

OLFACTORY PREY ATTRACTION IN *DROSERA*?

ANDREAS FLEISCHMANN • Botanische Staatssammlung München • Menzinger Strasse 67 • D-80638 Munich • Germany • fleischmann@lrz.uni-muenchen.de

Keywords: trap scent, prey attraction, prey analysis, Lepidoptera, ecology, *Drosera fragrans*, *Drosera finlaysoniana*, *Drosera slackii*.

The use of scented traps for prey attraction has been reported from a few genera of carnivorous plants: most prominently in the pitcher plant genera, where a sweet honey- or fruit-like scent is detectable to the human nose from the pitchers of some populations of *Sarracenia flava*, *S. alata*, *S. rubra*, *S. oreophila*, *S. leucophylla*, and *S. minor* (Miles *et al.* 1975; Slack 1979; Juniper *et al.* 1989; Jürgens *et al.* 2009; pers. obs.), certain species of *Heliampora* (a sweet, honey-like scent is produced from the nectar-spoons of *H. tatei*, *H. neblinae*, and *H. chimantensis*, while the pitchers of *H. sarracenioides* produce a notable chocolate-like odor when growing under natural or favorable conditions; Fleischmann & McPherson 2010), and the pitchers of some species of *Nepenthes* (e.g. *N. rafflesiana*; Moran 1996; Di Giusto *et al.* 2008). Interestingly, the Venus Flytrap *Dionaea* also has been discovered to attract prey to its traps not only by the vivid coloration, but also by producing scented volatiles (Kreuzwieser *et al.* 2014). Furthermore, a weak, musty, fungus-like fragrance is emitted from the leaves of several *Pinguicula* species such as the five species from the southeastern United States (e.g. *P. primuliflora* and *P. lutea*, pers. obs.) and *P. vallisneriifolia* (Zamora 1995), and was even generalized to be true for the whole genus (Lloyd 1942; Slack 1979). Interestingly, a large percentage of prey trapped by the sticky leaves of *Pinguicula* consists of fungus gnats (Diptera: Mycetophilidae, and Sciaridae; pers. obs.), which are attracted by this kind of flavor. Curiously, I observed that the green foliar leaves of three closely related members of *Utricularia* section *Folioliosa* (*U. tricolor*, *U. tridentata*, and *U. calycifida*) also have a clearly notable, characteristic scent (which, to my nose, smells identical in these three species, and reminds me of cardamom). Since in this genus, the subterranean bladder traps are clearly separated from the photosynthetic organs, the scent plays no obvious role in prey attraction—perhaps it is defensive in nature? The well-known, unpleasant smell of Martyniaceae shall be just briefly mentioned here, as *Proboscidea* and *Ibicella* are evidently not considered carnivorous anymore.

The most renowned and best-studied example of a carnivorous plant with fragrant traps, however, is the dewy-pine, *Drosophyllum lusitanicum*, which produces a strong, honey-like odor from its sticky passive flypaper traps (Lloyd 1942; Slack 1979; Juniper *et al.* 1989; Bertol *et al.* 2015). The perfume produced by this carnivorous subshrub is so strong that I could first smell natural populations from the car (driving with open windows in southern Andalusia) before actually seeing the plants themselves. Likewise, even when just a single plant of *Drosophyllum* is grown in a greenhouse, it will fill the entire greenhouse space with its intense honey scent during warm, bright days.

Curiously, in *Drosera*, the largest genus of carnivorous plants with ca. 250 species, there have been almost no reports about scented traps thus far, although a few species are obviously equipped with a typical scent of their leaves, which most likely is connected to prey attraction (in combination with the visually attractive coloration of the lamina, and the glistening mucilage of the glands). Prey attraction by a combination of olfactory and visual clues has been speculated for *Drosera* as early as Darwin (1875), who states: “I suspect from the number of insects caught by the English

species of *Drosera*, and from what I have observed with some exotic species kept in my greenhouse, that the odour is attractive.” Yet, surprisingly few studies focused on that topic—and those who did, examined only a single species, where they did not find a special trap scent: Jürgens *et al.* (2009) used *D. binata*, a species where I also did not observe any special scent in any of the cultivated forms I examined.

However at least in two different groups of *Drosera*, I noticed scented traps (both in cultivated specimens, as well as in plants in their natural habitat).

