhance prey capture rates. Overall, we conclude that fenestrations may be selected because of their effects on long-range attraction rather than aggressive mimicry of pitcher apertures leading to enhanced prey retention. Typically, capture efficiency of carnivorous plants is low, for example ranging from 0.34 to 1.6% in five $Nepenthes$ species [11]. Because hairs inside the pitcher effectively function to retain prey, we suggest that pitchers have been selected to exploit the senses of potential prey in ways that enhance visitation rate not retention efficiency.

Mimicry is an intuitively appealing idea; but this attractiveness can lead to premature assumption of the existence of mimicry in specific systems without careful consideration and elimination of simpler, more parsimonious, explanations. Our work should not be interpreted as evidence that fenestrations do not ever function in aggressive mimicry. Indeed, fenestration in $Nepenthes aristolochioides$ influences capture rates through increased attraction of prey into the pitcher [7]. While the study reported in [7] did not differentiate the frequencies with which $Drosophila$ flies flew into a pitcher with shaded versus unshaded fenestration from variation in the likelihood that they failed to emerge from the pitcher, it clearly showed that fenestration can be involved in short-range attraction of prey. Given that fenestration can apparently function in long- and short-range attraction, we recommend exploration of the concept of aggressive mimicry in concert with other mechanisms by which sensory and cognitive exploitation of potential prey of carnivorous plants might occur. Recently, Jackson & Cross [12] argued that aggressive mimicry holds exceptional potential for advancing our understanding of animal cognition. However, to explore that potential most effectively, we must first demonstrate the importance of aggressive mimicry in candidate study systems.

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References