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Diel activity of arboreal arthropods associated with a rainforest tree

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The diel activity of arboreal arthropods associated with the Australian rainforest tree *Argyrodendron actinophyllum* was investigated with interception traps during a week in the summer season. When all arthropods were considered, there were no significant differences in flight activity, expressed as either numbers of individuals, numbers of species or biomass, between day-time and night-time. Flights of fungal-feeding species were not restricted to night-time, presumably because scents may also spread well during day-time with the high humidity of the rainforest. However, arthropod activity was high during night-time in comparison with temperate woodlands, and herbivores were generally more active during night-time than during day-time, whereas this was the reverse for predators and parasitoids. These limited data tend to support the hypothesis that some herbivores may feed during night-time in rainforests in order to escape predators and parasitoids.

KEYWORDS: Diel activity, arboreal arthropods, rainforest, *Argyrodendron*, fungal-feeders, herbivores, predators, parasitoids.

Introduction

Usually insects fly during only part of the 24-h daily cycle, since their time of flight is determined by physiological responses to cyclic factors in the environment (Lewis and Taylor, 1964). Usually, light intensity is the major factor that affects the time of flight, whereas temperature influences its amplitude (Lewis and Taylor, 1964). Species sharing similar requirements may live collaterally in the same environment, with separation of periods of diel activity, thus reducing direct competition (Szujecki, 1987). While arthropod diel activity has been the subject of several studies within temperate environments (for reviews, see Lewis and Taylor, 1964; Couturier, 1973; Costa and Crossley, 1991), that of rainforest species, and particularly that of arboreal species, has received little attention. The study of the arboreal arthropod fauna associated with an Australian rainforest tree, *Argyrodendron actinophyllum* (Basset, 1991a, b; Basset and Arthington, 1992), provided the opportunity to investigate arthropod diel activity during a week in summer. Elucidation of general patterns was of greater interest to us than specific interactions. In particular, we tested the null hypothesis that arthropod activity does not differ between day-time and night-time, and does not differ among

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arthropod families and guilds. Thus, daily flight activity was analysed with reference to selected arthropod groups which represented the most abundant arthropod families and arboreal guilds associated with *A. actinophyllum* (for guild definition and assignment see Basset and Arthington, 1992).

Material and methods

The study was performed in a complex notophyll vine forest (warm subtropical rainforest) near Mount Glorious (27°19′20″S, 152°44′55″E, altitude 700 m), some 30 km northwest of Brisbane, Queensland, Australia. *Argyrodendron actinophyllum* (Bailey) Edlin (Sterculiaceae) is a tall tree, reaching up to 50 m. Detailed accounts of the phenology of this rainforest species are reported in Basset (1991c). Arthropods were sampled by five composite interception traps, each consisting of a window trap and a Malaise trap sub-units (Basset, 1988), set up at 25 m within the mid-crowns of five *A. actinophyllum*. Arthropods were collected continuously and removed weekly from February 1986 to February 1988 (weeks 1 to 104).

Arthropod diel activity was investigated in summer, during week 95 (10–17 December 1987). The traps were surveyed, manually, three times a day: at 5 a.m., 12 noon and 6 p.m. Support trees were climbed with the single rope technique and collecting jars of both sub-units were replaced. The five trees were always visited in the same order and each survey lasted no longer than 1·5 h. This procedure allowed segregation of the specimens collected during the day (period one: 5 a.m.–12 noon; period two: 12 noon–6 p.m.) and during the night (period three: 6 p.m.–5 a.m.). Crepuscular insects (i.e. those flying at dusk) were considered in this last category of catches (cf. Lewis and Taylor, 1964). Sampling was performed by the senior author.

During week 95 the sunrise occurred at 4.45 a.m. and sunset at 6.45 p.m. This week was unexceptional in the size of catches recorded (786 specimens collected; mean averaging 700 specimens per week during summer months), as were the climatic conditions (39 mm of rainfall during the week; two rainy days; maximum air temperature during the week 35°C; minimum air temperature 15°C; no prolonged windy periods). On average the study trees displayed more than 10% of young leaves during week 95.

