

The effect of trap colour and trap-flower distance on prey and pollinator capture in carnivorous *Drosera* species

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Summary

1. The functional features of carnivorous plants' traps have been mostly interpreted as adaptations to capture prey. Carnivorous plants that feed on insects, however, run the risk that increasing trapping effectiveness might in turn reduce reproductive success through capture of pollinators. Such a pollinator–prey conflict might play an important role in the evolution of trap features. In carnivorous plants with sticky leaves (e.g. *Drosera*, *Pinguicula*), both spatial distance between traps and flowers and their visual signals (e.g. colour, display size) likely play a role in attracting prey but it has also been suggested that they affect the risk of potential pollinators landing on a trap. It has been reported, for example, that red pigmentation in carnivorous plants may lure insect prey to traps. This idea remains controversial, however, because colour vision of most insects does not extend very far into the red part of the spectrum.

2. We tested an alternative hypothesis, namely that red pigmentation of the trapping leaves may reduce the risk of a pollinator–prey conflict. Experiments were conducted in a natural habitat of *Drosera arcturi* and *D. spatulata* in the Southern Alps of New Zealand. Using sticky model traps similar in shape to *Drosera* leaf traps and flowers, we investigated the effect of colour (green vs. red vs. white) and flower-trap distance (flower stalk length and leaf arrangement, that is upright as in *D. arcturi* vs. flat ground rosette as in *D. spatulata*) on composition and abundance of insects landing and being trapped.

3. Flower-trap distance had no significant effect on the risk of pollinators being trapped but model flowers higher above the ground received more pollinator landings. Across all model traps, the number of trapped potential pollinators was significantly lower in traps with red leaves compared to green ones.

4. The results suggest that the typical red pigmentation of the trapping leaves in *Drosera* may be a way to protect pollinators from being attracted and captured. However, our data also suggest that pollinator protection via red traps may come with a trade-off since total prey capture was also significantly reduced.

Key-words: carnivorous plants, *Drosera*, flower-trap distance, pollinator–prey conflict, trap colour

Introduction

Carnivorous plants that are living in nutrient poor conditions benefit from feeding on animals in multiple ways (e.g. Thum 1988, Thum 1989; Worley & Harder 1999; Ellison & Gotelli 2009; Ne'eman *et al.* 2006). It is therefore likely

that the features of the prey trapping leaves, such as arrangement or colour, are under strong selection pressure to optimize prey capture and nutrient uptake (Ellison & Gotelli 2009). Thus, trap features in carnivorous plants have been interpreted as adaptations to optimize prey capture. This might, however, not always be the case since prey capture may come with a trade-off in situations where part of the prey spectrum consists of pollinators. A

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pollinator–prey conflict (PPC) may be described as a trade-off between increasing the risk of pollinators being trapped to gain more resources (that can in turn be invested in reproduction) vs. reducing the effectiveness of traps to increase reproductive success via pollen import and export through pollinators (Jürgens *et al.* 2012). It seems possible that the pollinator–prey conflict can be partly resolved through the evolution of features that reduce the risk of pollinators being trapped, for example by increasing the distance between prey capturing leaves and flowers (Anderson & Midgley 2001; Anderson 2010). Another way to reduce the risk of pollinators being trapped might be to use specific olfactory and/or visual cues to lure non-pollinating animals to traps, while at the same time attracting pollinators to flowers (see Jürgens *et al.* 2012). However, our knowledge of the importance of visual and olfactory cues in carnivorous plants for attracting prey insects is still very limited.

The trapping leaves of many carnivorous plants have striking visual features, and it has been suggested that these are related to prey capture (e.g. Joel 1988; Newell & Nastase 1998; Schaefer & Ruxton 2008; Kurup *et al.* 2013). Red pigmentation is commonly found in leaf traps of carnivorous plants with different trap types such as pitcher traps, flypaper traps and snap traps (Juniper, Robins & Joel 1989). Because carnivorous plants turn red when they become nutrient deficient (Moran & Moran 1998; Ichiishi *et al.* 1999), it was hypothesized by Ichiishi *et al.* (1999) that this might increase the attractiveness of the plants to prey. If this hypothesis is correct, a change in the pigmentation of carnivorous plants from green to red could be interpreted as an adaptation to reduce nutrient deficiency by increasing the capture rate of insects. Experimental evidence that the red pigmentation may function as a visual attractant and significantly increase prey capture (particularly of Diptera) was provided by Schaefer & Ruxton (2008), who compared artificially red-coloured *Nepenthes ventricosa* pitcher traps with green controls. However, it remains controversial whether red pigmentation found in traps of carnivorous plants is an adaptation to increase attractiveness for prey (Bennett & Ellison 2009), especially since Schaefer & Ruxton (2008) did their experiment outside of the natural habitat of their study species. Furthermore, colour vision of most insects does not extend very far into the red part of the spectrum (Briscoe & Chittka 2001). It seems more likely that, to visually attract insect prey, carnivorous plants should produce traps with white, yellow or UV patterns (e.g. Joel, Juniper & Dafni 1985; Moran, Booth & Charles 1999; Kurup *et al.* 2013). These colours could be better perceived by most insects since they are easier to distinguish from green vegetation (Chittka & Waser 1997; Chittka *et al.* 2001; Lunau 2014). The situation might even be more complex, however, when considering that insect attraction to the deadly traps might also reflect learned responses to other visual signals in the environment. It is known that under natural conditions, flower-visiting insects may develop learned preferences for

the colours of their most important food plants (Giurfa 1991). Higher insect capture rate of red-coloured traps, as shown by Schaefer & Ruxton (2008), could therefore reflect learned rather than innate colour preferences and may therefore depend on the ecological context in which the traps are presented.

