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Abstract: Nectar secretion was measured at 6-h intervals over a 24-h period in flowers of the Red Bloodwood, *Corymbia gummifera* (family Myrtaceae). Secretion varied among time periods and among trees. There was no clear diurnal or nocturnal pattern. Flowers produced 0.5–3 µl of dilute nectar (9% concentration) per hour throughout the diel cycle. Standing crops of nectar averaged 1–12.6 µl per flower and also varied temporally and spatially. Flowers were visited by a wide array of nectarivores: insects, birds, gliding possums and bats. Although it is likely that these visitors vary considerably in their effectiveness as pollinators, it would appear that *Corymbia gummifera* has a generalised pollination system.

Introduction

Despite the enormous ecological value of eucalypts (species of *Eucalyptus* and *Corymbia*), to Australian biodiversity, relatively few studies have been conducted to assess the interactions between eucalypts and their nectar-feeding visitors (see House 1997). Hopper and Moran (1981) concluded 24 years ago that the study of the pollinators of eucalypts was in its infancy. However, this situation has improved little in the intervening period.

Several studies have been completed that document the feeding behaviour of eucalypt nectarivores. Field studies on petaurid gliding possums have revealed that eucalypt nectar and pollen are common elements of their diet and are likely to feature in the diet wherever these species occur (Kavanagh 1987; Howard 1989; Goldingay 1990; Quin et al. 1996; Sharpe & Goldingay 1998; Jackson 2001; Dobson et al. 2004). Only Goldingay (1990) has considered the implications for pollination of regular flower visitation by these marsupials. There have been few advances in the last 10 years of documenting visitation by birds, bats and insects to eucalypts despite the dominance of these trees in the Australian landscape (see McGoldrick & MacNally 1998; Horskins & Turner 1999; Palmer & Woinarski 1999; Palmer et al. 2000; Hingston & McQuillan 2000). Some work was conducted on honeyeater birds and their food plants prior to this (e.g. Ford et al. 1979; Pyke 1985) and on foraging by flying-foxes (Eby 1991). Therefore, our understanding of the pollinators of eucalypts has progressed little and we are a long way from describing the relative contribution to pollination of different pollinators.

The notion that plants exhibit specific traits (referred to as syndromes) that have co-evolved with their primary pollinators has been around for some time (e.g. Baker 1961; Rourke & Wiens 1977; Faegri & van der Pijl 1979). Despite this, there have been few attempts to test this among Australian plants. Hingston and McQuillan (2000) documented a large set of plant visitor profiles, including 11 species of eucalypt, to test visitor predictions based on floral morphology. They concluded there was a lack of specialisation. Saffer (2004) categorised six plant species as predominately bird or mammal-pollinated and determined whether patterns of anthesis and nectar production were consistent with predictions for these pollinators. She concluded that the lack of concordance was suggestive of a generalised pollination system.

Describing patterns of anthesis and nectar production is basic to understanding the ecology of different plant species. It is not only important in providing insights into whether plants are predominantly visited by diurnal or nocturnal pollinators, but will also provide insights into food resource availability and how this may influence foraging by specific floral visitors. Few studies have described patterns of nectar production in eucalypts but this is needed to properly understand interactions between these dominant trees in Australia and their visitors. The aim of this study was to describe the pattern of nectar production in the Red Bloodwood, *Corymbia gummifera* (formerly *Eucalyptus gummifera*), a dominant tree species in coastal New South Wales that is commonly visited by many species of vertebrate.

Methods

Study area

This study was conducted in Murramarang National Park (35° 35′ S, 150 ° 19′ E), approximately 20 km north-west of Batemans Bay on the New South Wales south coast. The study area was dominated by *Corymbia maculata*, *Corymbia gummifera* and *Eucalyptus pilularis*, but also contained *Eucalyptus scias* and *Eucalyptus piperita*. Tree canopies ranged from 20 to 45 m above the ground. At this site, *Corymbia gummifera* typically flowers between February and May but not every year (Goldingay 1990).