Results

Table 1 details the differences observed in arthropod flight-activity during day-time and night-time. When data from both sub-units of interception traps were pooled and all arthropods considered, arthropod activity was higher during day-time than during night-time, but not significantly so. Thus, we did not reject our first null hypothesis. Window-trap sub-units intercepted significantly more arthropods during day-time than during night-time, because of their high effectiveness in catching day-flying beetles. The proportions of day and night catches were similar in Malaise-trap sub-units. Although a general trend towards high activity was noted during the second day-time period for most groups, no significant difference existed between the flight activity of the first day-time period (mean individuals collected $\pm$SE, all arthropods: $5{\cdot}34 \pm 0{\cdot}69$) and that of the second day-time period ($7{\cdot}40 \pm 0{\cdot}93$; Kruskal–Wallis test, $W = 3{\cdot}21$, n.s.). More species were collected during day-time, and more biomass during night-time, but these differences were not statistically significant (Table 1).

Most of the taxa examined did not show distinct differences between their day-time and night-time activity (Table 1), presumably due to a high occurrence of crepuscular flights. Nevertheless the following groups, as individual entities, could be considered as

Table 1. Differences in flight activity (mean (SE) number of individuals collected daily per trap) during day-time and night-time for selected taxa and guilds. All figures refer to number of individuals collected in both trap sub-units, except otherwise stated.

Taxa/guild	Day-time Σ1	Mean 2		Night-time Σ1	Mean 2		Non-parametric ANOVA Kruskal–Wallis test
All arthropods—IT3	446	12·74	(1·43)	340	9·71	(0·98)	2·91 n.s.
All arthropods—WT3	239	6·83	(0·66)	150	4·29	(0·54)	8·68**
All arthropods—MT3	207	5·91	(1·03)	190	5·43	(0·80)	0·04 n.s.
All species 4	339	9·69	(0·80)	273	7·80	(0·68)	2·51 n.s.
All biomass 5	772	22·06	(3·52)	1349	38·55	(18·90)	0·01 n.s.
Araneae	11	0·31	(0·09)	11	0·31	(0·10)	0·34 n.s.
Blattodea	3	0·09	(0·06)	7	0·20	(0·08)	2·09 n.s.
Brachycera	38	1·09	(0·29)	31	0·88	(0·26)	1·03 n.s.
Chloropidae	1	0·03	(0·03)	9	0·26	(0·08)	7·36**
Dolichopodidae	5	0·14	(0·06)	9	0·26	(0·12)	0·02 n.s.
Empididae	7	0·20	(0·11)	3	0·08	(0·05)	0·21 n.s.
Phoridae	9	0·26	(0·10)	3	0·09	(0·05)	1·99 n.s.
Coleoptera	145	4·14	(0·52)	93	2·66	(0·36)	4·67*
Biphyllidae	23	0·66	(0·22)	8	0·23	(0·09)	2·10 n.s.
Chrysomelidae	19	0·54	(0·15)	28	0·80	(0·16)	1·90 n.s.
Corylophidae	21	0·60	(0·18)	5	0·14	(0·07)	6·29*
Curculionidae	11	0·31	(0·09)	2	0·06	(0·04)	6·41*
Lathridiidae	4	0·11	(0·05)	1	0·03	(0·03)	1·91 n.s.
Phalacridae	6	0·17	(0·07)	8	0·22	(0·10)	0·02 n.s.
Scarabaeidae	0	0		8	0·23	(0·08)	7·65**
Scolytidae	18	0·51	(0·15)	9	0·26	(0·09)	1·44 n.s.
Staphylinidae	6	0·17	(0·08)	1	0·03	(0·03)	2·91 n.s
Homoptera	47	1·34	(0·22)	31	0·89	(0·15)	1·82 n.s.
Achilidae	2	0·06	(0·04)	6	0·17	(0·07)	2·22 n.s.
Cicadellidae	20	0·57	(0·13)	15	0·43	(0·10)	0·33 n.s.
Cicadellidae—juveniles	12	0·34	(0·11)	0	0		10·13**
Fulgoroidea—juveniles	14	0·40	(0·10)	3	0·08	(0·05)	6·99**
Psylloidea	3	0·08	(0·05)	5	0·14	(0·06)	0·55 n.s.
Hymenoptera	80	2·28	(0·36)	25	0·71	(0·13)	17·33***
Bethylidae	8	0·22	(0·07)	0	0		8·90**
Formicidae	18	0·51	(0·15)	5	0·14	(0·07)	5·25*
Pteromalidae	29	0·82	(0·19)	13	0·37	(0·11)	3·17 n.s.
Lepidoptera	15	0·43	(0·13)	55	1·57	(0·37)	5·21*
Nematocera	100	2·86	(0·58)	75	2·14	(0·29)	0·07 n.s.
Cecidomyiidae	17	0·49	(0·15)	25	0·71	(0·15)	2·04 n.s.
Chironomidae	10	0·29	(0·09)	22	0·63	(0·16)	2·68 n.s.
Sciaridae	42	1·20	(0·31)	6	0·17	(0·07)	9·89**
Chewers	19	0·54	(0·15)	36	1·03	(0·17)	5·87*
Phloem-feeders	42	1·20	(0·21)	29	0·83	(0·14)	1·35 n.s.
Mesophyll-feeders	5	0·15	(0·06)	3	0·09	(0·05)	0·56 n.s.
Predators	60	1·71	(0·25)	37	1·06	(0·22)	4·38*
Parasitoids	57	1·63	(0·32)	23	0·66	(0·16)	8·13**
Fungal-feeders	63	1·80	(0·40)	23	0·66	(0·17)	5·17*
Wood-feeders	38	1·09	(0·20)	21	0·60	(0·12)	3·49 n.s.
Scavengers	6	0·17	(0·08)	13	0·37	(0·11)	2·18 n.s.
'Tourists'	143	4·08	(0·74)	148	4·23	(0·58)	0·31 n.s.
Uncertains	9	0·26	(0·09)	5	0·14	(0·06)	0·92 n.s.