Here we tested, within the natural habitat of carnivorous sundews, the alternative hypothesis that red pigmentation of sticky traps reduces the risk of trapping potential pollinators and may therefore be a way to reduce the effects of a pollinator–prey conflict. Carnivorous plants, by feeding on insects, run the risk that their reproductive success is reduced by trapping their potential pollinators (Moran 1996; Zamora 1999; Anderson & Midgley 2001; Murza, Heaver & Davis 2006; Jürgens *et al.* 2012). It can therefore be assumed that they have evolved mechanisms to avoid pollinator–prey overlap thereby protecting their pollinators from being captured (e.g. Jürgens, El-Sayed & Suckling 2009; Jürgens *et al.* 2012). One possibility to reduce the pollinator–prey overlap is to guide potential pollinators and non-pollinating prey (based on their innate and learned preferences) differently via visual cues to flowers and traps, respectively. Another possibility to protect flower visitors from being trapped would be to spatially separate flowers and traps. This can be achieved by positioning flowers further away from the trapping leaves on long flowering stalks (see Juniper, Robins & Joel 1989; Ellison *et al.* 2003) or by positioning traps away from the flowers, for example in flat ground rosettes rather than in an upright position. However, the role of spatial separation of flowers and traps for protecting pollinators has been debated (see Anderson & Midgley 2001), and there is limited evidence to support the hypothesis that spatial separation of flowers and leaves is related to pollinator–prey conflict. An alternative explanation for long peduncles in some carnivorous plants is that flower display height may positively affect pollinator attraction and in consequence reproductive success (Anderson & Midgley 2001). The results of a study on two *Drosera* species, *D. pauciflora* and *D. cistiflora*, by Anderson (2010) indeed suggest that long flowering stalks have evolved to improve the visual display of flowers to pollinators and not to protect them from being caught in sticky leaf traps.

Because learning might play a role in insect responses to different colours, it is important to test the effects of leaf colour and flower-trap distance on pollinator and total prey capture in the natural environments of carnivorous plants (see also Bennett & Ellison 2009). We therefore conducted our experiments in the Southern Alps of New Zealand, where two *Drosera* species with different leaf positions and flower stalk lengths (*Drosera arcturi* and *D. spatulata*) co-occur. Furthermore, the effect of visual signals for approaching and landing on flowers and leaves might also be affected by the arrangement (upright vs. on the ground), height above the ground and distances between them. For the experiment, we designed sticky model traps of flowers and leaves of different colours and

arranged them in different combinations to resemble those of the two *Drosera* species. Since it is possible that trap-flower distance, trap leaf arrangement and colour could act synergistically, we conducted experiments with model flowers that tested both single effects and combined effects on pollinator and non-pollinator landings on flowers and traps.

The following hypotheses regarding the effect of trap colour and spatial separation of flowers and traps (i.e. trap position, flower presence and flower to trap distance) on prey capture and the risk for a pollinator–prey overlap (PPO) were tested: (i) Does flower stalk length have an effect on the attraction of potential *Drosera* pollinators to model flowers? (ii) Does the presence and proximity of model flowers increase prey capture and the risk of *Drosera* pollinators being trapped by the model leaves? (iii) Does model leaf trap position (upright as in *D. arcturi* vs. flat on the ground as in *D. spatulata*) affect prey capture or pollinator landings on flowers? and (iv) Are model trap leaf colours (red vs. green) and model flower colour (white) differentially attractive to non-pollinating prey insects and known *Drosera* pollinators?

Based on the results of other studies (e.g. Anderson & Midgley 2001; Anderson 2010), we predict that stalk length has a positive effect on the number of pollinators landing on model flowers because of their better visual display. If the visual and olfactory features of the flowers provide weak guidance mechanisms for flower visitors, then we expect that model traps with non-sticky flowers trap more pollinators than model traps without flowers and that the closer the flower is to the leaf trap model the higher is the risk for pollinators of being trapped. Since pollinators in New Zealand show strong innate and/or conditioned responses to white and yellow flower colours (Campbell *et al.* 2010), our prediction is that colour has an effect on prey and pollinator capture with red and green attracting fewer pollinators than white. Finally, we expect that upright traps attract a different spectrum of insects, with a higher proportion of potential pollinators than traps flat on the ground.

Materials and methods

STUDY SITES AND SYSTEMS

The study was conducted in summer in December 2007 in the Arthur's Pass National Park in the Southern Alps of New Zealand at a natural site where two *Drosera* species (*D. arcturi* Hook., *D. spatulata* Labill.) co-occur. The study site was an easily accessible subalpine bog at the lower end of the Bealey Valley Track, ca. 2 km North of Arthur's Pass Village (Fig. 1). The bog is surrounded by beech forest, and, besides *Drosera arcturi* and *D. spatulata*, the flowering bog vegetation was characterized by *Donatia novae-zelandiae* Hook.f., *Celmisia graminifolia* Hook.f., *C. discolor* Hook.f., *Pentachondra pumila* (J.R.Forst. & G.Forst.) R.Br., *Utricularia monanthos* Hook.f. and *Aporostylis bifolia* (Hook.f.) Rupp & Hatch. *Drosera arcturi* typically grows in the sphagnum mosses and plant cushions from *Donatia*, but also grows in the drier grassy areas of the bog close to the forest edges, where the vegetation is taller. In contrast, *D. spatulata* seems less competitive

and is typically restricted to less overgrown areas such as the surface of *Donatia* cushions, rocky outcrops and the edges of small flat ditches and remnants of water pools.

COLOUR MEASUREMENTS WITH COLOUR SPECTROMETER

For comparison of colours, we measured spectral reflectance of *Drosera* leaves and artificial traps (without the sticky coating to avoid damage to the spectrometer) over the UV–visible range (300–700 nm) using an Ocean Optics S2000 spectrometer and an Ocean Optics DT-mini light source (200–1100 nm; Dunedin, FL, USA). Readings were taken through a fibre-optic reflection probe (UV/VIS 400 lm) held at 45° and about 5 mm from the surface of the object. Results were analysed with the Ocean Optics Spectra Suite software (Ocean Optics, Dunedin, FL, USA). Petals and leaves of the two *Drosera* species were measured freshly after collection. Ambient light was excluded with a small can when measurements were taken. Three replicates were taken for each measurement and curves were averaged for graphic display. In case of irregularities such as mucilage from the leaves, direct measurements of the surface were taken after removing the mucilage with tissue paper.

TRAP DESIGN

The natural models for artificial sticky traps were the two *Drosera* species, *D. arcturi* and *D. spatulata* (Fig. 1). We chose to use artificial sticky traps with simple colours (white for flowers, green and red for leaves) instead of natural plants, because observation and manipulation of individual *Drosera* plants in the natural habitat within the natural population was not possible without damage or including additional variables that affect the attraction of insects (e.g. added markers, volatile emission, colour change or wilting due to damage or ageing or previous prey capture or pollination) in the analysis. Furthermore, a sufficiently high number of standardized replicates of traps for statistical analyses of the effects of the variables under study (trap colour, trap position, flower presence and trap-flower distance) could only be generated by using simplified standardized artificial trap models.

