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Arthropod diel activity and stratification

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ABSTRACT

Many studies of canopy arthropods in rainforests rely on methods that do not permit comparison of day and night activities of the target fauna: accordingly, data on arthropod diel activity are scarce. Nevertheless, such information as is available suggests significant dissimilarities during the course of the day and a greater activity of insect herbivores during the day than at night. We studied faunal exchanges, particularly of insect herbivores, between day and night, and between the upper canopy and understorey of a lowland rainforest in Gabon. In total 14 161 arthropods were collected by beating, flight interception and sticky traps from six canopy sites during mid-January to mid-March 1999. Diel activity explained about 6–9% of the total variance in arthropod distribution, depending on the sampling method. In general, arthropod activity was higher during the day than at night. In particular, Thysanoptera, Psylloidea, Membracidae, Curculionidae, Scelionidae and Apidae were notably more active during the day in the upper canopy. Similarity values between day and night faunas from particular strata were often higher than between faunas of the understorey and the upper canopy at a particular time of day. This suggests that there are fairly distinct suites of herbivores foraging in the understorey and in the upper canopy. Faunal turnover between day and night was higher in the upper canopy than in the understorey, suggesting that changes in the microclimatic conditions between day and night in the upper canopy may be more severe than in the understorey, and that only a well-adapted fauna may be able to cope with these changes. In addition, certain groups, such as the Chrysomelidae, may migrate during the night from the understorey to the upper canopy, although there was no evidence of such mass insect movement overall. Our data suggest that insect herbivores of the upper canopy may be resident and well adapted to environmental conditions there.

INTRODUCTION

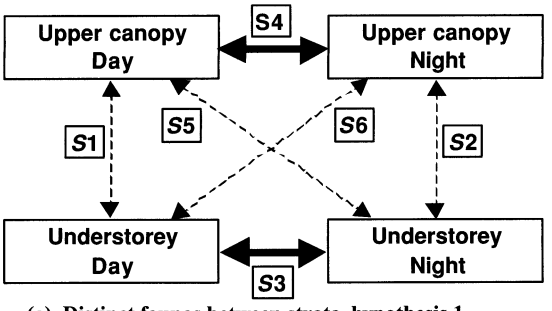
Although most entomologists would agree that different insect faunas can often be collected during the day or at night in the same location, there are surprisingly few data available on the diel activity of arthropods in tropical rainforests (other than biting flies), and, particularly, on that of canopy arthropods. Many entomological studies rely on methods such as pyrethrum knockdown and light traps, which are unsuitable for such day/night comparisons. Few protocols have been designed specifically to study the diel activity of canopy arthropods. Hammond (1990) used Malaise traps in Sulawesi and reported the extremely low levels of nocturnal flight activity in all major insect groups. Basset and Springate (1992) set up flight-interception traps within a species of canopy tree growing in a subtropical rainforest in Australia and showed that the activity of associated insect herbivores was significantly higher during the day than at night. Springate and Basset (1996) reached a parallel conclusion using similar traps operated in different tree species in Papua New Guinea. Davis *et al.* (1997) studied the activity of dung beetles in the canopy of a forest in Borneo using baited traps. They showed that most species were only active during the day, with clear differentiation in activity between two species groups, one peaking at dawn–dusk, the other at midday. Compton *et al.* (2000) used sticky traps in Borneo to show that the overall activity of Chalcidoidea was higher during the day than at night, in contrast with the Agaoninae, which preferred to fly over the canopy at night. Although arthropod activity often appears to be higher during the day than at night, the validity of this statement varies across particular insect species or guilds (e.g. Springate & Basset, 1996). Of particular interest, some species of insect herbivores concentrate their activity during the day, others at night (e.g. Johnson & Mueller, 1990; Duan *et al.*, 1996).