* = $P < 0·05$; ** = $P < 0·01$; *** = $P < 0·001$.

1. Sum of individuals collected.
2. Mean number of individuals collected daily per trap ($n = 7 \times 5 = 35$).
3. IT = interception traps; WT = window trap sub-units; MT = Malaise trap sub-units.
4. Number of species collected.
5. Biomass collected in mg DW.

being predominantly active during day-time in the tree crown: Coleoptera, Hymenoptera, Corylophidae, Curculionidae, Formicidae, Bethylidae, juvenile Cicadellidae, juvenile Fulgoroidea, Sciaridae, predators, parasitoids and fungal-feeders. However, Lepidoptera, Chloropidae, Scarabaeidae (Melolonthinae only) and chewers were active predominantly during the night. The following groups appeared to be equally active during both day- and night-time: Araneae, Nematocera, Chrysomelidae, Phalacridae, Cicadellidae and the 'tourist' guild. Therefore, we rejected our second null hypothesis.

Discussion

Interception traps, whether surveyed manually or automatically, do not represent the best sampling method to assess arthropod diel activity. Suction traps are certainly more suitable in this regard (Lewis and Taylor, 1964; Goodenough *et al.*, 1983). Our data are limited in their scope but remain interesting because, to the best of our knowledge, there is no published information about diel activity of rainforest arboreal arthropods. Our data are valid for a week only, but this week could be considered as average by several parameters for the summer period (see Material and methods). However, it is not known if the trends reported here would have been similar during an average week of the 'winter' period.

Pre-existing data on the diel activities of arthropod taxa are fragmentary and heavily selective toward the target group (e.g. Odonata: Inoue, 1988; Homoptera: Perfect and Cook, 1982; Diptera: Willmer, 1982). It was difficult to compare, in a sufficiently rigorous manner, other available data with our results since (a) the faunas were not comparable, in terms of corresponding taxa (e.g. Goodenough *et al.*, 1988); (b) previous studies on tropical faunas have not considered taxa at a higher resolution than arthropod orders (e.g. Janzen, 1973; Ricklefs, 1975; Lowman, 1982; Hammond, 1990) or (c) tropical data have been obtained from the field layer only.