According to our observations, *Drosera arcturi* typically has 2–4 more or less upright usually red, rarely green, active trap leaves per plant and a single white pentamerous flower on a flower stalk (Fig. 1). *Drosera spatulata* has up to 15 small usually bright red-coloured circular leaves arranged in a rosette pressed flat to the ground. At the study site, the species produces typically up to four white pentamerous flowers on a long flower scape, but usually only one flower is open at a time. In order to establish the size of the models random measurements of trap leaves, flowers and peduncle lengths were taken with a digital calliper from plants in observation plots at the end of the flowering season in February 2007: mean leaf length *D. arcturi* 3.6 ± 1.3 standard deviation (min–max 0.5–8.4 cm; $n = 461$), rosette diameter *D. spatulata* 1.6 ± 0.3 cm (min–max 0.8–2.6 cm; $n = 308$), average peduncle length to only *D. arcturi* flower 4.9 ± 1.8 (min–max 1.5–8.7 cm; $n = 461$), and to lowest *D. spatulata* flower 6.8 ± 1.9 cm (min–max 2.4–11.4 cm; $n = 308$). Based on these, we produced two types of artificial sticky leaves of equal size (surface area) and similar in size and shape to natural *D. arcturi* leaves and *D. spatulata* leave rosettes. The first model leaf type was of 3 cm length and 1 cm width and had an upright position similar to the trapping leaves of *D. arcturi* individuals. The second type was a disc 2 cm in diameter positioned on the ground, similar to *D. spatulata* leave rosettes. A simple white disc 1 cm in diameter served as a flower model.

Commercially available (Desire[R] pheromone lure and trap, Etec Crop Solutions, PO Box 51584, Pakuranga, Auckland, New Zealand) red-, green- and white-coloured delta traps were cut into



Fig. 1. *Drosera arcturi* (a and c), *D. spatulata* (b and d), leaf-shape (green and red) and flower-shape (white) format of artificial model traps (e), study site at the lower end of the Bealey Valley Track, Arthur's Pass (f).

leaf-shape and flower-shape format as described above (Fig. 1e). We used thin green coated wire to pin the different sticky leaf traps and to emulate a flower stalk when leaf traps were combined with white flower models depending on the hypothesis being tested. Using these building blocks, we designed combinations of white, green and red artificial sticky traps or non-sticky models to test the effect of leaf trap positioning (on the ground, *D. spatulata* disc type, vs. upright, *D. arcturi* leaf type), leaf trap colour (red vs. green), and the combination of trap leaves and flowers (white) with different stalk lengths on attraction and capture of insects in general and potential pollinators in particular (Fig. 2). Based on measurements of the two sundew species, flower stalks were chosen to be 5 cm for testing the effects of flower presence in general, and 2 and 8 cm for testing the effect of flower stalk length in particular. For an overview of trap types used to test the different hypotheses, see below and Fig. 2.

TRAP EXPOSURE AND SPECIMEN COLLECTION

A length of protruding wire at the bottom of the sticky traps served to hold them in styrofoam boards for storage and transport, or pin

them to the ground during exposure in the habitat. Once assembled, the exposed upper surfaces of the traps were evenly coated with 'Tangle-Trap' (The Tanglefoot Company, Grand Rapids, MI, USA). 'Tangle-Trap' is commonly used by ecologists and entomologists to capture insects and is extremely retentive.

Fifteen trap arrangements of each type and colour as shown in Fig. 2 were produced and were exposed at the same time on two consecutive sunny days for 16 h of daylight (deploying traps 10–1100 h on 21.12.2007, collecting traps 17–1800 h 22.12.2007); a separate second set of model flowers with different stalk lengths (again 15 each) was exposed on another relatively cloudy and windy day (30.12.2007) during 8 h of daylight (1000–1800 h). In preparation for the first trial, all different trap types to be exposed on the day were arranged in alternating lines on styrofoam boards. 'For logistic reasons and to keep the impact on the environment low we decided to use a random design for distributing the model traps in the field. Furthermore, because the experimental area was relatively homogenous in terms of vegetation and presence of *Drosera* we considered the risk that spatial autocorrelation would affect our results (by reducing the power of the statistical test) acceptable (see also Legendre *et al.* 2004)'. On the

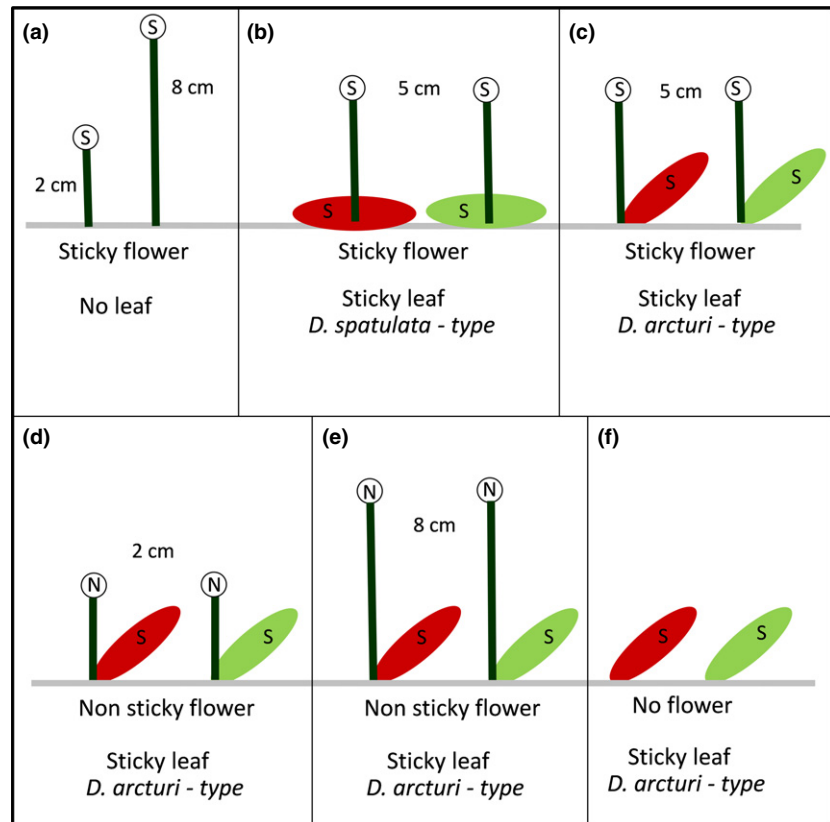


Fig. 2. Experiments with white, green and red artificial sticky traps to test the effect of: flower stalk length (2 cm vs. 8 cm) on pollinator attraction (a); trap positioning (on the ground, *Drosera spatulata* type, vs. upright, *D. arcturi* type) on prey (excluding pollinators) and pollinator capture (b, c); presence of flowers on prey and pollinator capture (d, e, f); and trap colour on prey and pollinator capture (d, e, f). S = sticky, N = non-sticky.

morning of the 21.12.2007, all traps were randomly distributed in the BV bog among the natural sundew population. One person walked in serpentine covering the entire bog evenly, while sticking an artificial trap from the styrofoam boards into the ground every three steps at a distance of at least 2 m. Traps were left in the bog overnight and collected on the evening of the second day by walking the same serpentine from beginning to end again to ensure that all traps were exposed for the same duration. Altogether traps had been exposed for 16 h of daylight on two days. The procedure for the second trial was similar, albeit model flower traps were exposed for only a single day.