Nectar sampling

Sampling of nectar from eucalypt flowers at the site was difficult because tree canopies were at least 10 m above the ground. In the first year of sampling (5–6/4/1987), only a single tree was sampled. A caving ladder was attached to a branch at about 10 m above the ground to gain access to flowers. In the second year of sampling (19–21/4/1988), a mini-cherrypicker was used which enabled access to four trees. These trees were located along 200 m of an unsealed forest road and were selected based on ease of access with the cherrypicker, which had to be repositioned to sample each tree.

On each of the five trees, 6–10 flowers on a single branch were initially emptied of nectar between 1300–1700 h. All flowers were in a middle development stage where they had some upright stamens while others were reflexed (see Bond & Brown 1979; Horskins & Turner 1999). This was assumed to be the time of highest secretion in *Corymbia gummifera* as it was for *Eucalyptus costata*. Once emptied of nectar, flowers were covered with a fibreglass mesh bag to prevent access by nectar-feeding animals. In year 2, each tree was sampled one after the other. The amount of nectar secreted by each flower was measured using a microcapillary tube at approximately 6-h intervals beginning at 1800 h. The exact times of sampling were recorded so the secretion rates
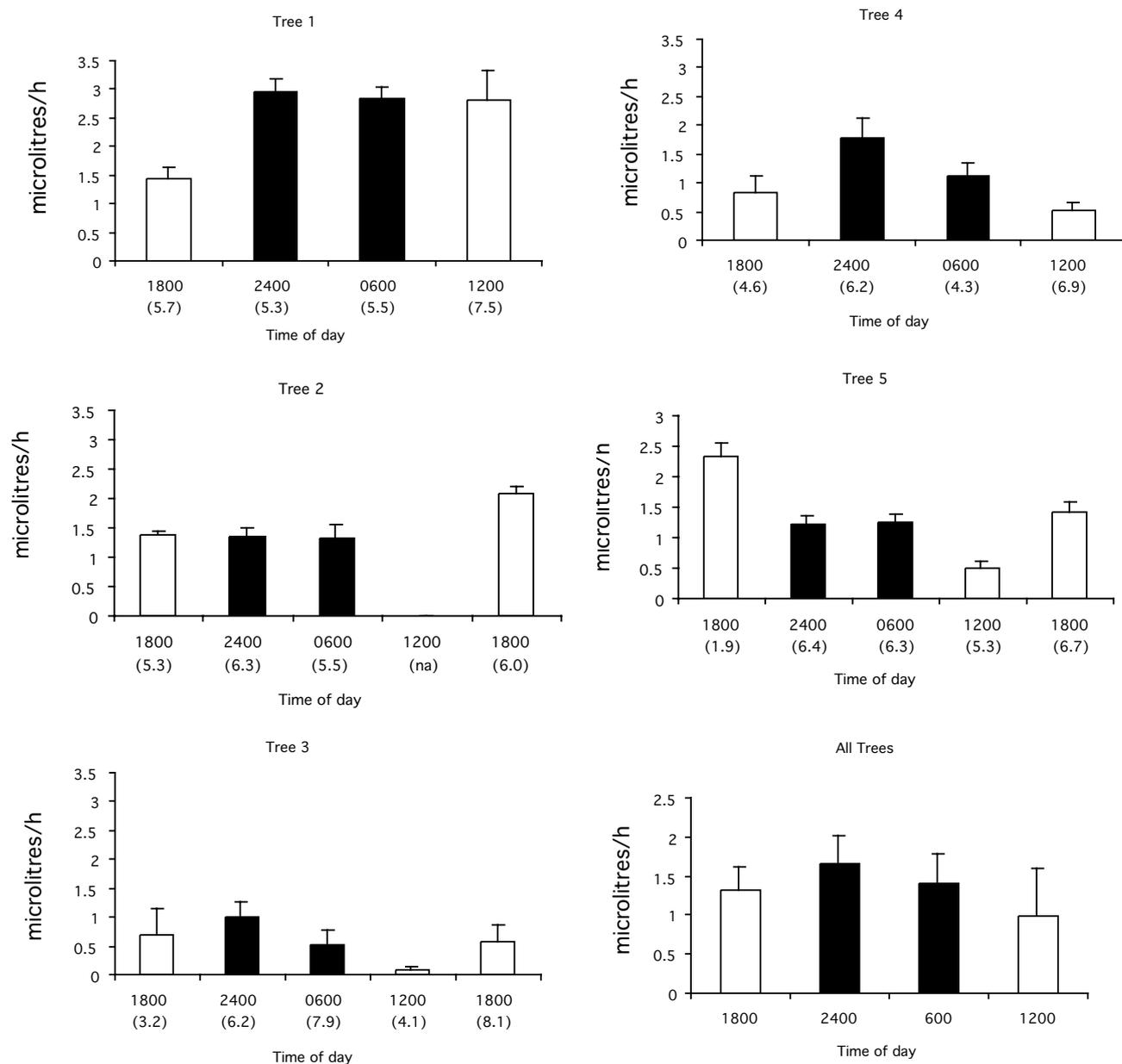

