Arthropod fauna of mammal-pollinated *Protea humiflora*: ants as an attractant for insectivore pollinators?

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*Protea humiflora* Andrews inflorescences are cryptic, but strongly scented and borne close to the ground (geoflorous) for ready access by small, non-flying mammals. During a study of *P. humiflora* pollination, we found that insectivorous elephant shrews (Macroscelididae: *Elephantulus edwardii* (A. Smith)) carried higher pollen loads on their snouts than simultaneously-trapped rodent species. Elephant shrews seem to be acquiring pollen while foraging for insects in the inflorescences. Compared with the larger bird-pollinated inflorescences of *P. repens* (L.), *P. humiflora* inflorescences have a substantially lower mass of arthropods, relatively fewer beetles (12 % of arthropod dry mass) and more ants (13 %). The large numbers of ants in these inflorescences may attract insectivore pollinators, suggesting an indirect, mutualistic relationship between plant, insect and insectivore.

**Key words**: non-flying mammal pollination, fynbos, satellite fauna, ants, nectar, mutualism.

**INTRODUCTION**

*Protea* species of the section Hypocephalae are known as the ‘rodent sugarbushes’, and are characterized by cryptic, strong-smelling inflorescences, borne close to the ground under dense foliage (Rebelo 1995). This allows ready access by small, non-flying mammals (‘therophily’), which account for half of the pollination events that lead to seed set (Wiens *et al.* 1983; Fleming & Nicolson 2002). *Protea* species are self-incompatible (Horn 1962), and it seems likely that the remaining pollination is carried out by insects (Coetzee & Giliomee 1985; Wright *et al.* 1991).

During a recent study of the pollination system of *Protea humiflora* Andrews (Fleming and Nicolson 2002), we were surprised to find that Cape rock elephant shrews (Macroscelididae: *Elephantulus edwardii* (A. Smith)) carried higher pollen loads on their snouts than simultaneously-trapped rodent species. The possibility that these medium-sized insectivores (mean ± 1 S.D.: 49 ± 5 g, n = 11 adults) could be significant pollinators of *Protea* species has not been seriously considered previously (Wiens *et al.* 1983; Rebelo & Breytenbach 1987). The preponderance of pollen on the snouts of *E. edwardii* compared with its scarcity in their faeces (pollen grain exines pass through the digestive system intact; van Tets 1997), suggests that these shrews are unlikely to feed directly on *Protea* pollen, as do rodent visitors (Muridae: *Acomys subspinosus* (Waterhouse) and *Aethomys namaquensis* (A. Smith)). It is more likely that pollen is acquired during foraging for insects in the inflorescences. The aim of the present study was to quantify and characterize the arthropod fauna in *P. humiflora* inflorescences to gain insight into why elephant shrews might be visiting these inflorescences, and compare this with published data for other, typically bird-pollinated, *Protea* species. In addition, we estimated the nectar standing crop and compared the energy available from nectar and arthropods.

**METHODS**

We examined *P. humiflora* inflorescences collected from two sites near Villiersdorp in the Riviersonderend Mountains, in the southern Cape, South Africa, between July and October 2000. We analysed inflorescences at all stages of opening; from early, recently opened, through to near-spent inflorescences, provided that pollen was still present.

Arthropods were collected from 48 inflorescences, which were cut and placed immediately in plastic bags and analysed on return to the laboratory. Nectar standing crop was quantified for an additional 36 inflorescences: arthropods were removed with forceps on site and stored in alcohol.

For nectar analysis, the styles of 12 about-to-open florets were marked with permanent marker.
pen and nectar was collected from their bases using 10 µl micropipettes and slight suction. (Nectar was found in florets that were about to open, while older peripheral florets and younger central florets were largely dry.) Nectar volume was recorded (proportion of micropipette length) and sugar concentration (% weight/weight) was measured with 0–50 % and 45–80 % refractometers (Bellingham & Stanley, U.K.) for each floret separately. After conversion to % weight/volume (Bolten et al. 1979), the quantity of sugar obtained from each floret was calculated. The average value was then extrapolated to estimate total nectar from each floret was calculated. The average value of sugar for the 265 ± 36 florets per inflorescence was then extrapolated to estimate total nectar from each inflorescence. The mean dry mass of arthropods (7.6 ± 10.8 mg per inflorescence) represents an energy content of 175 J (energy values from Mostert et al. 1980).

A total of 756 macro-arthropods (646 mg) representing seven orders was recovered. The dry mass of macro-arthropods was significantly higher during mid-winter (Table 1, K-S: P < 0.025). There were no differences in arthropod mass between the two sites sampled.

Over half the total dry mass of arthropods recovered (58 %) was lepidopteran larvae which were only found in inflorescences sampled during winter, at the beginning of the flowering season (Table 1). The larvae bore into inflorescence receptacles and sever the water supply to the florets, causing their abortion and death (A.G. Rebelo, pers. comm.). The dry mass of Lepidoptera larvae from inflorescences that appeared to be aborted (i.e. were dry, brownish, or had failed to open, n = 19) was around three times that of inflorescences that appeared fresh (n = 65, K-S: P < 0.05). Lepidoptera larvae were not recovered from inflorescences sampled from August onwards. A greater mass of Coleoptera was also recovered during winter (KS: P < 0.001).