After exposure in the habitat, captured specimens were removed from the sticky traps and cleaned by bathing the sticky traps in mineral turpentine until the glue dissolved and specimens came free. Specimens were stored in labelled vials filled with 70% ethanol for later identification.

STATISTICAL ANALYSES

Prior to analysis, all trapped and identified insects were classified either as non-pollinators or pollinators of the two sundew species in the habitat, according to flower visitor spectra given by Sciligo (2009; unpublished data). We used a robust approach for our statistical analysis by only considering flower visitor taxa where individuals had been found to carry *Drosera* pollen (Sciligo 2009; unpublished data) as potential *Drosera* pollinators.

To measure independent and interactive effects, all count data of all model traps were analysed in a generalized linear model (GLM) with Poisson error distribution and a log link function as implemented in Statistica 7 (StatSoft, Inc. 2004). We analysed hypotheses about the effect of trap colour (red vs. green), peduncle length (2 cm vs. 8 cm) and trap arrangement (upright vs. on the ground) on prey/pollinator capture with likelihood-ratio (type 3) tests of generalized linear models (McCullagh & Nelder 1989). We

also corrected for overdispersion of data. Because the effect of flower stalk length on pollinator attraction was tested on two different days under different weather conditions and different duration (16 h vs. 8 h), the data were statistically analyzed as frequency counts. The analysis of the frequency counts (effect of stalk length) therefore involved ln-transformation of the data and using an offset as implemented in the generalized linear model module in Statistica 7 (StatSoft, Inc. 2004).

To analyse patterns of prey overlap between the different model traps, Pianka's (1973) index (PNO = pairwise niche overlap) was calculated in the ECOSIM 7.0 software (Gotelli & Entsminger 2004). The PNO index ranges from 0.0 (no shared prey) to 1.0 (identical prey). The observed average PNO is then statistically tested against null models (expected mean) based on 1000 Monte Carlo randomizations (see Ellison & Gotelli 2009 for details). We used the RA3 algorithm (niche breadth retained/zero states reshuffled) to test for non-random patterns of prey composition (see Winemiller & Pianka 1990; Albrecht & Gotelli 2001).

Results

GENERAL OVERVIEW

Apart from a few Araneae, taxa from a variety of insect orders (Diptera, Coleoptera, Hemiptera, Hymenoptera, Plecoptera) were caught on the artificial sticky traps (Table 1). The spectrum was dominated by Diptera, especially *Hercostomus* flies (Dolichopodidae), several flower-visiting Syrphidae (*Allograpta* sp., *Anu una*, *Platycheirus eocheiloides*, and unidentified flower-visiting Tachinidae. In general, white sticky model flowers were very attractive to insects and showed higher capture rates than green or red

Table 1. Number (absolute number and, for better comparison, standardized per 100 traps) and identification of insects recorded on green, red and white model traps

Colour of traps Number of traps	Green <i>n</i> = 75	Red <i>n</i> = 75	White <i>n</i> = 120	Green Per 100	Red Per 100	White Per 100
Captured taxa						
Unidentified order	1	1	1	1.3	1.3	0.8
Araneae	6	5	1	8.0	6.7	0.8
Coleoptera						
Scirtidae	0	1	1	0.0	1.3	0.8
Unidentified Coleoptera	2	2	0	2.7	2.7	0.0
Diptera						
Calliphoridae*	0	0	1	0.0	0.0	0.8
Chironomidae	0	1	2	0.0	1.3	1.7
Dolichopodidae	0	5	5	0.0	6.7	4.2
<i>Hercostomus</i> sp.	33	15	88	44.0	20.0	73.3
Muscidae*	2	1	0	2.7	1.3	0.0
Phoridae*	0	0	1	0.0	0.0	0.8
Pipunculidae						
<i>Pipunculus</i> sp.	0	1	5	0.0	1.3	4.2
Stratiomyidae						
<i>Odontomyia</i> sp.	0	0	5	0.0	0.0	4.2
Syrphidae						
<i>Allograpta</i> sp.	0	1	17	0.0	1.3	14.2
<i>Anu una</i> [†]	7	0	52	9.3	0.0	43.3
<i>Helophilus</i> sp.	2	0	3	2.7	0.0	2.5
<i>Melangyna novae-zelandiae</i> [†]	0	0	3	0.0	0.0	2.5
<i>Platycheirus eocheilosia</i> [†]	3	2	51	4.0	2.7	42.5
<i>Sismosyrphus grandicornis</i>	0	0	1	0.0	0.0	0.8
Unidentified Syrphidae	2	0	14	2.7	0.0	11.7
Tachinidae*	14	4	19	18.7	5.3	15.8
Unidentified Diptera	53	28	54	70.7	37.3	45.0
Hemiptera						
Cicadellinae	7	5	3	9.3	6.7	2.5
Hymenoptera						
Formicidae						
<i>Monomorium</i> sp.	4	1	0	5.3	1.3	0.0
Halictidae						
<i>Lasiolossus maunga</i> [†]	1	0	11	1.3	0.0	9.2
Colletidae						
<i>Leioproctus pekanui</i> [†]	0	0	1	0.0	0.0	0.8
Proctotrupoidea	5	0	0	6.7	0.0	0.0
Unidentified Hymenoptera	7	7	14	9.3	9.3	11.7
Plecoptera	1	0	0	1.3	0.0	0.0
N for all arthropod taxa	150	80	353	200.0	106.7	294.2
N for all flower visitor taxa*	27	6	139	36.0	8.0	115.8
N for all flower visitor taxa with pollen**	11	2	118	14.7	2.7	98.3

*Flower visitors observed on the two study species according to Sciligo (2009) and unpublished data.