Fig. 1. Nectar secretion per flower (mean ± se; n = 6–10 per tree) at 6-h intervals in five *Corymbia gummifera* trees. Black bars are nocturnal periods, white bars are diurnal periods. The actual time (h) intervals between samples are shown is brackets below times of day. na = data not available.

could be expressed as the volume of nectar produced in the intervening interval. This assumes that rates of secretion are consistent within an interval and that if intervals are unequal it has not biased the comparison. Data were not available for Tree 2 at 1200 h because the exclusion bag had become dislodged. These flowers were emptied at this time and re-sampled at 1800 h. The flowers of Trees 3 and 5 were also resampled in this interval to allow a basic comparison of the two 1800 h intervals.

The sugar concentration of the nectar was determined from the above samples using a Brix temperature-compensated hand refractometer. The range in temperature during sampling in the second year was 14–22°C. Standing crop of nectar was also measured in the four trees sampled in the second year. This occurred at various times including after when the nectar secretion measurements were taken. A random sample of 10 flowers was removed from the tree to facilitate the measurement. Flowers were removed from branches away from those containing the bagged flowers. The constraints of positioning the cherrypicker precluded being able to disperse these flowers more broadly through a tree's canopy.

Results

Nectar secretion

Nectar secretion was highly variable among the five trees, ranging from 0.1 μl/h in Tree 3, to 3.0 μl/h in Tree 1. There was no consistent pattern among trees with regard to higher secretion in day or night samples (Fig. 1). Repeated measures analysis of variance of the diel cycle from 1800 h to 1200 h revealed that there were significant differences among the sample periods for three of the five trees (Tree 1: $F_{3,24}$=6.27, P=0.003; Tree 4: $F_{3,27}$=7.13, P=0.001; Tree 5: $F_{3,27}$=25.8, P=0.001). However, only Tree 4 showed a pattern of higher secretion in both nocturnal samples compared to diurnal samples. Each of the four other trees had a single diurnal period with equivalent or higher nectar secretion to those in the nocturnal period. For three of the trees, measurements were also recorded in a second 1800 h interval. This confirmed the variation in the rates of secretion.

The individual tree secretion data were averaged across all 5 trees to provide insight into any consistent pattern across the five trees (Fig. 1). This suggests that there is a trend for lower secretion in the 6-h period to 1200 h.