The only data set that could be compared with ours remained that of Lewis and Taylor (1964) and, to a lesser extent, those of Couturier (1973) and Costa and Crossley (1991). Our findings about arthropod diel activity were not substantially different from these studies but some differences emerged. In Britain, more insects fly during day-time (e.g. 'leaf-feeding' species; Brachycera (i.e. Chloropidae, Dolichopodidae, Empididae); Chrysomelidae) than in the Mount Glorious rainforest. Furthermore, high numbers of 'scavengers' (including fungal-feeders, wood-feeders and scavengers *s. str.*) are active during night-time in Britain. Lewis and Taylor (1964) suggested that these species may rely more on scents to locate their food, and these may be spread further in moist air, at night. In the rainforest, where the relative humidity of the air is always quite high in the lower strata, night-flying does not appear to be an adaptive advantage for certain 'scavengers', such as fungal-feeders, the majority of which were collected during day-time at Mount Glorious.

However, the most striking difference was related to the overall ratio of arthropods active during night to those active during day, which was much higher than in temperate conditions (percentage of arthropods collected during night-time to day-time collections: 9·6%, Lewis and Taylor, 1964; this study: 76%). Several authors reported that arthropod activity is generally higher by night in rainforests than in temperate forests, since air temperatures are higher during night-time than in temperate woodlands (Janzen, 1973; Ricklefs, 1975; Lowman, 1982). For example, Janzen (1973), sweeping tropical foliage in the field layer, found that the percentage ratio of night to day catches amounted to 105% in his samples. Ricklefs (1975) reported

that the biomass of night samples collected with Malaise traps was higher than that of day samples, a situation also observed in the sweep samples of Janzen (1973). Our crown data follow a trend in increased biomass for night catches but this is not statistically significant, because of the high variance among night samples. Conversely, Hammond (1990) found that night catches represented only 20% (including crepuscular insects) of day catches in Malaise traps and flight-interception traps established within the field layer of a lowland rainforest in Sulawesi (Hammond, 1990: fig. 27). Comparison with our data suggests that during night-time arthropod activity may be lower within the field layer than within tree crowns, but further investigations are needed in order to verify this.

Since their potential prey species are active at different times, predators are more likely to partition resources by being active at different times of the day than other trophic groups (Schoener, 1974). In the crowns of *A. actinophyllum*, arthropod predators and parasitoids exhibited a marked tendency to be more active during day-time. Elton (1973) was the first author to suggest that most of herbivore damage in rainforests may occur by night. This hypothesis explained why so few chewing species are usually collected during day-time, whereas the apparent leaf damage in rainforests is not notably lower than in temperate forests (Elton, 1973). Janzen (1983) added that most of herbivory should occur between sunset and midnight, when the day's photosynthate of leaves is highest and has not yet been translocated or respired. Janzen (1983) also predicted that concentration of herbivory during night-time was an escape from day-active predators. Lowman (1982) stated that the proportion of phytophagous insects was higher in her night-samples, but her data and conclusions were highly speculative (Lowman used non-comparable methods to obtain day and night samples and assigned adult moths attracted by light-traps to the 'phytophagous' trophic group).

Although interception-trap data provide a measure of foraging activity, it seems reasonable to assume that this activity is correlated with feeding activity. Thus, the foraging and, presumably, feeding activity of chewers within the foliage of *A. actinophyllum*, which occurred mostly during night-time, may have resulted in part from an escape from day-active predators and parasitoids. Heinrich (1979), studying different caterpillar species in the United States of America, suggested that one of the strategies adopted by palatable caterpillars to escape visually oriented predators, was to restrict foraging to night-time. However, Heinrich (1979) stressed that this strategy was costly under temperate latitudes, both in terms of time and energy, since short and cool nights may retard food ingestion rate and growth. In tropical rainforests these restrictions are probably less limiting for caterpillars and for chewers in general. Hygrothermal stress may also be reduced by feeding at night, particularly if chewers concentrate their activity in the upper levels of the canopy (see Basset, 1992). Night-feeding in rainforests may confer a selective advantage to chewing species, but careful experimentation is required to verify this suggestion.

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