IDEA

Food or sex; pollinator–prey conflict in carnivorous plants

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Abstract

Carnivorous plants potentially trap their own pollinators and it has been argued that considerable spatial separation of flowers and traps has evolved to protect pollinators. We investigated flower-trap separation of *Drosera* and *Utricularia*. Short *Drosera* had a greater element of floral–trap separation than tall *Drosera*. Such a relationship is unexpected for plants whose peduncles were evolved to protect their pollinators. *Utricularia* can not trap pollinators but this genus still produces exceptionally long peduncles. We propose that flower-trap separation evolved because carnivorous plants are often short and need to project their flowers well above ground level to make them more attractive to pollinators.

Keywords

Carnivorous plants, flower-trap separation, pollinator attraction, pollinator protection, pollinator-prey conflict.

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INTRODUCTION

Many carnivorous plants display considerable spatial separation between their flowers and traps. For example, *Drosera hamiltonii* has a flat rosette of leaves and a peduncle 30–40 cm tall (Marchant *et al.* 1982). Juniper *et al.* (1989), Givnish (1989) and Zamora (1999) hypothesize that such spatial separation in carnivorous plants may have evolved to avoid trapping potential pollinators; the pollinator protection hypothesis (PPH). This dilemma was studied in the carnivorous plant *Pinguicula vallisnerii-folia* that apparently traps its own pollinators (Zamora 1999).

However, long peduncles may also make flowers more attractive to pollinators by placing them in more visible positions (Givnish 1989; Peakall & Handel 1993); the pollinator attraction hypothesis (PAH).

Should PPH be true, we expect no relationship between plant height and peduncle length, nor a positive allometric (Midgley & Bond 1989) relationship. In addition, short *Drosera* typically trap nonaerial prey, whereas upright forms trap flying prey (Verbeek & Boasson 1993) and potential pollinators. Thus, it is expected that tall plants would need to separate traps and flowers more than short plants. If PAH is true, then one would expect an inverse relationship between plant height and flower-trap separation (short plants with long peduncles and tall plants with short peduncles).

We examined the relationships between plant height and flower-trap separation in South African and Australian *Drosera*. Peduncle lengths of *Utricularia* were also compared with those found in *Drosera*. Terrestrial *Utricularia* have underground traps and aerial flowers, ensuring that pollinators never get caught and that peduncle length plays no part in pollinator protection. Like *Drosera*, *Utricularia* is generally a plant of short vegetative stature, seldom exceeding a few centimetres from ground to leaf tips (Taylor 1989) and both occur in similar habitats. Since *Utricularia* can not trap its pollinators it should exhibit less floral-trap separation than *Drosera* (PPH).

METHODS

Seventeen species of South African *Drosera* were examined from the Bolus herbarium (UCT). Plant height (distance from ground to topmost leaves) and flower-trap separation (distance from stigma to nearest trap) were measured. Twenty measurements were made for each species (two species were under collected and five and seven measurements were made for these).

Plant height was plotted against floral-trap separation for South African *Drosera*. They were divided into tall and short plant height categories by using the median trap height (3.9 cm) as the cut off. The mean separation distance was also calculated for all *Drosera* (12.2 ± 7.5 cm) and compared with the mean flower-trap separation distances of each

species individually. Separations falling short of the average were designated "small" and those above the average were called "large".

Height and peduncle lengths in Australian *Drosera* were calculated using data from Marchant *et al.* (1982). Data was available for 36 of the 54 species listed. Species were numbered from 1 to 54 by Marchant *et al.* (1982); limited data were available for numbers 14, 15, and 18–30 (unused). Data were collected by calculating the average of the extremes given (e.g. if the range was 10–30 cm, 20 cm was used). Occasionally only average measurement was available and this was left unchanged. If only the upper extreme was given, this value was halved (e.g. if maximum height was 30 cm, 15 cm was used). Occasionally the words "short" and "very short" were used to describe stem height and these were designated the values 1 and 0.5 cm, respectively. Eighteen of the 36 plants were smaller or equal to 1 cm in height and the calculated median height was 1 cm. Plant height vs. peduncle length was plotted to test PPH and PAH. We also divided plants into two categories based on mean stem height (5.5 ± 9.5 cm), as total vegetative height was not available. Peduncle length was used as a surrogate for floral/trap separation (it is impossible to calculate floral/trap separation without total vegetative height) and the mean calculated was 7.6 ± 8.1 cm. Peduncle lengths were analysed using the same methods as in South African *Drosera*.

Measurements of *Utricularia* peduncle heights (Taylor 1989) established representative average and size class distribution of the genus. The midpoints of maxima and minima were used. When only the maximum measurement was given, this was halved. Only nonepiphytic, terrestrial species of *Utricularia* were used in the analysis ($n = 154$ of 214 species).

