A COMPARISON OF THE FORAGING BEHAVIOUR OF THE EASTERN PYGMY-POSSUM (CERCARTETUS NANUS) AND NECTARIVOROUS BIRDS IN A BANKSIA INTEGRIFOLIA WOODLAND

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The foraging behaviour of a non-flying mammal, the eastern pygmy-possum (Cercartetus nanus) and nectarivorous birds was compared in a Banksia integrifolia woodland at Wilson’s Promontory National Park, Victoria, Australia. Exclusion experiments performed previously in this woodland indicate that both non-flying mammals and nectarivorous birds are important pollinators of *B. integrifolia* (Cunningham 1991: *Oecologia* 87: 86-90). In this study it is shown that *C. nanus* and nectarivorous birds employ different foraging tactics. Nectarivorous birds tended to move further between trees (\(x = 8.16 \pm 1.06\) m) than *C. nanus* (\(x = 5.64 \pm 0.75\) m), although these differences were not significant. Nectarivorous birds were attracted to trees with a significantly larger number of inflorescences (\(x = 36.55 \pm 2.84\)) than *C. nanus* (\(x = 18.65 \pm 2.95\)), and visited a significantly greater number of inflorescences per tree (\(x = 4.24 \pm 0.33\)) than *C. nanus* (\(x = 2.33 \pm 0.22\)). Although the two pollinator groups were attracted to banksia plants by different cues, once in the plants they visited an equal proportion of the available inflorescences.

Key words: *Cercartetus nanus*, nectarivorous birds, *Banksia integrifolia*, pollination, foraging movements

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THE foraging behaviour of animals in plant-pollinator systems is important in determining both their effectiveness as pollinators, and the degree to which they promote gene dispersal (Harder and Barrett 1996). An ineffective pollinator may reduce the reproductive success of plants by limiting the quantity or quality of compatible pollen deposited on stigmata (Ramsey 1988), or by removing pollen from the system, thus decreasing the amount available for transfer by more effective pollinators (Snow and Roubik 1987). The effect of systematic foraging on flowers of adjacent plants has been shown both theoretically (Levin and Kerster 1974), and empirically (Turner *et al.* 1982) to produce significant inbreeding, homozygosity and patchiness in plant populations. In contrast, long-distance foraging and resulting gene flow produces greater levels of outcrossing within populations (Linhart *et al.* 1987).

Many flower-visiting animals have been identified as pollinators (Faegri and van der Pijl 1979). Pollination by nectarivorous birds and insects is both common and widespread (Vaughton 1992; Johnson 1996). Pollination by nectarivorous bats is also common (Woodside and Pyke 1995). However, until recently, pollination by non-flying mammals was often overlooked (Carthew and Goldingay 1997).

Previous studies have attempted to quantify and compare pollination services of different vertebrates to determine the relative importance of these animals as pollinators of the Proteaceae within Australia (Hopper and Burbidge 1982; Paton and Turner 1985; Cunningham 1991; Vaughton 1992; Carthew 1993). Although insects do visit the flowers of banksias (Vaughton 1992), the copious nectar production and large stigma to nectary distances typical of these plants suggest specialisation for pollination by vertebrates (Paton and Turner 1985). Studies demonstrate that both non-flying mammals and nectarivorous birds are effective pollinators (Cunningham 1991), but there has been little investigation into the differences in the foraging behaviour of these pollinators (Carthew and
Goldingay 1997). Early studies (Sussman and Raven 1978; Hopper and Burbidge 1982) suggested that non-flying mammals were more sedentary than bird pollinators, making fewer interplant movements, thus resulting in greater levels of self pollination and limiting their effectiveness as pollinators.

The aim of this study was to investigate differences in the foraging behaviour of a non-flying mammal, the eastern pygmy-possum (Cercartetus nanus) and nectarivorous birds in a Banksia integrifolia woodland.