Nectar sugar concentration varied among trees and sample periods. Values were arcsine-square root transformed for analysis. For Tree 1, there was a significant difference (P=0.001) in concentration among the time periods. At 1800 h, it averaged 21.1% while it ranged from 11.4% to 15.3% for the other three time periods. For Tree 2, there was a significant difference (P=0.001) in concentration among the time periods, but the range in mean values was quite low (7.1–9.9%). For Tree 3, concentrations varied from 8–13%
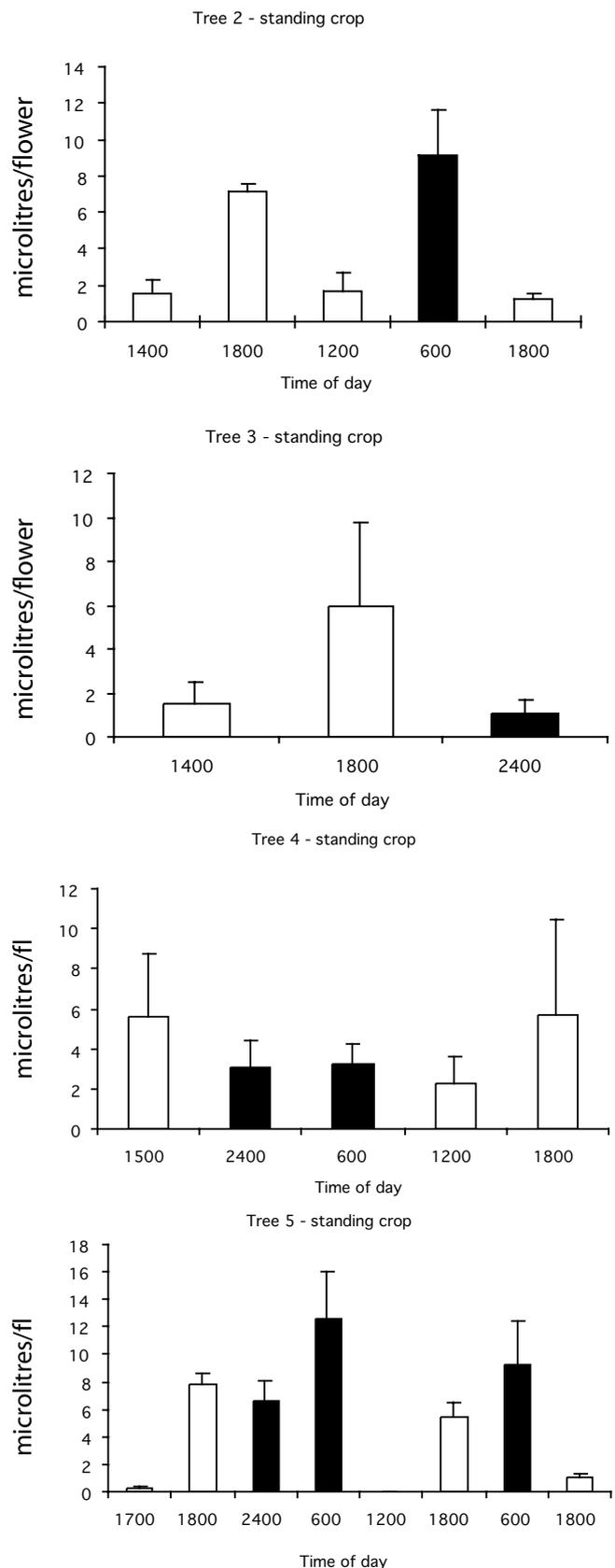

Fig. 2. Standing crop of nectar (mean ± se) measured in four *Corymbia gummifera* at different times. Different flowers (n=10) were measured in each time period. Black bars are nocturnal periods, white bars are diurnal period.

but the low volumes of nectar in many samples precluded determining the concentration and therefore analysis could not be conducted. There was no significant difference among sample periods for Tree 4 (7.5–17.5%) or Tree 5 (6–10%). Nectar concentration averaged 9.3 % overall for Trees 2–5 that were measured in the second year. There appeared to be little relationship between nectar volume and sugar concentration.

Nectar standing crop

Nectar standing crops varied greatly among the trees (Fig. 2). Standing crops varied from about 1 µl in Tree 3 to 12.6 µl in Tree 5. High standing crops of about 5 µl or higher were observed during the day in all trees while crops of that size were observed at night in Trees 2 and 5.

Discussion

Although only a small number of trees was sampled in this study, the variability in nectar secretion was such that there appears to be little temporal pattern to it, though there may be a trend of slightly lower secretion in the period 0600–1200 h. Flowers produced nectar at approximately 0.5–3 µl per hour throughout the diel cycle. Pyke (1985) described daily nectar production of 12.9 ± 1.5 µl per flower in *Corymbia gummifera* near Sydney. This value actually represents the dawn standing crop (assuming there were no nocturnal nectarivores). This is within the range of measurements in this study for a 12-h night. Standing crops at different times of the day or night were variable but often > 6 µl per flower.

