Fatal attraction: carnivorous plants roll out the red carpet to lure insects

H. Martin Schaefer1,* and Graeme D. Ruxton2

1Faculty of Biology, Department of Evolutionary Biology and Animal Ecology, University of Freiburg, Hauptstrasse 1, 79104 Freiburg, Germany
2Division of Environmental and Evolutionary Biology, Institute of Biomedical & Life Sciences, University of Glasgow, Glasgow G12 8QQ, UK

*Author for correspondence (martin.schaefer@biologie.uni-freiburg.de).

We provide the first experimental test of the hypothesis that the coloration of carnivorous plants can act as a signal to lure insects and thus enhance capture rates. An experimental approach was needed to separate effects of the visual appearance of plants from those of traits that may correlate with appearance and also affect capture rates. We compared insect capture rates of pitcher plants with artificially coloured red and green pitchers in a paired design, and found that plants with red pitchers captured significantly more flying insects. Thus, we present the first experimental evidence of visual signalling in carnivorous plants. Further, it has previously been suggested that carnivorous plants use contrasting stripes or UV marks on their pitchers to lure insects; our results emphasize that insect traps do not need to sport contrasting colours to be attractive; it might be sufficient to be different from the background.

Keywords: plant–animal interactions; visual signalling; insect vision; anthocyanins; traps

1. INTRODUCTION

The multiple, independent evolution of carnivory in plants is considered an adaptation to nutrient-poor habitats (Ellison & Gotelli 2001). In these habitats, the availability of animal prey is a key factor for plant fitness as it enhances biomass, flower and seed production (Moran & Moran 1998). To increase capture rates, plants might use a variety of deceiving signals to lure insects. While many carnivorous plants have nectaries and use olfactory signals, it has repeatedly been suggested that they also use visual signals to attract prey (Joel et al. 1985; Moran et al. 1999; Biesmeijer et al. 2005). This conjecture has, however, not been tested experimentally. Hence, and in contrast to the immense progress in understanding plant visual signals that are used for pollination and seed dispersal (Chittka et al. 2001; Schaefer et al. 2004), the design and efficiency of visual signals in carnivorous plants are poorly known.

The potential role of visual signalling in the remarkably diverse group of carnivorous plants is intriguing as the traps of all species examined in a large interspecific comparison sport visual characters that are considered to be attractive to insects (Biesmeijer et al. 2005). These include UV reflection and strong chromatic contrasts of radiating stripes on the traps (Joel et al. 1985; Biesmeijer et al. 2005). Remarkably, many unrelated plants sport red coloration, particularly on the structures used to capture prey. For example, pitcher plants from the genus Nepenthes sport no or very little UV reflectance but large inter- and intraspecific variation (from green to red) in the coloration of pitchers (Joel et al. 1985; Moran et al. 1999). Although the human eye perceives strong contrasts between red colours and the generally green background of most plants, red is considered dull or cryptic to most insects since their colour vision does not extend as far into the red as that of humans (Chittka et al. 2001). However, red colours are not invisible to insects (Chittka & Waser 1997), and the capture rates of Sarracenia pitcher plants correlated with the amount of red venation (Cresswell 1993; Newell & Nastase 1998). However, given that red veins are lined with nectaries (Cresswell 1993) and red is often not a strongly contrasting colour to insects, it is uncertain whether the nectaries or the red colour enhanced capture rates in these studies.

From the perspective of plant–animal communication, the development of red coloration on insect traps might be non-adaptive since the expression of anthocyanins, the pigments producing red hues, is often related to stress responses in plants (Schaefer & Rolshausen 2006). In particular, foliar anthocyanin production is often related to N and P deficiencies (Steyn et al. 2002). Consistent with this view, prey-deprived individuals of Nepenthes rafflesiana were characterized by smaller and fewer pitchers and by increased anthocyanin production (Moran & Moran 1998).

To test the adaptive value of red coloration in attracting prey, we conducted an experiment comparing capture rates in artificially coloured red and green pitchers. If red coloration is primarily a stress response, we expect no difference in the capture rates of individuals with red or green pitchers. In contrast, if red coloration is a visual signal functioning to lure insects, we expect that red pitchers would capture more insects than green ones do.

2. MATERIAL AND METHODS

We bought 20 same-aged Nepenthes ventricosa plants from a commercial supplier. In this species, originating from Southeast Asia, pitchers differed in their coloration from red to green. To exclude the effects of correlated selection, i.e. that traits associated with differential coloration (e.g. olfactory cues) may bias prey capture, we coloured pitchers artificially either completely red (experimental group) or completely green (control group) using a mixture of opaque white (Milan no. 306), yellow (Eberhard Faber no. 8801-1), and green and red paints (Buntlack, Obi). Because both colours consisted of a mix of acrylic and tempera paints, we minimized biases caused by different colours associated with the paint (albeit not entirely eliminating them). Therefore, if insects reacted differently to the colours, we assumed that this is primarily due to visual differences. Indeed, in a previous experiment, we used similar colours and found that aphids did not discriminate between these artificial colours and natural red and green plant coloration (Schaefer & Rolshausen 2007).