METHODS

This study was conducted in a B. integrifolia subsp. integrifolia L.f. woodland within Wilson's Promontory National Park (38° 57'S, 146° 17'E), approximately 230 km south-east of Melbourne, Australia. Cercartetus nanus is a small (15 - 43 g) arboreal marsupial which feeds largely on nectar and pollen from banksias, eucalypts and bottlebrushes (Turner and Ward 1983). Both C. nanus and nectarivorous birds are common visitors to the inflorescences of B. integrifolia at this site (Cunningham 1991; Bunce 1996). There are no nectarivorous bats or gliding marsupials present in this woodland (Bunce 1996).

Foraging movements of pollinators were investigated between April and October 1996, and April and August 1998. During this time, C. nanus was captured over twelve periods by placing between 30 - 200 Elliott traps (33 x 10 x 10 cm: Elliott Scientific, Victoria), each night of trapping in the branches of banksia trees. Traps were checked and cleared at intervals throughout the night.

Trapped individuals were weighed, measured, ear-notched for identification, and a spoil of fine thread (nylon quilting thread bobbin 70/7, Penguin Threads Pty. Ltd., Victoria), wrapped in adhesive tape, was attached to their backs using skin bond cement (following Carthew 1994). Each spool weighed approximately 2.4 g and was 165 m in length. The free end of the thread was attached to vegetation at the point of capture and the animal released. The path of the possum, as described by the thread, was followed the next day. Recording of foraging movements started at the first visit to an inflorescence to allow for the effect of any escape response. A thread that passed within 10 cm of an inflorescence or was tangled within the inflorescence itself, was taken to indicate a visit.

The foraging behaviour of nectarivorous birds was investigated by observing flowering banksia trees. Observations were conducted throughout the day ranging from 0700 to 1630. Once located, foraging birds were followed with binoculars until lost from sight.

For each banksia plant visited by C. nanus or a nectarivorous bird, the following information was collected:

1. the total number of available inflorescences in visited plants (those at the pollen presentation stage).
2. the number of inflorescences visited per plant.
3. the distances (to the nearest half metre) moved between plants.

RESULTS

Cercartetus nanus

The overall trapping success rate of C. nanus over the two seasons was 2.5% (71 captures from 2,899 trap nights). Other non-flying mammals captured were the house mouse (Mus musculus), and the bush rat (Rattus fuscipes). Of the 71 C. nanus individuals trapped, 45 were successfully tracked using the spool-and-line method. The remainder were either fitted with spools which subsequently either fell off or broke early on, or chemiluminescent ‘cyalume’ tags were attached to investigate the time spent by C. nanus at individual inflorescences. However, due to the difficulty of following the animals, insufficient data were collected.

Individuals were found to regularly move through the canopies of plants at a height of 1 - 2 m, or less often along the ground. In both cases, flowering inflorescences were approached by climbing onto the stem below the inflorescence. Multiple tracking of some individuals (n = 6) revealed that animals usually followed different foraging routes each night, but often revisited plants. Cercartetus nanus also passed through non-flowering banksia plants and plants of other species.

Nectarivorous birds

Six species of nectarivorous birds were identified as visitors to B. integrifolia inflorescences (little wattlebird (Anchochaera chrysoptera), red wattlebird (Anchochaera carunculata), eastern spinebill (Acanthorhynchus tENUrostris), New Holland honeyeater (Phylidonyris novaehollandiae), crescent honeyeater (Phylidonyris pyrrhoptera), rainbow loriikeet (Trichoglossus haematodus). The most frequently observed species were the red and little wattlebirds. Birds generally landed on the lateral branches immediately below inflorescences and probed between the most recently opened flowers to extract nectar. Nectarivorous birds were often difficult to follow due to the dense nature of the B.
**integripolia** woodland. As a result, there are more observations of foraging movements within trees than between trees (Table 1). The foraging behaviour of the rainbow lorikeet differed from that of the honeyeaters with lorikeets visiting a larger number of inflorescences per plant. However, due to small sample sizes, differences in foraging behaviour between species of nectarivorous birds could not be investigated fully. Nectarivorous birds visited fewer non-**integripolia** plants than **C. nanus**.