[†]Flower visitors of the two study species found with either *Drosera arcturi* or *D. spatulata* pollen according to Sciligo (2009) and unpublished data.

model leaf traps, especially with regard to flower-visiting insects such as the flower-visiting halictid bee *Lasioglossum maunga* and syrphid flies *Allograpta* sp., *Anu una*, *Platycheirus eocheiloisa*, as well as non-flower visitors such as *Hercostomus* sp. (Dolichopodidae), *Pipunculus* sp. (Pipunculidae) and *Odontomyia* sp. (Stratiomyidae) (Table 1).

THE EFFECT OF COLOUR ON PREY AND POLLINATOR CAPTURE OF MODEL LEAF TRAPS

In all experiments, regardless of the presence or absence of non-sticky or sticky model flowers, green sticky model

traps had significantly higher prey capture counts than red traps (Table 2). The same was true for the number of pollinators captured on green model traps compared to red ones. In summary, white is the most attractive colour and had the highest trapping success, followed by green and then red. Green traps were more successful than red traps in trapping pollinators and non-pollinators (Fig. 3).

PREY OVERLAP BETWEEN DIFFERENT TRAP TYPES

Using family level data of observed prey, we found high overlap in the prey composition between traps with

Table 2. Results of generalized linear models analysing the effect of: (A) flower stalk length, (B) trap position in combination with trap colour (B1) and (C) trap colour in combination with presence and distance of a flower from model leaves (C1)

Tested effects	<i>n</i>	d.f.	Prey on traps			Pollinators on traps			Pollinators on flowers			Figure
			Mean, SE	χ^2	<i>P</i>	Mean, SE	χ^2	<i>P</i>	Mean, SE	χ^2	<i>P</i>	
(A) Flower stalk length	60	1	–	–	–	–	–	–	0.11 ± 0.011	486	<0.05	2a, 4
2 cm	30		–	–	–	–	–	–	0.083 ± 0.012			
8 cm	30		–	–	–	–	–	–	0.138 ± 0.017			
(B) Trap position*	60	1	1.38 ± 0.18	1.82	0.177	0.27 ± 0.06	0.245	0.62	1.23 ± 0.13	4.62	<0.05	2b–c, 6
Upright	30		1.13 ± 0.23	10.2	<0.01	0.27 ± 0.08	10.19	<0.01	0.97 ± 0.13	1.84	0.174	
(B1) Colour	15		1.0 ± 1.13			0.07 ± 0.07			1.13 ± 0.19			
Red	15		1.27 ± 0.37			0.47 ± 0.13			0.8 ± 0.175			
Green	30		1.63 ± 0.26			0.267 ± 0.52			1.5 ± 0.22			
Red	15		1.33 ± 0.33			0.13 ± 0.09			1.66 ± 0.37			
Green	15		1.93 ± 0.39			0.4 ± 0.17			1.33 ± 0.23			
(C) Trap colour	90	1	1.33 ± 0.19	11.72	<0.001	0.21 ± 0.05	9.15	<0.01	–	–	–	2d–f, 5
Green	45		1.91 ± 0.33	1.35	0.51	0.33 ± 0.09	0.617	0.734	–	–	–	
(C1) Flower†	2								–	–	–	
No flower	15		1.73 ± 0.63			0.33 ± 0.13			–	–	–	
2 cm flower	15		1.67 ± 1.42			0.27 ± 0.15			–	–	–	
8 cm flower	15		2.3 ± 0.66			0.74 ± 0.19			–	–	–	
Red	45		0.76 ± 0.16			0.09 ± 0.05			–	–	–	
No flower	15		0.73 ± 0.23			0.13 ± 0.13			–	–	–	
2 cm flower	15		0.60 ± 0.24			0.07 ± 0.07			–	–	–	
8 cm flower	15		0.93 ± 0.34			0.07 ± 0.07			–	–	–	

*Was tested in combination with sticky model flower on a 5 cm stalk.

†Was tested in combination with non-sticky model flower or no flower.

Bold numbers indicate significant effects.

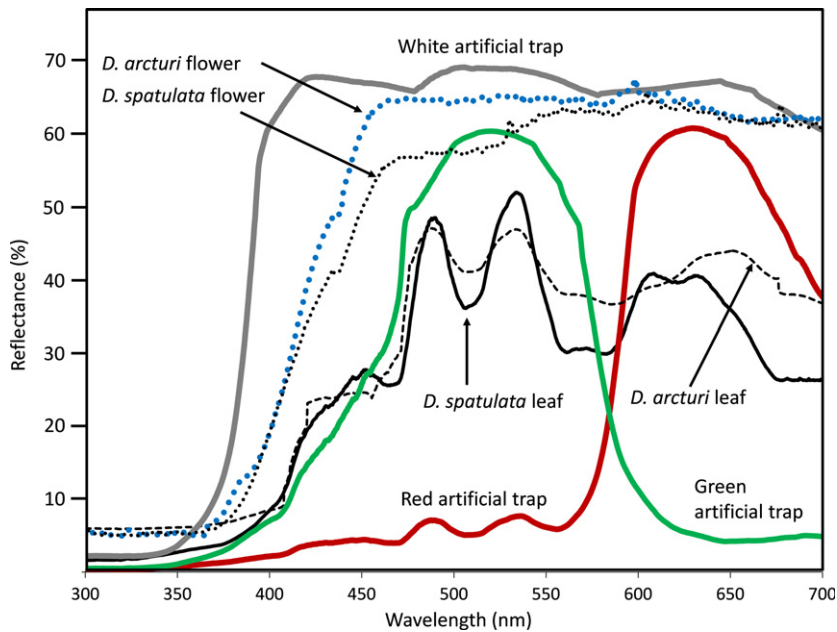


Fig. 3. Spectral reflectance patterns of *Drosera arcturi* and *D. spatulata* leaves and flowers, and artificial traps (white, green, red).

