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Diel activity of arboreal arthropods associated with Papua New Guinean trees

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The diel activity of arboreal arthropods foraging within the crowns of nine species of trees native to submontane rain forests in Papua New Guinea was studied. Data were collected over a 30-day period, using modified flight-interception traps, which are described briefly. Sampling was designed to enable segregation of material into day- and night-catches. Arthropod activity (measured by the number of individuals collected) was correlated positively with minimum air temperature. As a probable consequence, overall arthropod activity was significantly higher during day-time than night-time and night catches represented 72% of day catches. Predators, parasitoids, wood-eaters, ant workers and entomophagous arthropods were significantly more active during day than night. Few arthropod groups showed an inverse behaviour. Regression slopes comparing entomophages versus herbivores during day- and night-time were not significantly different. The data do not support the hypothesis that herbivores are particularly active during night-time in rain forests in order to escape day-active predators. However, this hypothesis may apply in specific situations, which are reviewed briefly. Additional hypotheses explaining the relatively low densities of insect herbivores in tropical rain forests but a level of leaf damage comparable to that estimated for their counterparts in temperate forests are suggested.

KEYWORDS; Arboreal arthropods, diel activity, Papua New Guinea, prey–predator ratios, rain forests.

Introduction

Despite much scientific interest in arboreal arthropods associated with tropical rain forests, studies upon the composition and organization of their communities have been, with few exceptions, limited and sporadic. Both the autoecology and synecology of arboreal species (review of the latter in Basset, 1993) remain virtually unknown. An example of this is the relative paucity of data upon arthropod diel activity, both at ground level and within the crown and canopy layers (review in Basset and Springate, 1992). Several ecologists reported the relative rarity of insect herbivores on foliage during day-time in rain forests (e.g. Elton, 1973; Janzen, 1983). Since leaf damage in most rain forests is not much lower than in temperate forests (e.g. Lowman, 1985), this apparent paradox was resolved by the prediction that herbivore activity should be particularly high during night-time in rain forests (Elton, 1973). One of several reasons invoked to explain this possible shift in activity is escape from day-active predators (Janzen, 1983). However, to date, data sets to test this hypothesis are lacking.

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In an earlier work (Basset and Springate, 1992), it was shown that the activity of chewing insects associated with a rainforest tree in Australia was generally higher during night-time than during day-time, and that the activity of insect predators and parasitoids followed an inverse trend, thus lending support to Janzen's hypothesis. However, the limitations of the data were stressed, since they were restricted to one rain forest tree species and to one week of sampling. As a part of a larger study, which investigated the species richness and host specificity of chewing insects associated with ten tree species native to Papua New Guinea (PNG) (Y. Basset, unpubl. data), it has been possible to repeat the previous study for a greater number of tree species, during a one month sampling period. This larger data-set permitted a more detailed investigation of possible differences in diel activity of entomophagous arthropods and insect herbivores, and of possible differences in the ratio of these groups during day- and night-time.

Material and methods

Study site

Sampling was performed within the grounds of the Wau Ecology Institute, Wau, PNG (7°24′S, 146°44′E, 1180 m). The Institute is located on the lower slopes of Mount Kaindi and encompasses a mosaic of vegetation, including remnant and replanted submontane forest and coffee plantations. The climate may be classified as 'humid to

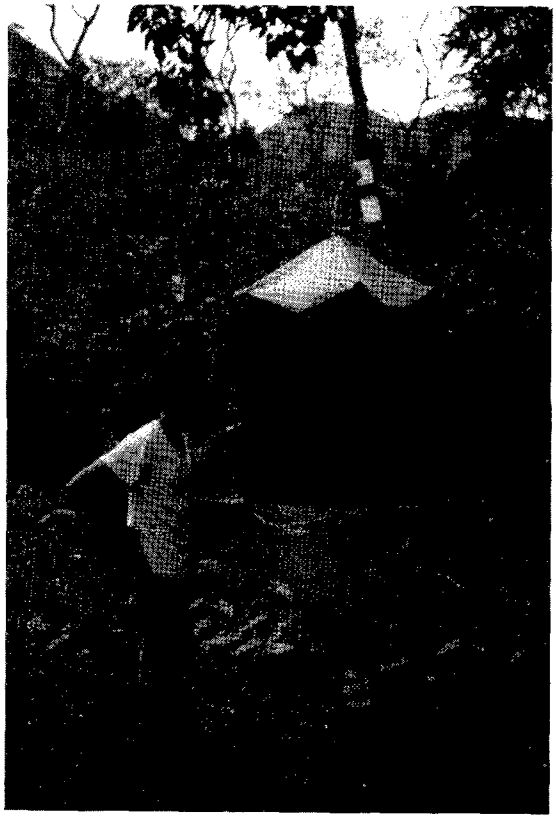

FIG. 1. General view of the intercept flight trap, at ground level.