Few studies have measured nectar secretion in eucalypts. Horskins and Turner (1999) found that 90% of the daily production of nectar by *Eucalyptus costata* occurred overnight. They reported secretion of about 0.6 µl per hour overnight compared to about 0.02–0.17 µl per hour during the day. This was largely consistent with an earlier assessment of the same species (referred to as *E. incrassata*) by Bond and Brown (1979), though these authors reported an average of only 0.11 µl of nectar per hour overnight. McCoy (1990) has also documented greater levels of nectar production at night in *Eucalyptus porrecta* and *Eucalyptus confertiflora* in northern Australia. These findings contrast with the present study that showed reasonably consistent secretion during the day and night.

The complete array of floral visitors to *Corymbia gummifera* was not documented in this study. However, detailed nocturnal research at the site revealed that three species of gliding possums (*Petaurus australis, Petaurus breviceps, Acrobates pygmaeus*) were abundant and regularly visited blossoms of *Corymbia gummifera* and other eucalypts. Indeed, eucalypt-nectar feeding accounted for 70% of feeding observations on *Petaurus australis* (Goldingay 1990). Nocturnal insects also

visited flowering *Corymbia gummifera* though they were not quantified, while grey-headed flying foxes (*Pteropus poliocephalus*) were abundant and fed in flowering *Corymbia gummifera* when flowering trees were abundant (Goldingay 1990). Diurnal insects, honeyeaters and lorikeets were present in large numbers and fed in the blossoms of *Corymbia gummifera* during the day. The relative contribution of these different floral visitors to pollination in *Corymbia gummifera* is unknown but the abundance of such an array of visitors is suggestive of a generalised pollination system. This is likely to prove a rich area of research in future years because the advent of new genetic techniques may allow resolution of contributions to gene flow from different pollinator groups, possibly simply by sampling pollen that they carry. However, the fitness consequences of pollen transferred over different spatial scales would remain unknown.

It is very common among plant species to be visited and pollinated by more than a single species of animal. Indeed, plant species are commonly visited by diverse types of pollinators (e.g. bats & hummingbirds, Sahley 1996; lizards, flies & wasps, Travest & Sáez 1997; moths & bees, Groman & Pellmyr 1999; bees & flies, Kephart et al. 1999; bats, birds & non-flying mammals, Tschapka & von Helversen 1999; moths and bats, Arizaga et al. 2000). Most studies are unable to identify whether all floral visitors pollinate equally or whether some may be more effective than others, though some attempt is usually made by authors to highlight the species they considered most important, based on visitor observation. Relatively few studies have assessed the contribution to seed production made by different pollinators for plants with mixed pollinator guilds (e.g. Goldingay et al. 1991; Groman & Pellmyr 1999; Hingston et al. 2004).

There has been some speculation that flying-foxes and birds may be more significant pollinators of eucalypts than other floral visitors because they have the potential to carry pollen over long distances (see McCoy 1990; Eby 1991; House 1997; Palmer & Woinarski 1999). Although eucalypts show higher seed set from cross compared to self pollination (Potts & Wiltshire 1997), it is yet to be established that highly mobile floral visitors transfer high loads of interpopulation pollen or that this is beneficial to the plants. It is worth noting that wider-ranging flying pollinators may deliver pollen that leads to out-breeding depression, due either to a disruption of local adaptation or to genetic incompatibilities (e.g. Waser & Price 1994). Moreover, flying pollinators may be more likely to carry mixed pollen loads from different species that reduce pollination success. This is clearly an area where many hypotheses can be generated regarding the effectiveness of various pollinator groups. Such research is needed if we desire to adequately manage and conserve our eucalypt-dominated ecosystems that continue to be fragmented and in which significant pollinators may be declining in abundance.

Acknowledgements

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