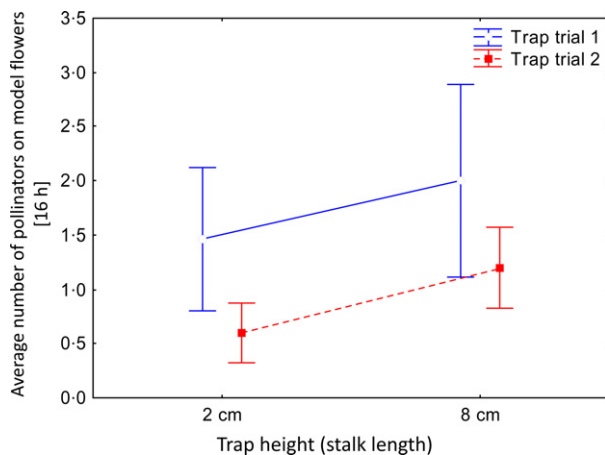


Fig. 4. Generalized linear model showing the effect of stalk length (2 cm vs. 8 cm) on the average number of *Drosera* pollinators captured on artificial sticky flowers (Fig. 2a) at two sites and two days ($\chi^2_{1,60} = 4.86$; $P < 0.05$).

different colour (red vs. green) and even higher overlap for traps with different position (basal vs. upright rosette). For model traps with different colour, the observed prey overlap ($PNO_{obs.} = 0.869$) was significantly higher than the expected PNO ($PNO_{exp.} = 0.31$; $P = 0.003$). The overlap between upright and ground traps was even higher ($PNO_{obs.} = 0.944$; $PNO_{exp.} = 0.264$; $P = 0.002$).

THE EFFECT OF DISPLAY HEIGHT OF STICKY MODEL FLOWERS ON POLLINATOR CAPTURE

Independent of the different days the experiment was conducted, significantly higher numbers of potential *Drosera* pollinators were trapped on sticky model flowers with 8 cm long stalks than on those with 2 cm long stalks

(Table 2, Fig. 4) indicating that pollinators are more attracted to flowers on longer stalks.

THE EFFECT OF FLOWERS ON PREY AND POLLINATOR CAPTURE OF STICKY LEAF MODELS

The presence and/or proximity of a flower to the trapping model leaf had no effect on the capture rate of pollinators on the model leaf, nor did it have an effect on total prey capture (Table 2; Fig. 5). In other words, spatial separation of traps and flowers did not affect prey abundance or composition.

THE EFFECT OF TRAP POSITIONING ON PREY AND POLLINATOR CAPTURE ON MODEL LEAVES

When testing the effect of leaf positioning of model traps together with sticky model flowers on 5 cm long stalks, there was a high similarity regarding the number and types of prey taxa caught in basal traps and upright traps. We could not detect an effect of positioning of leaf traps on their prey and pollinator capture (Table 2).

THE EFFECT OF LEAF POSITIONING AND LEAF COLOUR ON POLLINATOR CAPTURE OF MODEL FLOWERS

Sticky model flowers in combination with upright sticky model leaves trapped a significantly lower number of pollinators than model flowers in combination with traps positioned on the ground. This means that at constant flower height, the amount of pollinators landing on flowers increases with increasing spatial separation of flowers from traps. The trap colour (green vs. red) of sticky model leaves had no significant effect on pollinator capture on sticky model flowers (Table 2, Fig. 6).

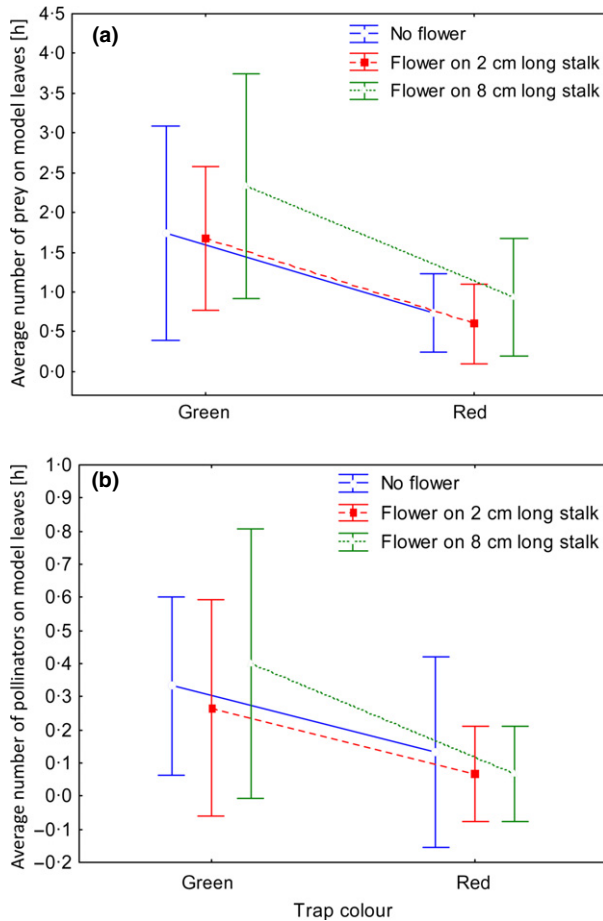


Fig. 5. Generalized linear model showing the effect of different colours (green vs. red) of model leaves (Fig. 2d–f) on number of captured (a) prey (excluding *Drosera* pollinators) and (b) potential *Drosera* pollinators (all prey: $\chi^2_{1,90} = 11.72$; $P < 0.001$; pollinators: $\chi^2_{1,90} = 9.15$; $P < 0.01$). The presence or absence of non-sticky flowers (2 cm and 8 cm) had no effect on capture of sticky model leaves (prey: pollinators: $\chi^2_{1,90} = 0.617$; $P = 0.734$ all prey: $\chi^2_{1,90} = 1.35$; $P = 0.51$).

Discussion

Not many studies have tested the specific adaptations of carnivorous plants in the context of potential trade-offs between different functions such as nutrient supply (prey capture) and pollination (reproductive success) (Jürgens *et al.* 2012). We tested several hypotheses regarding the morphology and colour features of carnivorous *Drosera* species using artificial model flowers and leaves. However, plant morphology (flower stalk length, leaf position) and colour both contribute to the visual features of the plant. It is therefore difficult to clearly separate effects that are the result of colour (chromatic effects) from effects that are related to the visual display (e.g. distance, visibility). Furthermore, the risk of a prey insect (including pollinators) to land on a trap is not only affected by the visual cues displayed by the plant. The trap-flower distance may affect the manoeuvrability of an insect so that in plants where traps and flowers are in close proximity pollinators may