perhumid mesothermal with little or no water deficit' (McAlpine *et al.*, 1983). Mean annual air temperature and rainfall are 21·1 °C and 1887 mm, respectively (Gressitt and Nadkarni, 1978).

Sampling of arthropods

Arthropod diel activity was measured by counting individuals collected during day- and night-time in flight-interception traps set up in tree crowns. These traps were developed specifically for sampling arboreal faunas and their design was derived from an earlier version (Basset, 1988). They are non-attractive and combine features of Malaise- and window-traps. The main body of the trap consists of a rectangular cross-panel of black netting (mesh width of 0·5 mm, collecting surface of 3·24 m^2) with a roof of white netting connected to a collecting jar via a clear plastic tube of 4 cm diameter. A clear plastic funnel is attached below the main body of the trap (upper and lower diameter of funnel of 83 cm and 11 cm, respectively) and connected to a large collecting jar (Figs 1, 2). The height of the trap, from the tip of the upper collector to the base of the lower jar, is 246 cm. An overflow grid in the middle of the lower jar allows overflow of water during heavy rainfall. During protracted periods of trapping, collecting fluids in the upper and lower jars respectively consisted of ethanol 70% and of water saturated with salt mixed with a few drops of detergent. However, due to the

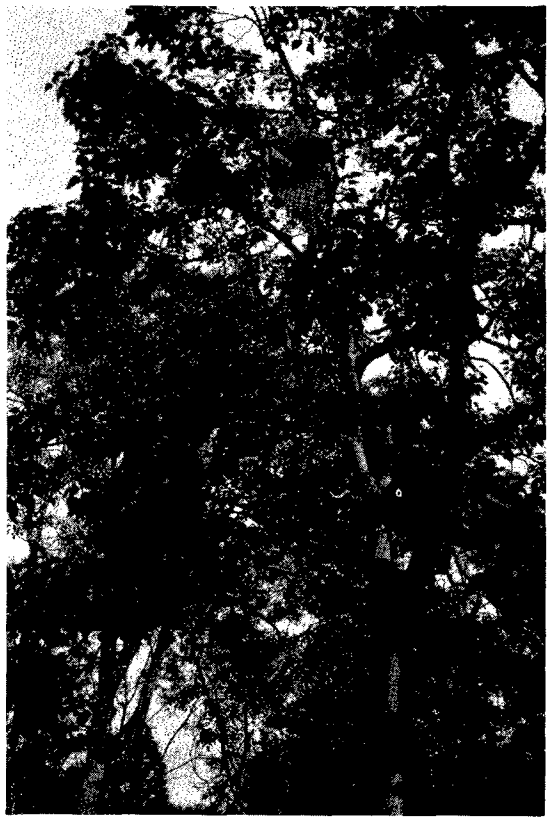

FIG. 2. Intercept flight trap established in the crown of *Ficus nodosa*.

Table 1. Identity of trees species in which the traps were established, distance from the ground to the top of trap when in position, phenology of trees and number of arthropods collected during the sampling period.

Species	Plant family	Height (m)	Phenology†	No. arthropods
1. *Elmerrillia tsiampacca* (L.) Dandy	Magnoliaceae	19·3	5%, fl.	671
2. *Cinnamomum culilaban* (L.) Presl.	Lauraceae	7·3	5%, fl.	2865
3. *Piper plagiophyllum* K. Sch. and Laut.	Piperaceae	4·0	5%, s.	1536
4. *Ficus nodosa* Teys. and Binn.	Moraceae	13·6	0%, s.	1909
5. *Pipturus argenteus* Wedd.	Urticaceae	5·0	5%, s.	937
6. *Castanopsis acuminatissima* A. DC.	Fagaceae	15·0	5%, s.	841
7. *Aleurites moluccana* Willd.	Euphorbiaceae	13·0	5%	1741
8. *Melicope denhamii* (Seem.) T. Hartley	Rutaceae	9·6	20%, fl.	1156
9. *Cordia dichotoma* Forst.	Boraginaceae	12·1	0%	824

† Maximum % of young leaves present; fl. = flowers; s. = seeds.

intended regularity of surveys during the diel activity study, both jars contained water and detergent solution only.