The distinct microclimates in the understorey and canopy of tropical forests (e.g. Blanc, 1990; Parker, 1995; Barker, 1996) may well influence the diel activity of arthropods in these strata. In particular, the volume immediately below the canopy surface, the upper canopy, experiences much larger fluctuations in air temperature, wind, relative humidity and water condensation than the understorey does (e.g. Blanc, 1990; Parker, 1995). However, these seemingly adverse conditions may be offset by the greater availability of foliage, flower and fruit resources for insect herbivores (e.g. Basset *et al.*, 1992; Basset, 2001a).

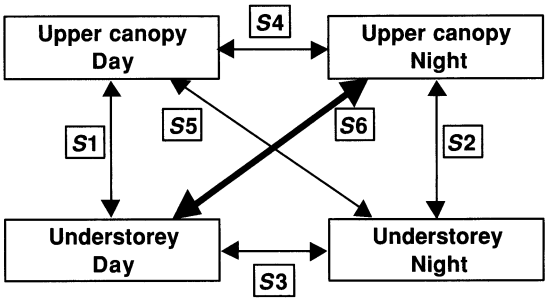
Insect herbivores foraging and feeding in the upper canopy of closed tropical forests may encounter serious hygrothermal stress during the day, and threatening water condensation at night. Three strategies may overcome these obstacles:

1. The development of a specialized, distinct fauna well adapted to the extreme microclimatic conditions of the upper canopy – this could include day-active herbivores resistant to desiccation or night-active herbivores untroubled by water condensation, or even a blending of several adaptations
2. Interchanges of fauna between the upper canopy and lower layers, for example, in which individuals resting in lower layers during the day may move to the upper canopy to feed at night, perhaps taking advantage of air movements (e.g. Haddow & Corbet, 1961a; Sutton, 1989; Compton *et al.*, 2000)
3. A combination of both strategies 1 and 2.

Hereafter, the first two hypotheses are designated by their respective numbers. If hypothesis 1 is correct, little overlap of herbivore faunas will be expected between the upper canopy and the understorey, both during the day and at night (Fig. 27.1a). In this case, the highest faunal similarities are likely to be between the day and night faunas of the upper canopy on the one hand, and the day and night faunas of the understorey on the other (Fig. 27.1a). If hypothesis 2 is correct, a high similarity (Fig. 27.1b) will be expected between the fauna in the understorey during the day and that in the upper canopy at night. Further, a relatively high herbivore turnover will be expected between day and night in the upper canopy (Fig. 27.1b). In addition, the abundance and activity of herbivores in the upper canopy at night will be similar to those in the upper canopy during the day. If hypothesis 3 is correct, the results will be intermediate and difficult to interpret.



(a) Distinct faunas between strata, hypothesis 1



(b) Interchanges between strata, hypothesis 2

Fig. 27.1. Hypothetical faunal relationships between the understorey and upper canopy during the day and at night within a closed tropical rainforest: (a) distinct faunas between strata, hypothesis 1; and (b) interchange between strata, hypothesis 2 (see Introduction). *S1* to *S6* refer to coefficients of similarity among the faunas of the four situations. A bold line denotes a particularly high similarity, a broken line a particularly low similarity.

In this contribution, we present data on the diel activity of arthropods in the understorey and upper canopy of a lowland rainforest in Gabon. In particular, we focus on the insect herbivores, estimate their turnover between strata and time of day, and discuss the results against hypotheses 1 and 2.

METHODS

Study sites and canopy access

Arthropod samples were obtained from a lowland tropical rainforest in the Forêt des Abeilles, near the station of La Makandé, Gabon (0° 40′ 39″ S, 11° 54′ 35″ E, 200–700 m above sea level). The height of the upper canopy varies between 35 and 45 m. The main features of the

forest are described in Doucet (1996), Fréty and Dewynter (1998) and Hallé (2000). The canopy was accessed from mid-January to mid-March 1999 using the canopy raft, the sledge and the treetop bubble (see Ch. 2). The canopy raft is a 580 m^2 hexagonal platform consisting of air-inflated beams from which is suspended a platform of Aramide™ (PVC) netting. An air-inflated dirigible raises the raft and sets it upon the canopy. The raft is positioned at specific sites upon the canopy and moved every fortnight by the dirigible. Access to the raft is provided by single-rope techniques (Ebersolt, 1990; Hallé & Blanc, 1990). The sledge is a triangular platform of about 16 m^2 that is suspended below the dirigible and which 'glides' over the canopy at low speed (Ebersolt, 1990; Lowman *et al.*, 1993a). The treetop bubble is a 180 m^3 helium balloon, 6 m in diameter, that runs along a fixed line set up in the upper canopy by the dirigible (Cleyet-Marrel, 2000).