Eight species of ants were identified from P. humiflora flowers: Anoplolepis custodiens (F. Smith), (31 % of individuals, 20 % of dry mass), Crematogaster sp. 1 (31 %, 45 %), Camponotus nivosetosus Mayr (18 %, 24 %), Crematogaster sp. 3 (6 %, 9 %), Lepisiota capensis (Mayr)(9 %, 2 %), and small numbers of individuals of Crematogaster sp. 2 (2 % of total ant individuals), Camponotus sp. 2 (nr angusticeps Emery) (2 %), and Tetramorium erectum Emery (1 %). Ant specimens have been lodged with the South African Museum. No Argentine ants (Linepithema (Iridomyrmex) humilis (Mayr)) were present. Ants were present throughout flowering, even during the middle of winter. An average of 6.5 ants (1.55 ± 3.07 mg) was recovered from each inflorescence sampled later in the flowering season (61 % of the macro-arthropod dry mass), compared with only 1.6 individuals (0.78 ±
1.34 mg) in winter (8.5%; K-S: P < 0.01). We found ants present at all stages of opening, from buds to near-spent inflorescences (Fig. 1B). Ant abundance was associated with a decrease in nectar volume (Fig. 1C), presumably as a result of their feeding on nectar (Fig. 2).

**DISCUSSION**

In this study, we found that *P. humiflora* nectar was highly concentrated and extremely viscous. Our average concentration of 49% (w/w) was considerably higher than the mean of 37.8% measured for freshly secreted *P. humiflora* nectar by Wiens *et al.* (1983). Our energy estimates of about 66 J of energy available per day from nectar may therefore be an underestimate of the energy available to a small flower visitor that would be able to feed on quantities not measurable by ourselves. Estimates of energy available from macro-arthropods (175 J) were therefore higher than that for the nectar standing crop. Calf (2000) similarly found much greater arthropod energy available for sugarbirds in bird-pollinated *Protea*.
inflorescences than in the nectar. These inflorescences are much larger than those of *P. humiflora* and contain a much greater mass of arthropods (Mostert et al. 1980; Calf 2000).

Comparison of the macro-arthropod fauna of *P. humiflora* inflorescences with published data for other *Protea* species (e.g. Collins & Rebelo 1987) revealed similarities as well as some differences, which should be interpreted with caution. Lepidoptera and Coleoptera larvae were similarly numerous in bird-pollinated *Protea* species, particularly *P. lepidocarpodendron* (L.) L. (36% of individuals recorded during July and August, Rebelo & Seiler, unpubl. data, cited by Collins & Rebelo 1987). Differences in records of larvae may reflect different sampling regimes, since inflorescences heavily infested with larvae appear to be dying and may therefore be ignored. In addition, we found that larvae were present only in inflorescences sampled during July, so that differences in the time of sampling could greatly affect arthropod composition; previous studies of *Protea* arthropod fauna have been confined to autumn and winter (Mostert et al. 1980; Coetzee & Giliomee 1985) or winter only (Rebelo & Seiler, unpubl. data).

Numbers of adult Coleoptera appear to be very different in *P. humiflora* and the bird-pollinated species (Collins & Rebelo 1987). Around 77% of the arthropods in *P. repens* (L.) L. (Mostert et al. 1980; Coetzee & Giliomee 1985; Rebelo & Seiler, unpubl. data), 82% in *P. nitida* Mill. (Visser et al. 1996), and 60% of those from *P. lepidocarpodendron* (Rebelo & Seiler, unpubl. data) are beetles which may play an important role in pollination (Coetzee & Giliomee 1985; Wright et al. 1991). In particular, protea flea beetles (*Chirodica* sp.) are the majority in numbers of individuals as well as mass in these bird-pollinated species (Mostert et al. 1980; Coetzee & Giliomee 1985; Visser et al. 1996). This contrasts with *P. humiflora*, for which beetles comprised 54% of individuals, but only 12% of the mass. The most numerous beetle was a species of the little-known family Corylophidae (around 1 mm long); these beetles feed on fungi in decaying

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### Table 1. Arthropod dry mass composition for *Protea humiflora* inflorescences sampled in mid-winter (July, n = 62) and late winter/spring (August to October, n = 22). Figures are the mean mass per inflorescence (mg ± 1 S.D.) and percentages of total macro-arthropod dry mass. *P*-values are for results of analysis by Kolmogorov-Smirnov test comparing seasons.