These traps were winched into the centre of the crowns of trees native to Papua New Guinea. Nine traps were established, one in each of nine different tree species. These included small and large trees, pioneer and persistent species and they all belonged to different plant families (Table 1). Traps were raised and lowered on lines passed over supporting branches. A thread line connecting the bottom of the trap with the ground allowed precise and convenient resetting of the trap after each survey.

Sampling was performed from 11 December 1992 to 9 January 1993 (30 sampling days). During this period, sunrise was at 05.45 h and sunset at 18.45 h. The traps were surveyed twice daily and always in the same order, with the surveys commencing at 06.00 h and at 17.30 h. Usually, the survey of all traps was completed in 55 min. Thus, the material was segregated into day catches (sampling period of 11 h 45 min) and night catches (sampling period of 12 h 15 min), the latter including most of the early morning and late afternoon crepuscular activity. At the end of each survey, maximum and minimum air temperatures, as well as rainfall, were recorded.

Sorting of arthropods

Arthropods were sorted to families and these were assigned to arboreal guilds following Basset (1991). For certain taxa (e.g. Curculionidae), species were assigned to the chewer guild based upon the results of feeding trials (Y. Basset, unpublished data). Where sorting to higher taxonomic level still produced a homogenous feeding category, this approach was employed in order to speed up the assessment of material collected (e.g. Araneae: all predators; Psocoptera: all epiphyte grazers; adult Microlepidoptera: all tourists). In the absence of information upon the biology of some taxa, these were assigned to the 'uncertain' category, the majority of these being larvae of Cecidomyiidae; Thysanoptera; juvenile Heteroptera not readily assignable to a family; and Miridae (mostly hemizoophages). For the purposes of performing regression analysis upon collated data (see below), three broad 'guilds' were defined: 'entomophages' (predators, including ants, and parasitoids), 'herbivores' (chewers and

sap suckers) and 'prey' (all individuals with the exceptions of predators, parasitoids, ants and 'uncertains').

Statistical analyses

Most of the arthropod material was collected in the lower collectors of the traps. For the sake of clarity, individuals collected in both upper and lower jars of the same trap were pooled for the analyses. Further, the totals of the nine traps, during either day or night periods, were combined to examine the general validity of the results. Data were log $(x + 1)$-transformed in order to satisfy the assumptions of normality (Kolmogornov-Smirnoff-Liliefors tests, $p > 0{\cdot}05$). Since the climatic data did not suggest that day and night sampling periods were related, they were considered as independent events. Therefore, statistical differences in arthropod activity between day- and night-time were tested using independent t-tests on transformed variables. However, untransformed means with their standard errors are presented throughout the text.

Predator–prey ratios were investigated using Bartlett's three-group regression method (Sokal and Rohlf, 1981). This regression is particularly suitable for determination of the relationship between two variables which are both subject to error (i.e. it does not assume that sampling results are unaffected by both prey and predator behaviours; see Lockwood *et al.*, 1990; Basset, 1992 for examples). In order to examine Janzen's hypothesis further, differences in the slope of regressions obtained during day- and night-time were tested for, using 'entomophages' as an independent variable and either 'prey' or 'herbivores' as dependent variables. An initial analysis was performed with the pooled totals from the nine traps. In order to identify, subsequently, whether the characteristics of the study trees could influence our regression analyses, we considered several groupings of variables and defined two states for each variable, usually low and high, as detailed in Table 2. The data was then combined according to each variable and state and regression analyses were performed for day and night separately. This procedure ensured enough replicates in each data set (usually, four or five traps) and, therefore, enough arthropod numbers for regression analyses. Regression analyses were also made when the data set was restricted to warm day or night periods (see Table 2). In these various subsets of data, regressions were tested with herbivores as the dependent variable. The rationale for selecting these data subsets is explained in the Discussion.