**Comparison of pollinators**

The foraging behaviour of the pollinator groups was compared using 2-tailed t-tests. Where necessary, data were logarithmically transformed. A correlation coefficient was used to test if the variables were independent.

There was a trend for birds to move further than **C. nanus** between **integripolia** plants (Table 1: 2-tailed t-test with equal variances: $t = -1.97, df = 72, P = 0.053$), although this difference was not significant. Maximum interplant movements were similar with nectarivorous birds moving a maximum recorded distance of 35 m between plants and **C. nanus** a maximum of 32 m between plants. The majority of interplant movements by both **C. nanus** and nectarivorous birds were under 5 m (Fig. 1: 71% for **C. nanus**; 55% for nectarivorous birds).

Birds were more attracted to trees with a greater number of available inflorescences than **C. nanus** (Table 1: 2-tailed t-test with unequal variances: $t = -5.73, df = 55, P < 0.0005$).

The number of inflorescences visited per plant differed between nectarivorous birds and **C. nanus**, with birds visiting a significantly greater number than **C. nanus** (Table 1: 2-tailed t-test with equal variances: $t = -4.95, df = 97, P < 0.0005$).

However, the number of inflorescences visited per plant and the total number of available inflorescences were found to be dependent ($P < 0.0005$ for both **C. nanus** and nectarivorous birds). Nectarivorous birds and **C. nanus** visited a similar proportion of inflorescences per plant (Fig. 2). An ANCOVA was used to assess whether the number of inflorescences visited per plant was similar for **C. nanus** and nectarivorous birds, after adjusting the data for the effect of the total number of available inflorescences per plant visited. An ANCOVA requires that the slopes of the regressions of the dependent variable (number of inflorescences visited per plant) on the covariate of interest (total number of available inflorescences on plants visited), be the same for the two groups (**C. nanus** and nectarivorous birds). This was tested by examining the interaction between the groups and the independent variable, yielding $F = 3.117, df = 1, P = 0.082$. Thus, it may be assumed that the slopes of these two lines are the same. The ANCOVA accounting for the effect of the total number of available inflorescences on plants visited on the number of inflorescences visited per plant, then resulted in $F = 0.360, df = 1, P = 0.550$. Thus, from these data these two groups have no effect on the relationship between the number of inflorescences visited per plant and the total number of available inflorescences per plant visited.

**DISCUSSION**

The distances moved by pollinators between flowering plants provide an indirect estimate of pollen transfer distances (Schmitt 1980). In the present study, nectarivorous birds tended to move further between **integripolia** plants than **C. nanus**. Although maximum interplant distances were similar for **C. nanus** and nectarivorous birds, it is likely that due to the difficulties of following birds over long distances, there is a downward bias in distance estimates. Therefore, it is probable that nectarivorous birds do move greater distances than 35 m between plants within a foraging bout. However, the majority of moves by both pollinator groups were between near-neighbours (i.e., less than 11 m away). In