Five sites (coded A to E), separated by at least 100 m and at most by 4 km, were sampled for arthropods. The sites occurred within similar forest types and at similar altitudes. For collection purposes, a site included the portion of foliage directly accessible in the upper canopy from either the raft (sites A, B and D) or the bubble (sites C and E), and the projected area of the raft or transect of the bubble (*c.* 100 m) in the understorey below. In addition, samples were obtained from the sledge at various locations in the upper canopy early in the morning and equivalent samples were obtained at various locations in the understorey for direct comparison (sixth 'site', coded L). Canopy cover was similar for all sites but differed in floristic composition. Their main characteristics and that of arthropod collections are detailed in Basset *et al.* (2001a).

Sampling methods

The sampling methods assessed the following at all sites: (i) the density of arthropods per unit area of foliage obtained by beating; (ii) the relative activity of arthropods along a transect of three flight-interception traps, situated at ground level, in the canopy and in the upper canopy; and (iii) the relative activity of arthropods collected with sticky traps. These methods are complementary and provide a better assessment of the overall arthropod fauna present than use of any single method (e.g. Basset *et al.*, 1997b). The sampling methods employed were intended to collect macroarthropods, particularly insect herbivores.

Arthropods were collected on square beating sheets 0.397 m^2 in area, conical in shape (with internal slopes of 45°), ending in a circular aperture (7 cm in diameter) that was fitted with a removable plastic bag. Sheets were inserted below the foliage so that the layer of leaves above occupied approximately the entire area of the sheet. Arthropods were dislodged from the foliage with three sharp strokes of the beating stick and gently brushed inside the plastic bag, which was then closed and replaced by a new one. At each site, 20 samples were obtained per stratum (upper canopy or understorey), either during the day (between 13:00 and 16:00) or the night (between 21:00 and 24:00). Upper canopy samples were taken from the periphery of the raft, or with the sledge. Understorey samples were collected at a height below 2 m and originated either from immediately below the projected area of the raft, or from sampling at random in the understorey for comparison with the samples obtained with the sledge ($n = 78$ samples). The size of the samples obtained by beating averaged 2492 ± 267 cm^2 of leaf area.

Nonattractive flight-interception traps, combining features of Malaise and window traps, were used at the raft and bubble sites. The main body of the trap consisted of two intersecting rectangular cross-panels of black netting (mesh width 0.5 mm, double-sided collecting surface of 1.2 m × 1.4 m × 4 = 6.7 m^2) with a roof of the same black netting, connected to a vertical duct and collecting jar. A clear plastic funnel was attached below the main body of the trap (upper diameter of 1.12 m) connected to a large collecting jar. A plastic grid with a 2 cm mesh covered the plastic funnel, preventing larger debris, but not arthropods, from falling into the suspended jar. Collecting fluids were 70% alcohol in the upper jar and water saturated with salt in the lower jar. A similar trap model is described elsewhere (Springate & Basset, 1996).

At each site, one vertical transect of three flight-interception traps was operated for at least 3 days. The traps were set on a rope, with a pulley system that allowed convenient surveying and resetting of the traps in the same position. On the transect, the third trap was set immediately below the canopy raft or within the upper canopy at bubble sites (upper canopy trap), the second one 6 m below (canopy trap) and the first at 2 m above ground (understorey trap). Day and night catches were segregated by surveying the three traps at sunset (18:00) and sunrise (06:00),

respectively. A sample represented the pooled catches of the upper and lower collecting jars of each trap for 12 hours.