Results

Characteristics of the sampling period and material collected

A total of 12480 arthropods were collected by the nine traps during the one month sampling period. Sums of arthropods collected in each trap are detailed in Table 1. Table 3 presents the most common groups of arthropods collected, ordered by arboreal guilds. During the sampling period, minimum temperatures averaged $17{\cdot}7 \pm 0{\cdot}19$°C (mean ± s.e.), maximum temperatures $25{\cdot}7 \pm 0{\cdot}47$°C, and rainfall amounted to 135·7 mm. Overall, the occurrence of all arthropod groups in the nine traps during the 12 h sampling period was positively correlated with air temperatures recorded during these periods. In particular, overall arthropod activity was better correlated with minimal temperature ($r = 0{\cdot}392$, $p < 0{\cdot}01$) rather than with maximum temperature ($r = 0{\cdot}297$, $p < 0{\cdot}05$). However, during day-time, arthropod activity was better correlated with maximum temperature ($r = 0{\cdot}396$, $p < 0{\cdot}05$) whereas, during night-time, it was better correlated with rainfall ($r = 0{\cdot}463$, $p < 0{\cdot}05$).

Table 2. Grouping variables considered in regression analyses, the definition of their two states and the trap data included into these categories (numbers refer to species number in Table 1, see text for details).

Code of grouping variable and meaning		States	Traps no.
SUCCESS	successional status of the tree species	pioneer persistent	3, 4, 5, 9 1, 2, 6, 7, 8
HEIGHT	average height of the tree species when mature†	< 10 m > 20 m	2, 3, 5 1, 4, 6, 7, 8, 9
FLUSH	tree species presenting regular leaf flush events†	no yes	1, 3, 5, 7 2, 4, 6, 8, 9
AREA	average leaf area of leaves†	< 125 cm^2 > 125 cm^2	2, 5, 6, 9 1, 3, 4, 7, 8
N	foliar nitrogen (total)†	< 1·9% DW > 1·9% DW	1, 2, 4, 6 3, 5, 7, 8, 9
ALD	apparent leaf damage†	< 10% > 10%	1, 3, 4, 7, 8 2, 5, 6, 9
SPECIES	species richness of associated insect chewers†	< = 22 sp. > 22 sp.	1, 3, 7, 8 2, 4, 5, 6, 9
BIOMASS	average biomass of one associated chewing species†	< 5·0 mg DW > 5·0 mg DW	1, 6, 7, 9 2, 3, 4, 5, 8
HERBIV	percentage of herbivores collected per trap during the study	< 12% > 12%	2, 7, 8, 9 1, 3, 4, 5, 6
TMIN	sampling periods during which minimum air temperature was above the average recorded during the study (> = 18°C during day; > = 17°C during night, $n = 18$)	—	all pooled
TMAX	sampling periods during which minimum air temperature was above the average recorded during the study (> = 27°C during day; > = 23°C during night, $n = 18$)	—	all pooled

DW = dry weight; † Y. Basset, unpubl. data.

Diel activity of arthropods

When all arthropod groups were considered together, significantly more arthropods were active during day than during night (Table 3). Night catches represented 72% of day catches. In particular, larvae of Geometridae and of other Lepidoptera, juvenile Fulgoroidea, Staphylinidae, Encyrtidae, Scolytidae, Formicidae and adults of Cecidomyiidae were more active during day than during night. As a result, predators, parasitoids, wood-eaters, ants, all entomophages and all prey were more active during day than during night. Only two taxa were significantly more active during night than during day (Melolonthinae, Biphyllidae). There was a trend for chewers, epiphyte grazers, tourists and all herbivores to be more active during day than during night, but this was not statistically significant. The reverse, also non-significant, trend was noted for Cerambycidae, Tenebrionidae, Blattellidae, adult Microlepidoptera, Psychodidae and Miridae.

Table 3. Distributions of individuals collected in the nine traps within arboreal guilds and taxonomical groups and mean number of individuals collected with the nine traps during day- and night-time. Percentages refer to total of material collected in the case of guilds, and to total of material collected within the guild in the case of taxonomical categories. Significant t-tests denote significant differences between day and night.