<table>
<thead>
<tr>
<th>Arthropod Group</th>
<th>Mid-winter mg ± 1 S.D.</th>
<th>%</th>
<th>Late winter &amp; spring mg ± 1 S.D. %</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arachnida</td>
<td>0.32 ± 0.94</td>
<td>3.45</td>
<td>0.11 ± 0.52</td>
<td>&gt;0.10</td>
</tr>
<tr>
<td>Blattodea</td>
<td>0.96 ± 3.84</td>
<td>10.49</td>
<td>0.72 ± 2.34</td>
<td>&gt;0.10</td>
</tr>
<tr>
<td>Coleoptera</td>
<td>1.17 ± 3.34</td>
<td>12.80</td>
<td>0.07 ± 0.17</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Dermaptera</td>
<td>0.02 ± 0.13</td>
<td>0.17</td>
<td>0.04 ± 0.21</td>
<td>&gt;0.10</td>
</tr>
<tr>
<td>Hemiptera</td>
<td>0.18 ± 0.43</td>
<td>1.97</td>
<td>0.05 ± 0.17</td>
<td>&gt;0.10</td>
</tr>
<tr>
<td>Hymenoptera (Formicidae)</td>
<td>0.78 ± 1.34</td>
<td>8.51</td>
<td>1.55 ± 3.07</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Lepidoptera (larvae)</td>
<td>5.73 ± 10.98</td>
<td>62.60</td>
<td>0.00</td>
<td>&gt;0.10</td>
</tr>
<tr>
<td>Total biomass</td>
<td>9.41 ± 11.99</td>
<td></td>
<td>2.59 ± 4.00</td>
<td>&lt;0.025</td>
</tr>
</tbody>
</table>

1: largely Corylophidae.

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![Fig. 2. Anoplolepis ants recovered from *Protea humiflora* inflorescences. These individuals are obviously replete with nectar. Scale = 250 µm.](image-url)
plant material (Scholtz & Holm 1985) and were more abundant in inflorescences which were heavily infested with Lepidoptera larvae. While Chironicta were not recovered from *P. humiflora*, conversely Corylophidae have not previously been recorded in inflorescences of other *Protea* species.

Indigenous ants were a significant component of the arthropod fauna of *P. humiflora* (35% of numbers and 13% of mass), but in bird-pollinated inflorescences they are scarce. For example, in *P. repens*, Coetzee & Giliomee (1985) recorded that the alien Argentine ant was the most abundant of eight ant species, while Mostert et al. (1980) recovered only Argentine ants. Similarly, indigenous ants are extremely rare in *P. nitida* inflorescences (Visser et al. 1998). Ants are efficient nectar collectors and are easily able to handle sugar solutions as concentrated as the nectar of *P. humiflora* (Josens et al. 1998). However, ants are generally described as nectar thieves (Hickman 1974; Inouye 1980; Galen 1983). They are considered to be ineffective pollinators due to their small size (limiting contact with anthers and stigmas), smooth integument, frequent grooming, antibiotic metapleural gland secretions, and, finally, their rather limited mobility (Schubart & Anderson 1978; Beattie 1985; Peakall et al. 1991). Many plants therefore have developed protective devices designed to keep ants out: hiding nectar in tubes and closed blossoms, closed throats or sticky hairs (Geurrant & Fiedler 1981; Peakall et al. 1991). Other plants may distract ants by luring them away from flowers to extra-floral nectaries (e.g. Zachariades & Midgley 1999).

Therophilous *Protea* species, including *P. humiflora*, seem to have little defense against nectar-thieving ants. Their inflorescences are geoflorous, a short distance separating them from ants on the ground, and there is little protection of nectar within the flowers. *Protea* species do not possess extra-floral nectaries (Rebelo 1995). Nectar may in fact be more accessible to insects than it is to vertebrate would-be pollinators, particularly mammalian visitors that lack the finesse of an avian beak. The role of ‘satellite’ arthropods in *Protea repens* inflorescences as an attractant and energy source for bird pollinators was emphasized by Mostert et al. (1980), who analysed stomach contents of Cape sugarbirds. We suggest a similar role of arthropod fauna in pollination of *P. humiflora* by the elephant shrew *E. edwardii*. Elephant shrews trapped during flowering of *P. humiflora* (Fleming & Nicolson, in press) produced faeces containing pieces of ant exoskeleton (three out of eight scats samples from *E. edwardii* individuals trapped during winter contained positively-identifiable ant exoskeletons; however, the majority of the exoskeleton material is not identifiable). Ants (and termites) are recorded as the main diet of Macroscelididae (Perrin 1997). When foraging on ants in *P. humiflora* inflorescences, elephant shrews would be additionally rewarded by the nectar already consumed by these ants (e.g. Fig. 2).

Having an insectivore as pollen vector has advantages for the plant, since these animals are less likely to consume flower parts than rodent visitors (e.g. Vlok 1995) and also have greater home ranges (Withers 1979; Fleming & Nicolson, unpubl. data). Insectivores may also pollinate Australian Proteaceae: a number of dasyurid marsupial species recorded as regular visitors to *Banksia* inflorescences (Turner 1982; Carthew & Goldingay 1997; Goldingay 2000). These observations may change the perceived role of arthropods, particularly ants, in pollination of Proteaceae. If arthropods contribute in some part to attract insectivores, then Proteaceae would derive an indirect benefit from their arthropod visitors. The relationship between ant and plant under these circumstances may therefore be more mutualistic (Maloof & Inouye 2000) than illicit, and the blanket description of ants as ‘nectar robbers’ may be doing them an extreme injustice.

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