<table>
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<th>Interplant movement (m)</th>
<th>Inflorescences visited per plant</th>
<th>Available inflorescences per plant visited</th>
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<tbody>
<tr>
<td><strong>C. nanus</strong></td>
<td>5.64 ± 0.75 (39)</td>
<td>2.33 ± 0.22 (43) *</td>
<td>18.65 ± 2.95 (39) *</td>
</tr>
<tr>
<td>birds</td>
<td>8.16 ± 1.06 (35)</td>
<td>4.24 ± 0.35 (56) *</td>
<td>36.55 ± 2.84 (56) *</td>
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<tr>
<td>little wattlebird</td>
<td>(14)</td>
<td>(20)</td>
<td>(20)</td>
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<tr>
<td>red wattlebird</td>
<td>(11)</td>
<td>(18)</td>
<td>(18)</td>
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<tr>
<td>eastern spinebill</td>
<td>(5)</td>
<td>(7)</td>
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<tr>
<td>New Holland honeyeater</td>
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<td>rainbow lorikeet</td>
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* Table 1. Summary of foraging data for **C. nanus** and nectarivorous birds in the **integripolia** woodland. Mean values are shown ± standard errors. * indicates means differed significantly at $P < 0.05$. ( ) indicates the number of observations both for the two groups and for each bird species separately.
**Fig. 1.** Interplant movements made by nectarivorous birds (light shading) and *C. nanus* (dark shading).

**Fig. 2.** Relationships between the number of inflorescences visited per plant and the total number of available inflorescences per plant visited for nectarivorous birds (□, $r^2 = 0.38$) and *C. nanus* (●, $r^2 = 0.30$).
contrast, Carthew (1994) found that approximately 50% of movements by small marsupials visiting B. spinulosa were greater than 10 m. This variation between studies is likely to reflect differences in the distribution and densities of flowering plants between the sites.

Nectarivorous birds preferentially visited plants with a greater number of available inflorescences than C. nanus. This suggests that these pollinators are attracted to plants by different cues or plant traits. For nectarivorous birds, using sight to forage, inflorescence density and availability appear to be distinct attractants. The cues used by C. nanus, which forages at night, are less obvious (Carthew 1994). The odour of some banksia inflorescences is stronger at night (Carpenter 1978), thus it is likely that small marsupials are using odour as a cue when foraging. As a result, C. nanus may tend to visit any plant as long as there is at least one available inflorescence. Differences in the relative mobility of pollinators may also influence foraging decisions. Nectarivorous birds are relatively unrestricted in terms of foraging movements and may move freely between inflorescences and plants. Conversely, foraging movements of small marsupials are restricted in the sense that these animals are moving through an interlinked woodland, and thus are unable to move as freely or as quickly between inflorescences and between plants. However, C. nanus can perhaps access inflorescences towards the centre of the plant more easily than nectarivorous birds.

Although these pollinators were attracted to B. integrifolia by different cues, once within the canopy they foraged in a similar manner. Nectarivorous birds visited almost twice as many inflorescences per plant as C. nanus, but the proportion visited per plant was statistically indistinguishable from the proportion per plant visited by C. nanus. Therefore, differences in foraging behaviour between birds and C. nanus arise through the selection of trees or movements between trees, but not through behaviours once within the canopy.

It is likely, therefore, that both pollinator groups affect similar levels of geitonogamous pollination (self-pollination among inflorescences within a single plant) and pollen carry-over to other trees. However, there may be differences between nectarivorous bird species, for example lorikeets were observed to visit a larger number of inflorescences per plant than other species, and thus may affect a higher level of geitonogamous pollination. The carry-over of pollen, as pollinators move from inflorescence to inflorescence, is an important function of pollen dispersal (Harder and Barrett 1996). Although the amount of donor pollen rapidly declines after the first flower visit, some pollen continues to be deposited even after many visits (Morris et al. 1994). Although pollen carry-over was not measured in this study, it is likely to be considerable, since pollen loads carried by animals are generally high (up to several thousand pollen grains per head; Goldingay et al. 1991).

Exclusion experiments performed previously in this woodland by Cunningham (1991), indicate that both non-flying mammals and birds are important pollinators of B. integrifolia. Thus, although the two pollinator groups employ different foraging tactics, they are both effective pollinators of B. integrifolia at Wilson’s Promontory.

For future studies differences in foraging behaviour between nectarivorous birds should be investigated. In this study, sample sizes of each bird species were not large enough to allow more detailed analyses. In addition, genetic markers such as microsatellites should be used to provide a direct indication of pollen flow.

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