RESULTS

Short *Drosera* have variable flower-trap separation, whereas most tall plants show small separation and low variability (Fig. 1). The general trend is negative and opposes the PPH, which predicts a positive trend or no trend. Short *Drosera* differ significantly from tall *Drosera* ($P = 0.030$ for South African *Drosera* and $P = 0.033$ for Australian *Drosera*) because many short species and few tall species have considerable flower-trap separation (Fig. 1). The average peduncle length of *Utricularia* is 15.4 ± 10.8 cm whereas similarly short (< 5 cm) Australian *Drosera* have a mean peduncle length of 8.6 ± 8.9 cm ($n = 28$). Size class distributions of peduncle length in small Australian *Drosera* are skewed strongly towards the smaller size classes (Fig. 2). In contrast, *Utricularia* has a greater proportion of medium to extremely large peduncle lengths (Fig. 2).
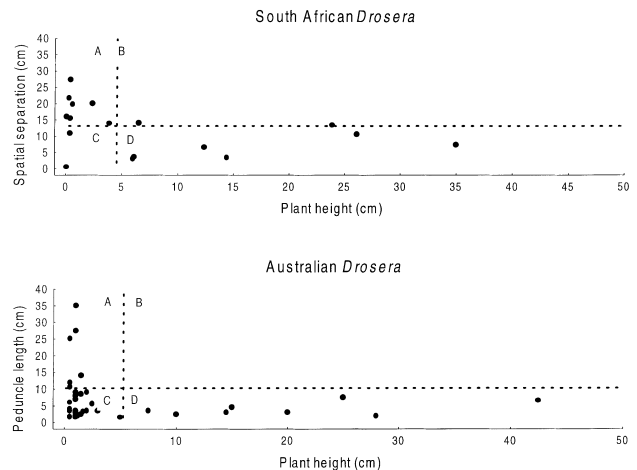
Figure 1 The distance between traps/leaves and flowers vs. plant height in South African *Drosera* and Peduncle length vs. plant height in Australian *Drosera*. Plots have been divided into four quadrants A = short plants with large floral-trap separation, B = short plants with small separation, C = tall plants with large separation and D = tall plants with small separation.
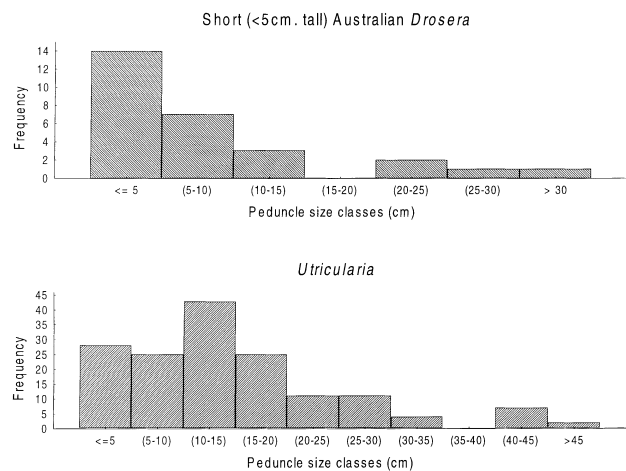
Figure 2 Size class distributions of peduncle lengths in small (< 5 cm) Australian *Drosera* and *Utricularia*.

DISCUSSION

Utricularia's peduncles are comparable in length or exceed those of *Drosera*. There are also higher frequencies of long flower stalks in *Utricularia* than in *Drosera*. Thus, the selective pressure for tall flower stalks in *Utricularia* seems to be as strong or stronger than for *Drosera*. Since *Utricularia* does not face the pollinator-prey conflict, other factors must select for long peduncles in this genus. Long peduncles may be a response to improved pollinator attraction or seed dispersal.

We also found a negative relationship between plant height and spatial separation in the Droseraceae (PAH). This suggests that PPH is not the primary mechanism driving the evolution of extreme spatial separation of flowers and traps in *Drosera*. This may be because *Drosera* seldom catches its pollinators, even if peduncles are short. Pollinators are either too "intelligent" or the mucilage is most suited to catching very small prey items and not pollinators. Alternatively, the positive effects on plant growth may outweigh the negative effect of trapping pollinators. *Drosera* and *Utricularia* probably evolved long peduncles for the same reasons (both are short plants needing to project their flowers). We predict that short, noncarnivorous plants will also exhibit long peduncles and that taller plants will have shorter peduncles.

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BIOSKETCH

Bruce Anderson's main interests are in the fields of evolutionary ecology, and in particular with mutualisms, symbiotic relationships and pollination biology. He is presently in his final year of PhD, working on mutualisms between insects and carnivorous plants.