Group/Taxa	Σ (%)	Mean day (s.e.)	Mean night (s.e.)	t-tests
All arthropods	12480 (100·0)	242·2 (12·74)	173·8 (10·32)	4·47***
Chewers	498 (4·0)	9·0 (0·66)	7·6 (0·66)	1·94 n.s.
Lepidoptera†	147 [29·5]	2·97 (0·36)	1·87 (0·37)	2·69**
Geometridae†	86 [17·3]	1·93 (0·40)	0·93 (0·31)	2·26*
Chrysomelidae	76 [15·3]	1·10 (0·21)	1·30 (0·20)	0·90 n.s.
Melolonthinae	75 [15·1]	0·50 (0·37)	2·00 (0·33)	4·74***
Sap suckers	1102 (8·8)	21·0 (3·65)	15·7 (2·53)	1·14 n.s.
Psylloidea	428 [38·8]	9·20 (3·20)	5·00 (2·19)	1·38 n.s.
Fulgoroidea†	192 [17·4]	3·67 (0·39)	2·70 (0·39)	2·03*
Cicadellidae	135 [12·2]	2·17 (0·32)	2·33 (0·33)	0·42 n.s.
Lygaeidae	54 [4·9]	0·90 (0·20)	0·90 (0·20)	0·05 n.s.
Predators	1021 (8·2)	24·2 (1·43)	9·8 (0·91)	8·23***
Staphylinidae	415 [40·6]	11·20 (1·42)	1·80 (0·67)	7·17***
Araneae	302 [29·6]	5·37 (0·41)	4·57 (0·48)	1·67 n.s.
Cantharidae	82 [8·0]	1·77 (0·31)	0·93 (0·20)	1·95 n.s.
Coccinellidae	47 [4·6]	1·07 (0·21)	0·63 (0·15)	1·46 n.s.
Parasitoids	337 (2·7)	6·9 (0·63)	4·4 (0·54)	2·88**
Encyrtidae	83 [24·6]	1·90 (0·34)	0·87 (0·20)	2·56*
Eulophidae	52 [15·4]	0·83 (0·18)	0·90 (0·18)	0·38 n.s.
Scelionidae	37 [11·0]	0·77 (0·17)	0·50 (0·14)	1·26 n.s.
Fungal-feeders	90 (0·7)	1·3 (0·28)	1·7 (0·30)	1·15 n.s.
Biphyllidae	28 [31·1]	0·30 (0·15)	0·63 (0·16)	2·03*
Wood-eaters	211 (1·7)	4·5 (0·51)	2·5 (0·39)	3·20**
Scolytidae	57 [27·0]	1·50 (0·25)	0·40 (0·12)	3·93***
Curculionidae	48 [22·7]	0·90 (0·18)	0·77 (0·19)	0·72 n.s.
Cerambycidae	36 [17·1]	0·47 (0·17)	0·73 (0·14)	1·73 n.s.
Epiphyte grazers‡	141 (1·1)	2·8 (0·38)	1·9 (0·26)	1·74 n.s.
Scavengers	1021 (8·2)	18·4 (1·87)	15·6 (1·70)	1·14 n.s.
Entomobryidae	745 [73·0]	13·90 (1·91)	10·87 (1·44)	1·03 n.s.
Tenebrionidae	83 [8·1]	1·10 (0·19)	1·60 (0·25)	1·52 n.s.
Blattellidae	48 [4·7]	0·60 (0·23)	1·00 (0·24)	1·68 n.s.
Ants§	1532 (12·3)	33·6 (5·00)	17·5 (3·00)	3·89***
Tourists	4283 (34·3)	76·2 (4·09)	66·6 (4·52)	1·82 n.s.
Microlepidoptera	1195 [27·9]	16·33 (2·54)	23·43 (3·28)	1·65 n.s.
Cecidomyiidae	901 [21·0]	18·23 (1·64)	11·10 (1·39)	3·52**
Psychodidae	653 [15·2]	9·27 (1·19)	12·33 (1·58)	1·79 n.s.
Chironomidae	351 [8·2]	5·53 (0·71)	6·07 (0·78)	0·29 n.s.
Uncertains	2244 (18·0)	44·3 (6·83)	30·5 (2·51)	1·32 n.s.
Cecidomyiidae†	1503 [67·0]	26·80 (6·01)	22·70 (3·58)	0·03 n.s.
Thysanoptera	180 [8·0]	4·83 (3·16)	1·17 (0·18)	1·65 n.s.
Heteroptera†	116 [5·2]	2·40 (0·34)	1·57 (0·36)	1·96 n.s.
Miridae	85 [3·8]	1·20 (0·25)	1·63 (0·27)	1·51 n.s.
Entomophages	2890 {23·2}	64·7 (5·22)	31·7 (3·61)	6·16***
Prey	7346 {58·9}	133·2 (7·22)	111·6 (7·64)	2·35*
Herbivores	1600 {12·8}	30·0 (3·46)	23·3 (2·50)	1·80 n.s.