The first example is the volatile lemon-like scent emitted from the blood-red rosettes of *Drosera slackii* (*D.* section *Drosera*), as was observed both in cultivated specimens (originating from Palmietriver and Hermanus, South Africa) and in plants studied *in situ* at Hermanus. Curiously, I did not notice any comparable scent in any other *Drosera* I tested, not even in the closely related South African species. *Drosera slackii* catches comparatively large prey in the greenhouse, predominately large flies (mainly Muscidae), but it is not tested yet if there is a connection to the leaf scent and/or dark red coloration¹ of the species.

Secondly, I noticed odoriferous leaves in at least two “forms” of the annual plants that were all previously called “*Drosera indica*” from tropical South Africa and tropical Australia in my greenhouse; the sweet honey-like scent that is emitted from their leaves is comparable (regarding strength and fragrance) to the scented traps of *Drosophyllum*.

The South African plant, which I obtained as “*D. indica* ‘large’, Transvaal” from Paul Debbert, Munich, clearly belongs to *D. finlaysoniana*, following the new classification of *D.* section *Arachnopus* (the “*D. indica* complex”) of Lowrie (2013). However I cannot ascertain for sure that the seeds, which I obtained from greenhouse-grown plants of Debbert in Munich in the mid-1990’s, indeed originated from Africa, or perhaps from a mix-up with material from Australian or Asian provenience (thus far, I have not found herbarium evidence for an occurrence of *D. finlaysoniana* in Africa). Nevertheless, scented leaves seem to be frequent in some populations of Australian *D. finlaysoniana*, as I also grow several plants from different locations from northern Australia which display a strong, honey-like odor emitting from their leaves, filling the entire greenhouse given warm temperatures and strong sun light.

Another member of the *D. indica* complex which has scented leaves is *D. fragrans* (the very obvious sweet, honey-like scent was even the source of the species’ name, see Lowrie (2013)); again, I was able to confirm the scent of the leaves this species (which is very similar to that of *D. serpens*) both in greenhouse grown plants, as well as in plants I observed near Darwin, Northern Territory, in July 2014. I did not detect any notable trap scent in the closely related, sympatrically growing *D. aquatica*, however, nor in *D. serpens* which I found co-occurring with scented *D. finlaysoniana* in the Keep River area (nor does Lowrie (2013) mention perfume for any other species of *D.* sect. *Arachnopus* than *D. fragrans*). In cultivated specimens of *D.* sect. *Arachnopus* tested, I observed trap scent only in *D. fragrans* (all specimens) and *D. finlaysoniana* (only from some locations), but not in any of the other members of that affinity.

The fact that plants of some populations of *D. finlaysoniana* have no obvious scent has no taxonomic meaning of course, and in flower scent of various (non-carnivorous) plants the same has

¹ The role of leaf coloration for prey attraction is still not clear in *Drosera*. While Jürgens *et al.* (2015) concluded that the red color of the leaves of *D. spatulata* and *D. arcturi* serves for prey attraction, Foot *et al.* (2014) found no evident connection between red trap color and prey attraction in *D. rotundifolia*. Certainly the bright red rosettes and leaves of many *Drosera* species do contrast well with the soil background of their habitats – but usually the plants are the redder the more exposed the habitat is. Some species occurring at high altitudes (e.g. above-mentioned *D. spatulata* and *D. arcturi* from New Zealand) are strikingly red in their natural alpine habitat, but have more greenish leaves at lower elevations – it is not known if they will catch significantly lower prey under such conditions. Most prey insects cannot detect colors of the red spectrum anyway, thus are more likely attracted by color contrasts than the color itself.