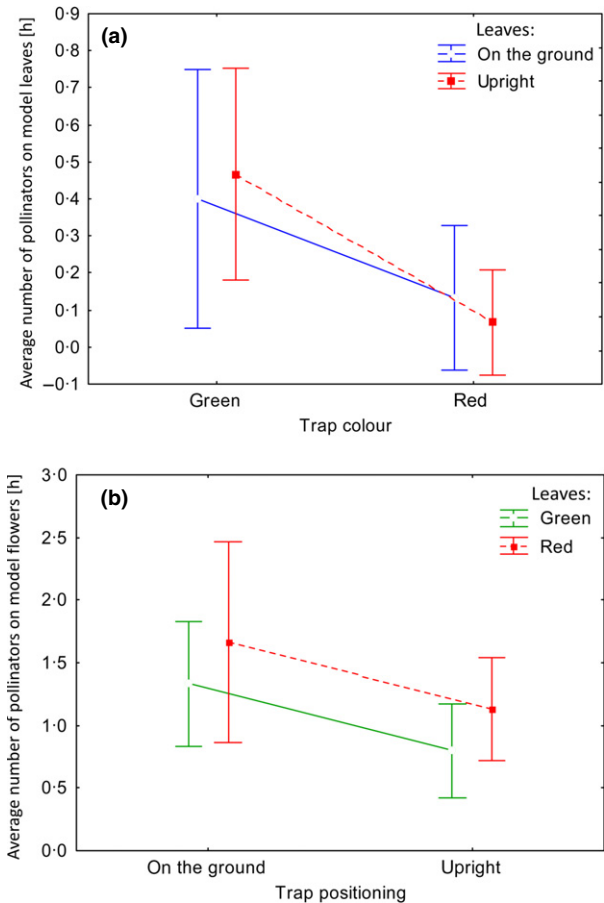


Fig. 6. Generalized linear models showing the effect of trap colour and trap positioning on pollinator capture on model leaves (a) and model flowers (b), respectively (see Fig. 2b,c). (a) Effect of trap colour ($\chi^2_{1,60} = 10.19$; $P < 0.01$) on pollinator capture of model leaves. (b) Trap positioning (upright vs. on the ground) showed no significant effect on pollinator capture in model traps ($\chi^2_{1,60} = 0.245$; $P < 0.62$). (b) Effect of trap positioning ($\chi^2_{1,60} = 4.62$; $P < 0.05$) but not trap colour ($\chi^2_{1,60} = 1.85$; $P < 0.174$) on pollinator capture of model flowers.

land on traps because they touch them when approaching flowers or while taking off. Thus, it is to be expected that complex interaction effects between visual features (chromatic effects and display effects) and flower-trap distance. Interestingly, our results suggest that the colour effect is much stronger than the effect of flower-trap distance. In general, white sticky model flowers were very attractive to insects and showed higher capture rates than green or red model traps, but the difference was even more pronounced when only considering insect taxa known to visit the flowers of the two model species *D. arcturi* and *D. spatulata* (Table 1). White traps received about 4 times more visits by insects visiting sundew flowers than green traps and 20 times more than red traps. Across all model leaf traps, the number of trapped potential pollinators was significantly lower in traps emulating red leaves compared to green ones suggesting that red pigmentation of the trapping leaves in *Drosera* may be a way to protect pollinators from being attracted and captured. The proximity of a flower

from a trap, either by placing them on longer stalks or by arranging the trapping model leaves closer to flowers, had only a weak (non-significant) effect on the risk of pollinators being captured. Furthermore, we found that model flowers higher above the ground (on longer stalks) received more pollinator landings than flowers on shorter stalks. This is consistent with the findings of several studies that the reproductive success of plants with flowers on longer scapes is higher than in plants where flowers are on shorter scapes (Ågren, Fortunel & Ehrlén 2006). This suggests that the selection for the relative display height of flowers in *Drosera*, and other carnivorous plants with sticky traps, is related to pollinator attraction and not to the pollinator–prey conflict.

EFFECT OF SPATIAL SEPARATION OF FLOWERS AND TRAPS ON PREY/POLLINATOR CAPTURE

Neither stalk length nor positioning of the leaves (upright vs. on the ground) had an effect on pollinator capture on model leaves. This is also supported by similar findings of Anderson (2010) who investigated the effect of peduncle length on *Drosera pauciflora* and *D. cistiflora* in South Africa. He found that peduncle length had no effect on pollinators being captured in traps but that plants with longer peduncles had higher pollinator visitation. In the present study, we also found that display height had a significant positive effect on the number of pollinators landing on model flowers giving further support to the hypothesis that inflorescence height is an adaptation to increase visual floral display and is probably not linked to pollinator–prey conflict (e.g. Peakall & Handel 1993; Lortie & Aarssen 1999). Furthermore, the presence of a non-sticky model flower had no significant effect on prey/pollinator capture of model traps. This suggests that visual signals of the flowers might be a sufficient mechanism to achieve landing of specific target insects on flowers (pollinators) and others on traps (non-pollinators). This is also supported by the fact that a significant difference in the prey composition of upright model leaves (*D. arcturi* type) and leaves positioned on the ground (*D. spatulata* type) was not observed.

Interestingly, our results suggest that leaf position (upright vs. on the ground) might have an indirect effect on pollinator protection. Significantly more pollinators were found on model flowers combined with model leaves positioned on the ground than on model flowers combined with upright model leaves. This may be because the risk for a flower visitor of ending up in a trap likely depends on the flight angle at which the flower is approached and if the sticky leaves are positioned as obstacles within its flight path. The other main flowering species in the community, *Donatia novae-zelandiae*, an abundant species forming large cushions, is positioned on the ground and often served as a substrate for *Drosera* plants growing on its cushions. It is therefore likely that flower visitors after departure from *Donatia* would approach *D. arcturi* and *D. spatulata* from below. Thus in the case of *D. arcturi*,

with its upright leaves and the relatively shorter flower-trap distance, the risk for a flower visitor being trapped would be higher than in *D. spatulata* which has a ground rosette which is not obstructing the flight path of flower visitors leaving the *Donatia* flowers. Furthermore, even if not caught, flower visitors could be prevented from landing on the sundew flowers if the leaves are positioned as an obstacle in their flight path.

THE ROLE OF TRAP COLOUR ON PREY AND POLLINATOR CAPTURE

The often striking colour features of the trapping leaves of carnivorous plants have fascinated scientist for a long time (Darwin 1875). Not all explanations for red pigmentation are based on the assumption that they are the result of adaptation, and not all explanations apply only to carnivorous plants (for a review, see Lev-Yadun & Gould 2009). The red pigmentation in carnivorous plants has been suggested to be: (i) an adaptation to attract prey (e.g. Schaefer & Ruxton 2008) (ii) a photoprotective response (see also reviews by Chalker-Scott 1999; Close & Beadle 2003), (iii) a result of nutrient deficiency (Hodges & Nozzolillo 1996; Ichiishi *et al.* 1999) and (iv) a protection against herbivory (see Lev-Yadun & Gould 2009). Based on our results that indicate pollinators are *not* attracted to red pigmentation as much as green, we suggest an additional hypothesis that the red pigmentation in carnivorous plants might be an adaptation to protect pollinators from being captured. The different hypotheses explaining red pigmentation in carnivorous plants are not mutually exclusive. It is likely that the production of anthocyanin serves multiple functions, for example photoprotection, herbivore defence, protecting pollinators. Furthermore, anthocyanin production might come with a trade-off between different functions, for example attracting prey vs. protecting pollinators.