† Juveniles, ‡ including all Psocoptera, § including workers but not alates; $*p < 0·05$; $**p < 0·01$; $***p < 0·001$.

Prey–predator regressions

Bartlett's regressions comparing entomophages and either prey or herbivores were significant both during day- and night-time (Fig. 3). However, their slopes were not significantly different from each other during these periods, apparently contradicting Janzen's hypothesis ($t = 0{\cdot}77$ and $t = 0{\cdot}06$, n.s., for regressions involving prey and herbivores respectively).

When subsets of data were considered, it became more difficult to fit regressions between entomophages and herbivores (Table 4). Regressions appeared to be more consistent during day than during night. For the following the regression slopes could be compared during day- and night-time: small trees, trees which did not present regular leaf flush events, trees supporting chewing insects of high average biomass, trees in which a high percentage of herbivores were collected and when the analysis was restricted to sampling periods with minimum and maximum temperatures above average. For all of these, the regression slopes were not significantly different between day and night. In fact, there was a trend for slopes to be higher during day than during night (i.e. for each individual herbivore there were more entomophages active during night-time than during day-time), although not when the data were restricted to small trees and to trees supporting chewers of high biomass. None of these results support Janzen's hypothesis.

Discussion

The data set of the present study is more comprehensive than the Australian data of Basset and Springate (1992), which used a similar methodology. The length of the sampling period in Wau was four times longer (one month instead of one week) and the amount of material 15 times greater (12480 individuals instead of 786). A single species of tree was investigated in Australia, *Argyrodendron actinophyllum* Edlin (Sterculiaceae), in comparison with nine in the present study (although no trap replicates were available for the latter and, therefore, it was not attempted to fit Bartlett's regressions to results obtained with particular traps). The amount of rainfall was comparable between the two studies (39 and 34 mm per week in Australia and PNG respectively), as was minimum air temperature (15 and 17°C respectively). However, maximum air temperature was higher in Australia than in PNG (35 and 25°C respectively) and, during study periods, the percentage of young leaves present in the crown of study trees was generally higher in Australia than in PNG (10 and 5% respectively). The latter may explain the lower proportion of herbivores collected in PNG than in Australia (12·8 and 17·0% respectively).

Despite these differences, general conclusions with regard to contrasts in arthropod activity during day- and night-time do not differ greatly between the two studies. However, in some cases the much smaller sample size from the Australian study may have precluded some comparisons achieving statistical significance. In particular, in both Australia and PNG arthropod activity was correlated with minimum air temperature. As a probable consequence, arthropods were generally more active during day-time and night catches represented only 70% of day catches. Also in both studies, predators, parasitoids, wood-eaters and ants were significantly more active during day than during night; sap-suckers less significantly. By contrast, in Australia fungal feeders were mostly active during day-time and, more notably, chewers during night-time, whereas these trends were reversed in PNG. Chewing insects in Australia included a high proportion of night-active Chrysomelidae, foraging and feeding within the crowns of *Argyrodendron actinophyllum.* This emphasizes that different insect species