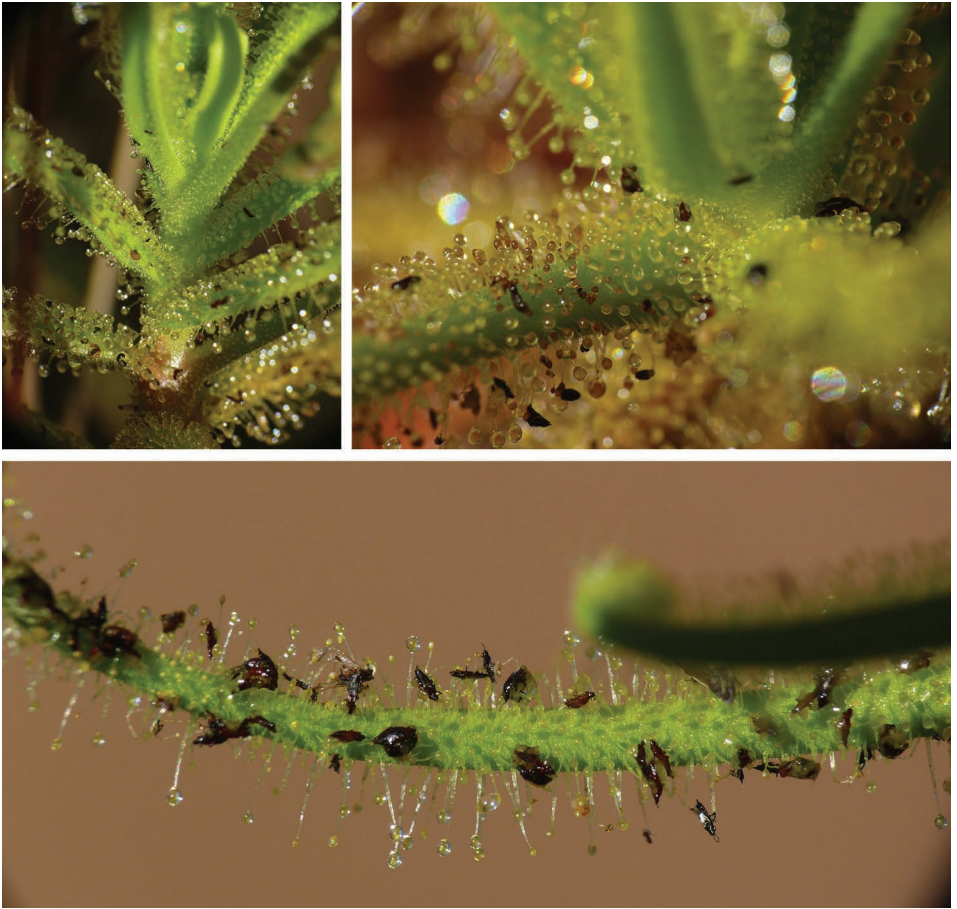


Figure 1: In *D. finlaysoniana*, carnivorous glands cover the leaf down to the very base (an obvious “petiole” is lacking). The small-sized prey items consisted mainly of Thysanoptera (thrips), a rather frequent small prey of other *Drosera* species with upright leaves. Keep River NP, Northern Territory, Australia.

repeatedly been observed: some populations or individuals within a given population might have floral odor, while others don't; the same holds true for sweet-honey scent in the pitchers of *Sarracenia flava* populations.

Lowrie (2013) assumed that the curious outgrowths at the leaf bases of *D. fragrans* could serve as osmophores which produce the perfume, a hypothesis that still has to be tested. In *D. finlaysoniana*, likewise strongly scented in some populations, such organs are missing (Fig. 1). Whatever the foliar source, these two annual species emit a strong, sweet, honey-like perfume, which is discernable to the human nose even at some distance from the plants. In a river valley at Ginimum Walk, Northern Territory, the sweet honey-like scent of some large individuals of *D. finlaysoniana* could be detected by myself even before I found the plants growing there. Interestingly the few large plants had captured a rich variety of large insect prey, almost exclusively consisting of medium-sized to large butterflies and moths (mainly diurnal, but also some apparently nocturnal species). Some individuals of *D. finlaysoniana* were literally covered in dead Lepidoptera (Figs. 2 & 3).



Figure 2: A single individual of strongly honey-perfumed *D. finlaysoniana* covered with prey. Besides Diptera (various small flies, midges and mosquitoes), Hymenoptera (small solitary wasps) and Thysanoptera (thrips), prey mainly consisted of Lepidoptera: 1. Geometridae (a species of geometer moth), 2. Pterophoridae (species of plume moth), 3. day-flying Tiger Moth (probably *Amata* sp.; Arctiidae), 4. Grass Yellow (*Eurema* sp., Pieridae), and 5. Eight individuals of *Acraea terpsicore* (Nymphalidae). The accompanying pink-flowered plant at the bottom is the glandular, annual *Styloidium adenophorum*.

On a single large plant I counted an astonishing total of 35 butterflies and moths adhering to the numerous gland-covered, thread-like leaves of the plant. Most impressive was not only the large number of butterflies caught by the plant, but the many different species (both males and females) of Lepidoptera from different families which were found attracted to and killed by *D. finlaysoniana*.

A few of them could be tentatively identified from the photographs (Fig. 2). Very common prey was the Tawny Coster (*Acraea terpsicore*; Lepidoptera: Nymphalidae), an invasive butterfly species from India which spreads widely in Northern Australia; frequently, three or more individuals of that species (mainly males, but also females) were caught by a single plant of *D. finlaysoniana* (Fig. 2).