While some studies could demonstrate that red pigmentation had a positive effect on prey capture (Schaefer & Ruxton 2008), others did not find an effect (Green & Horner 2007). For example, in the pitcher plant *Sarracenia alata*, coloration differences (measured as a percentage of red coloration) were found to have no effect on prey capture (Green & Horner 2007). As already pointed out by Schaefer & Ruxton (2008), their results are puzzling because most insects would find red colouring difficult to distinguish from green vegetation (see also Chittka & Waser 1997; Briscoe & Chittka 2001). However, it is likely that insects respond to both wavelength and intensity of a coloured object and there has been evidence for insect responses to red (see Briscoe & Chittka 2001 and references therein). It is therefore possible that insects can see and respond to red traps of carnivorous plants, in terms of the contrast to the visual background (see Dafni, Lehrer & Kevan 1997). Our results using green- and red-coloured model traps were contrary to the findings of Schaefer & Ruxton (2008) and Newell & Nastase (1998) that reported increased capture rates in carnivorous plants with red

pigmentation or red venation. In our experiments, prey landed significantly more often on green models than on red ones. However, our results need to be interpreted with caution because chromaticity of the colour stimulus, in our case red vs. green, is not necessarily the only aspect that might have attributed to the fly response. Other aspects associated with colour, such as intensity and polarization pattern, may provide an additional visual stimulus to flies that needs to be tested in the future. Furthermore, we used model traps with colours that had a much narrower reflectance pattern (either red or green) compared to *Drosera* leaves, which reflect in the red and green part of the spectrum. Future studies could test more complex colour models that are closer to the reflectance patterns of carnivorous plants. We see our simplified colour models, however, as a first step for testing the effect of different visual features in carnivorous plants on insect behaviour.

The effect of colour on prey attraction in general might also depend on the target prey and other features such as display size, height and shape. While we investigated plants with a flypaper trap system, Schaefer & Ruxton (2008) used carnivorous plants with pitcher traps. In the pitcher trap system, the dark entrance of the pitcher might lure insects, particularly Hymenoptera, with receiver biases for dark centres into the traps (Biesmeijer *et al.* 2005). Using sticky traps with a glistening surface, similar to that of the mucilage secreting glands on *Drosera* leaf traps, could have also added an additional visual aspect to the system that attracts certain insects such as nectar feeding bees and flies but not others. For a better understanding of the role of red pigmentation for prey attraction (or pollinator protection) in carnivorous plants, it seems therefore important to disentangle the role of different visual properties of traps (e.g. dark centres, glistening, shape and contrast to background) for prey and pollinator attraction.

That red pigmentation may serve as a photoprotective response to visible light and UV has been shown in several studies (see Close & Beadle 2003 and references therein). The production of anthocyanins could therefore correlate to the high light intensity of the typical habitats, such as alpine bogs, in which carnivorous plants grow.

Nutrient deficiency has been linked with red pigmentation and anthocyanin production in plants in general and in carnivorous plants in particular (Ichiishi *et al.* 1999). However, not all carnivorous plants produce trapping leaves with red pigmentation. The pitfall traps of some *Sarracenia* species (North American pitcher plants), such as *S. leucophylla* and *S. flava*, have visual and olfactory features similar to flowers (Jürgens, El-Sayed & Suckling 2009) and it has been suggested that their target prey are anthophilous insects (see Wickler 1968; Wiens 1978), although not necessarily their own pollinators.

The production of anthocyanins in plants has been discussed as a direct and/or indirect defence mechanism against herbivores (Karageorgou & Manetas 2006; Schaefer & Rolshausen 2006; Lev-Yadun & Gould 2009). It is

likely that mucilage secretion found in carnivorous plants with flypaper traps initially evolved as a defence mechanism against herbivores (Adlassnig *et al.* 2010). It can be speculated that the same might be true for red pigmentation to protect against arthropod herbivores and that during the course of evolution, the function of the mucilage and the red pigmentation has then changed. Since evolution of sticky traps ('If you cannot beat it, eat it'), the red colour serves another purpose, for example protecting pollinators from capture.

Conclusions

Carnivorous plants run the risk of reducing their reproductive success by feeding on their pollinators (Jürgens *et al.* 2012). Such a pollinator–prey overlap has only been shown in a few studies (e.g. Zamora 1999; Murza, Heaver & Davis 2006; Sciligo 2009). Nonetheless, the potential for a PPO, whether resolved or not, might have implications for the evolution of the trap structures in carnivorous plants. The results of our experiments with models of flowers and traps, similar to those of carnivorous plants with sticky leaves, suggest that the red pigmentation of sticky traps in *Drosera* might be a way to protect pollinators from being captured. Our finding that the total prey capture was lower in red model leaves compared to green ones contrasts with the findings and suggestions of other authors that red coloration might be an adaptation to attract prey (e.g. Ichiishi *et al.* 1999; Schaefer & Ruxton 2008). On the contrary, our data suggest that red pigmentation represents a trade-off between pollinator protection and nutrient supply through prey capture. Furthermore, it seems likely that the different functions that have been suggested to explain the red pigmentation in carnivorous plants, such as protecting pollinators, herbivore defence and photoprotection, may operate simultaneously. More experimental studies are needed to analyse functional cause and effect relationships between plant characteristics and prey capture in carnivorous plants.

Acknowledgements

We thank Dan Pearson, John Dugdale and Barry Donovan for identification of arthropod specimens. We are grateful to Jane Gosden for her help in the field. We are especially thankful to Janice Lord, Otago University, New Zealand for providing the spectrometer. This work has been supported by the New Zealand Royal Society (Marsden Fund title: 'Do carnivorous plants actively separate reproduction and feeding?').

Data accessibility

Prey capture data of artificial models of carnivorous plants and high resolution versions of figures are deposited in the Dryad Digital Repository (doi:10.5061/dryad.dj0gr) (Jürgens *et al.* 2015).

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Received 6 May 2014; accepted 9 January 2015

Handling Editor: Manfred Ayasse