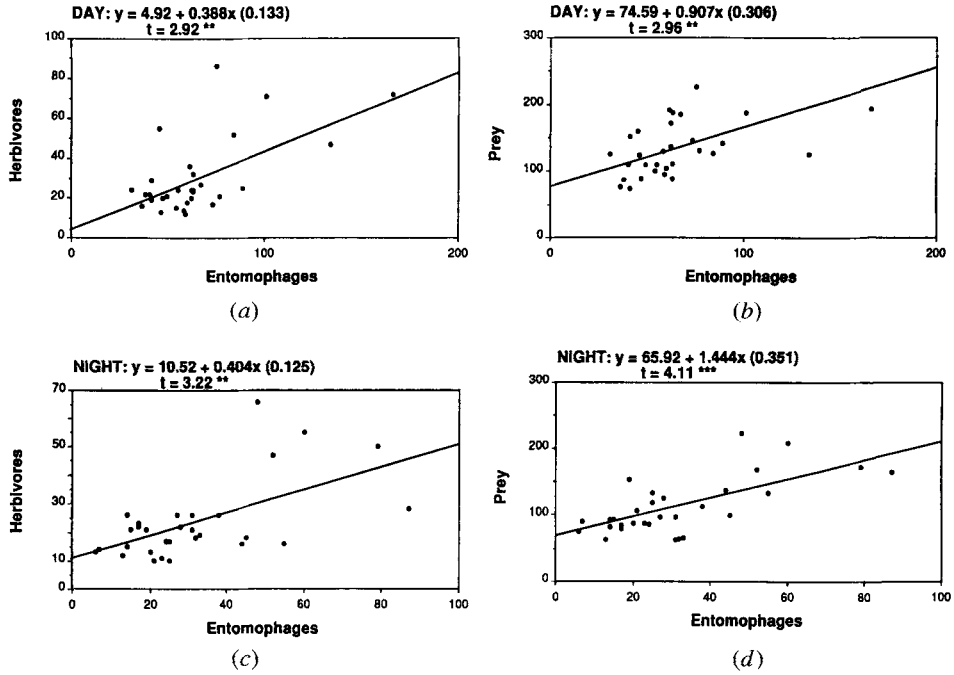

FIG. 3. Scatter plots and regressions fitted (Bartlett's three-group method) between entomophages and either herbivores or prey during day-time (*a*) and (*b*) and night-time (*c*) and (*d*). For each the full equation is indicated, including the standard error of the parameter estimate (in brackets) and *t*-values testing whether the slope is significantly different from zero.

Table 4. Slopes of regressions comparing entomophages versus herbivores obtained with Bartlett's method for subsets of data arranged by grouping variable and state (low and high, see Table 2). Significant *t*-tests denote significant differences in the slopes.

Grouping variable	Slope—day (s.e.)	Slope—night (s.e.)	*t*-tests
SUCCESS—pioneer	n.s.	1·348 (0·390)	—
SUCCESS—persistent	n.s.	n.s.	—
HEIGHT—small	0·425 (0·134)	0·615 (0·168)	0·70 n.s.
HEIGHT—tall	n.s.	n.s.	—
FLUSH—no	2·624 (0·641)	1·383 (0·606)	1·13 n.s.
FLUSH—yes	n.s.	n.s.	—
AREA—low	n.s.	0·152 (0·040)	—
AREA—high	n.s.	0·920 (0·408)	—
N—low	n.s.	n.s.	—
N—high	n.s.	1·273 (0·454)	—
ALD—low	n.s.	0·920 (0·408)	—
ALD—high	n.s.	0·152 (0·040)	—
SPECIES—low	2·260 (0·589)	n.s.	—
SPECIES—high	n.s.	0·103 (0·048)	—
BIOMASS—low	n.s.	n.s.	—
BIOMASS—high	0·415 (0·137)	0·519 (0·153)	0·36 n.s.
HERBIV—low	n.s.	0·143 (0·039)	—
HERBIV—high	1·215 (0·424)	0·803 (0·308)	0·40 n.s.
TMIN	0·498 (0·105)	0·284 (0·133)	0·91 n.s.
TMAX	0·442 (0·102)	0·297 (0·120)	0·67 n.s.

associated with different tree species may have different behaviours. It must be considered whether Janzen's hypothesis, which attempts to explain possible shifts of activity of insect herbivores as an escape from day-active predators, is robust enough to exclude these interspecific differences and to be validated generally.

The sampling scheme used in the present study has certain limitations that should be acknowledged before discussing this hypothesis in relation to the results obtained. Flight-interception traps do not represent the best sampling method to estimate arthropod activity (see discussion in Basset and Springate, 1992). In particular, they underestimate the activity of sedentary and flightless arthropods, many of which are herbivores. Arthropod activity and, more significantly, predation pressure were measured in terms of number of individuals collected, not in terms of either species richness or biomass collected. However, trends were identical for the number of individuals and species richness in our previous study (Basset and Springate, 1992). Our design did not address the importance of vertebrate predators (i.e. birds and bats). Activity of insect herbivores is assumed to be correlated with feeding activity but, depending on taxa, this may not be always true.