Figure 3: Three individuals of day-flying Tiger Moth (Arctiidae – Ctenuchinae, probably *Amata* sp.; left: 2 males, right: female) sticking to *D. finlaysoniana* at Keep River NP.

I also observed this and other butterfly species (especially Grass Yellows—*Eurema* species; Pieridae) being caught as frequent prey by non-scented members of the *D. indica*-complex (e.g. *D. serpens* and odorless *D. finlaysoniana* populations). However, these captures were usually rather solitary, and never in such high numbers as in the perfumed plants. Greg Bourke (pers. comm.) has found (non-scented) *D. serpens* with good numbers of Grass Yellow butterflies near Mareeba, northern Queensland, but only as many as maybe six or seven on an individual plant. Like my observations reported here, his finding was made in July, late in the growing season. Greg assumes that the presence of butterfly prey might also be dependent on the season, and earlier in the rainy season might be before the peak for the butterflies. Greg reported to me large populations of *D. hartmeyerorum* (non-scented) and *D. fragrans* (scented) between Broome and Derby, northern Western Australia, early in the season with just a few individuals of butterflies caught per plant. Any comparative prey observations from such large non-scented *Drosera* populations late in the season (at the height of butterfly presence) would be very interesting. Greg (pers. comm.) made a good point that also the habitat for these *Drosera* species might impact the number of available butterflies, especially where the sundew plants are concentrated in seepage habitats beside creeks where the only available moisture for butterflies is present, and where the insects might be more easily “channeled” to the *Drosera* traps, than in large, open swampy areas. Yet, it was quite obvious in the sympatrically growing species, *D. fragrans* (scented) and *D. aquatica* (non-scented) which I observed in a rather open swampy spot near Darwin in July, that the former had conspicuously more butterfly prey than the latter.

So what does attract these flower-visiting insects to the sticky traps of these *Drosera* species? Both color and scent can be connected with floral reward for pollinating insects (Chittka & Thomson 2001). Although foraging butterflies are generally more visually attracted to the flowers that they visit, guidance by olfactory floral cues also plays an important role (especially for distance attraction), and their antennae are very sensitive and receptive to floral scents (Dudareva & Pichersky 2006). Thus it is quite likely that some butterflies and moths might also have been attracted to *D. finlaysoniana* by the plant’s sweet honey-odor, but not so much by its coloration¹, as the yellowish-green sundew did not contrast much from the surrounding herbaceous vegetation during the dry season.

Once one individual of a certain butterfly or moth species is sticking to the *Drosera*, it is of course possible that it unintentionally will attract more individuals of the same species, males as well as females (especially male butterflies are generally very territorial, and will approach or attack any other males and females of the same species that come close). This intraspecific attraction

to the caught individuals might be caused both by visual stimuli and transmitted pheromones from the living prey, and might explain the high numbers of caught Lepidoptera. However then why only the honey-scented *D. finlaysoniana* – I’m almost tempted to call it “the Australian dewy-pine” in dependence on *Drosophyllum* – were fully covered in Lepidoptera, but not their odorless congeners? By the way, the phenomenon of “intraspecific prey attraction via caught but still alive prey” can also be observed in dark-winged fungus gnats (Diptera: Sciaridae) caught by yellow sticky traps (or likewise *Pinguicula* leaves) on the windowsill or in the greenhouse: a single female fungus gnat struggling on the sticky surface will usually soon attract a large number of males, which are then also caught nearby. Interestingly I have not found any published evidence about such observations, or similar reports from a comparable system of natural sticky trap: spider webs (but see Bjorkman-Chiswell *et al.* 2004 for the attraction of saprophagous insects to dead prey in sticky traps).

Interestingly, those few *Drosera* species which have scented leaves altogether have non-perfumed flowers. On the other hand, in those *Drosera* species that have perfumed flowers (see Fleischmann *et al.* 2007; Gibson 2013; Lowrie 2013), I could detect no evident odor from the leaves. Both are reasonable, to separate pollinators from prey, which will be either attracted to the traps or the flowers by visual signals or scent, or vice versa.

Acknowledgements: To Allen Lowrie for many inspiring discussions, and for confirming identification of the *Stylidium* species, to Greg Bourke and Richard Nunn for sharing their field observations with me, and to Barry Rice for helpful comments on the manuscript.

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