To measure natural and artificial pitcher colours, we used an Avantes 2048 spectrometer (Avantes, Eerbeek, The Netherlands) that was connected with a coaxial fibre cable to a Deuterium–Halogen lamp (Ava-lamp DHS) as a standardized light source.
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insects that were caught during the last 8 days of the experiment.
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active figure, we subtracted the number of insects caught on day 7
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2.9 (mean ± s.e.: experimental group: 2.9 ± 0.37 pitchers; control group
0.37 pitchers; t-test, n = 20, t = 0.0, p > 0.99). It is well known that
differences in the microhabitats might influence capture rates
(Schaefer et al. 2007). The angle of illumination and reflection was
fixed at 45°. Spectra were processed with A VASOFT v. 6.1 software
and calculated in intervals of 5 nm from 300 to 700 nm. The
artificial colours matched the natural colour variation found in
N. ventricosa (figure 1).

We categorized plants into two groups according to the number
of active pitchers. One group contained plants with one or two
pitchers; the other group included plants with three to five pitchers.
From each group, we randomly assigned plant individuals to the
experimental (red) or control (green) group. There was no
difference in the number of pitchers per plant between groups
(mean ± s.e.: experimental group: 2.9 ± 0.37 pitchers; control group
2.9 ± 0.27 pitchers; t-test, n = 20, t = 0.0, p > 0.99). It is well known that
differences in the microhabitats might influence capture rates
(Cresswell 1993). To minimize such effects, we positioned one red
and one green plant in pairs at 40 cm distance from each other
outside the Institute of Biology in Freiburg. This site was
characterized by several freshwater pools; pairs of plants were
placed at 4 m distances from other pairs and from ponds. We
randomly determined the position of plants within a pair.

At the start of the experiment, we inspected the pitchers without
removing the cap of the pitchers. We only found Collembola (in
almost every plant). After 7 days since the start of the experiment,
we removed the cap of the pitcher to examine the entire interior
and counted all insects. Some of these insects might not have been
visible at the start of the experiment. We therefore continued the
experiment until day 15 when we extracted insects with forceps and
identified the major taxonomic groups of prey. To use a conserva-
tive figure, we subtracted the number of insects caught on day 7
from the total number of insects on day 15 to obtain the number of
insects that were caught during the last 8 days of the experiment.
We used this number, which excluded all Collembola, to test for
differences between groups with paired two-sided t-tests as data
were normally distributed.

3. RESULTS

We found a total of 133 prey items in the pitchers. Fifty of these were caught during the last 8 days
of the experiment with a mean capture rate of 2.5
(± 0.4 s.e.) prey items per plant. These prey items
consisted of Diptera (58%), Homoptera and Acari
(14% each), Hymenoptera (10%, mainly Sympytha
which only occurred in red pitchers) and Araneae
(4%). Only Diptera were common enough to test
for differences in capture rates. Artificially coloured
red individuals caught more Diptera (paired t-test,
t = 3.25, p < 0.01) and a higher overall number of
insects than artificially coloured green individuals
(paired t-test, t = 2.98, p < 0.01; figure 2).

4. DISCUSSION

Our experiment shows that carnivorous plants can
increase their foraging success using visual signals.
More specifically, we show that red coloration can be
an adaptive trait for carnivorous plants as it increased
the overall capture rates of insects, particularly that of
Diptera. These results extend our understanding of
the evolutionary ecology of carnivorous plants for two
reasons. First, we present the first experimental
evidence of visual signalling in carnivorous plants.
Second, it has previously been suggested, based on
correlations between capture rates and pitcher color-
ation, that carnivorous plants use UV signals or
contrasting stripes to lure insects (Joel et al. 1985;
Moran et al. 1999; Biesmeijer et al. 2005). The higher
capture rates of unicoloured red pitchers in our
experiment thus extend the array of potential visual
signals that carnivorous plants might use. Our results
emphasize that insect traps do not need to sport
contrasting colours to be attractive; it might be
sufficient to be different from the background.

The higher efficiency of red pitchers might be
surprising at first glance, since it contrasts with the
traditional belief that red coloration is an inefficient
signal to insects. While humans can see colour farther
into the red than most insects, some insects such as
Symphyta also possess photoreceptors with peak
sensitivity in the red. More importantly, red colours
are not invisible to insects (e.g. Diptera) lacking such
photoreceptors (Chittka & Waser 1997). Artificial red
objects are even used for pest control owing to their
success in luring fruit flies (Cyrtynowics et al. 1982;
Katsyumannos & Kouloussis 2001), which is consistent
with our results of increased capture rates of Diptera
by red pitchers. Even bees that cannot discriminate
red colours based on differences in hue are able to
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Anthocyanins from other colours based on differences in the blue or green part of the spectrum (Chittka & Waser 1997). In our experiment, the reflectance of natural and artificial red pitchers differs from that of natural and artificial green pitchers both in the green (520–570 nm) and in the red parts (greater than 610 nm) of the spectrum. It thus remains open whether insects perceived red pitchers as different because they reflected more red light or less green light and had a lower overall luminance. In both the cases, red pitchers are more different (i.e. red and dark) from the background of green foliage than green pitchers. We propose that red pitchers are more effective because they represent, in addition to the olfactory signals of nectaries, a visual stimulus that might direct insects to the trap.

We conclude that the multiple, independent evolution of carnivory in plants (with more than 600 species described to date) presents an ideal, but hitherto overlooked, model system to analyse signalling in plant–animal interactions. Elucidating the mechanisms that plants employ to capture insects will greatly enhance our understanding of the evolutionary ecology of carnivory. Moreover, in light of the great variability of pitcher coloration in N. ventricosa is puzzling.

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