With these caveats in mind, it was shown that insect herbivores were not statistically more active during night-time than during day-time. Indeed, a general reverse trend was noted, albeit statistically non-significant, which was further confirmed statistically by the activity patterns of many larvae of Geometridae and of other Lepidoptera. This appears to be at variance with Janzen's prediction but it does not invalidate it necessarily, since predator–prey ratios may be different during day- and night-time and in a balance which is ecologically favourable to herbivores. Still, the data did not demonstrate, either when arthropod prey or insect herbivores were considered, that there were significantly less entomophages for each item of prey during night-time than during day-time. Therefore, it is concluded that the data do not support the hypothesis that insect herbivores are particularly active during night-time in order to escape day-active entomophagous arthropods.

However, since this hypothesis was apparently supported by the arthropod community associated with an Australian rain forest tree (Basset and Springate, 1992; with the reservations detailed in this paper), it is possible that it may also be valid for other situations. Using the data subsets detailed in Table 2, the regressions between entomophagous arthropods and insect herbivores, for which Janzen's hypothesis was originally formulated, provided exploratory tests of this. However, these tests were not sufficient: for example, the grouping of data according to apparent leaf damage and to leaf area had to be identical (Table 2). We considered several instances in which Janzen's hypothesis had a high probability of being substantiated. The situation in lowland rain forests, where conditions are warmer, may be different from that experienced in sub-montane rain forests. However, our analysis, restricted to warmer sampling periods, did not support the hypothesis. The hypothesis may be valid during specific periods of the year, such as during periods of intense leaf-flush and herbivore activity. Our sampling was performed during an active period of the year in this respect, but there is no doubt that there was a potential for the particular trees in which the traps were positioned to have exhibited a higher leaf turnover at other times of the year. When the data set was restricted to traps collecting above-average numbers of herbivores, the hypothesis was still not supported. The hypothesis may apply to arboreal communities associated with specific tree species only. One reason for this may be related to the influence of tree architecture and growth strategy on the searching behaviours of predators and parasitoids. Factors that are likely to be important in this regard may

include height of tree, leaf area and compactness of foliage, presence of leaf-flushing events, successional status of tree, etc. Another reason may be related to the attractiveness of particular tree species to day-foraging vertebrate predators, such as insectivorous birds. For example, Heinrich and Collin (1983) stressed that certain bird species in preference forage within heavily-damaged foliage. In Australia, birds forage in preference on eucalypt trees supporting a high biomass, species richness and numbers of invertebrates, and forage more often on trees with high foliage nutrient levels (Recher *et al.*, 1992). The various exploratory tests in this regard do not support Janzen's hypothesis. Finally, as the data for *Argyrodendron* suggest, Janzen's hypothesis may apply to particular interactions between herbivore, predator and parasitoid groups only and, particularly, those involving specialist species, since they are more likely to be active at different times of the day (Koskela, 1979). These different suggestions await further investigation.

Elton (1973) and others observed that herbivores in tropical rain forests were scarce, but noted a level of leaf damage comparable to that in temperate forests. Therefore, we envisage explanations, alternative to Janzen's hypothesis, which might explain this apparently paradoxical situation. These relate to the putative reasons for herbivore density being higher in the canopy of rain forests but the level of leaf damage being higher within the shrub layer (Basset *et al.*, 1992). In particular, grazing pressure may be higher in rain forests because young leaves are proportionately scarcer than in temperature deciduous forests. Alternatively, compensatory grazing rates may be common in rain forests in order to overcome the low nutritional value of foliage of evergreen trees (Mattson, 1980). Furthermore, the greater longevity of rain forest leaves, in comparison with that of temperate leaves, may result in high accumulated leaf damage. In addition, despite densities of insect herbivores being generally lower in tropical rain forests (Basset *et al.*, 1992), their biomass and, therefore, their feeding requirements may be higher than those of their temperate counterparts. Indeed, it has been theorized that tropical insect herbivores are larger than temperate insect herbivores (Lawton, 1991). Testing these different hypotheses will be challenging but may lead to a greater improvement of our understanding of ecosystem functioning in tropical, as well as temperate forests.

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