At each site, 21 sticky traps (Temmen GmbH, Hattersheim, Germany) were established in the upper canopy and in the understorey. Each trap was yellow, with glue (Tanglefoot™) on both faces, each 29 × 12.5 cm in area (total collecting area per trap 725 cm^2). In the upper canopy, traps were set up in the foliage along the periphery of the canopy raft (maximum distance available 84 m) or along the transect of the bubble (*c.* 100 m). In the understorey, traps were set up along a transect line of 80 m situated below the raft or below the transect of the bubble, at a height of 1.5 m. At each raft site and for each stratum, traps were operated for 3 hours in the afternoon (13:00–16:00) then replaced by fresh and inactive traps (with their protection sheet in place) at the same location; these were later operated at night for 3 hours (21:00–24:00). A similar protocol was used at the bubble sites (C and E) but, for logistical reasons, traps had to be surveyed at 07:00 and 17:00, both in the understorey and upper canopy. As a result, traps at sites C and E ran for 10 hours during the day and for 14 hours at night. A sticky trap sample represented the catches of a trap standardized to catch for 3 hours (see below).

Processing of arthropod material and statistical methods

Arthropods were counted and sorted to family or higher taxonomic level. Adults of insect herbivores (*sensu lato*: leaf-chewing, sap-sucking and wood-eating insects) from beating and flight-interception trap samples were mounted and sorted to morphospecies (hereafter termed species). The poor quality of the material collected with sticky traps did not justify this approach and, in this case, specimens were only sorted to the level of the family. Scolytinae were considered as distinct from Curculionidae for the analyses. Collections of insect herbivores were deposited at the Laboratoire Entotrop (Faunistique-Taxonomie) of the Centre de Coopération Internationale en Recherche Agronomique pour le Dévelopment (CIRAD-Amis), Montpellier, France.

Four sample sets relevant to hypotheses 1 and 2 presented in the Introduction were considered: from the understorey during the day; the upper canopy during the day; the understorey at night; and the upper canopy at night. For each sampling method, data on the 10 most common higher arthropod taxa are presented. For beating and flight-interception trap data, measurements of faunal similarity for herbivores across each pair of sample sets (Fig. 27.1) were estimated using the Morisita–Horn index (Magurran, 1988) and the Shared Species Estimator, V (Chen *et al.*, 1995). In the latter, the estimator V augments the observed number of shared species by a correction term based on the relative abundance of shared, rare species (Colwell, 1997b). Further, the rarefied number of species present in a sample of n individuals was estimated with Coleman's curve (e.g. Colwell & Coddington, 1994). The Morisita–Horn index, Shared Species Estimator and Coleman statistics (based on 50 randomizations) were calculated using the program Estimates (Colwell, 1997b). The evenness of herbivore communities was estimated with the index E, proposed by Bulla (1994).

For all sampling methods, we tested differences in the abundance of the higher taxa in the upper canopy between day and night using Mann–Whitney tests (beating data) and Wilcoxon signed ranks tests (flight-interception and sticky trap data). Following Stewart-Oaten (1995), we judge Bonferroni's correction for multiple tests uninformative and do not use it. An additional index of 'abundance change', AC, was calculated in order to estimate the magnitude of change in taxa abundance in the upper canopy between day and night, as follows:

$$AC = (X_d - X_n)/(X_d + X_n) \qquad (27.1)$$

where X_d and X_n are the means of numbers of individuals collected per sample of a particular taxa with a particular method in the upper canopy during day and night, respectively. AC may vary from −1 to +1.

To account for the longer exposure of sticky traps at sites C and E, arthropod catches at these sites were corrected by a factor of 0.3 for day catches (10 × 0.3 = 3 hours) and a factor of 0.214 for night catches (14 × 0.214 = 3 hours). Analyses were performed using these corrected data. Unless otherwise stated, means are presented with the associated standard errors throughout the text. In the interests of clarity standard errors of means in the Figures are not indicated.

RESULTS

Overview

In total, 14 161 arthropods were collected across the three sampling methods (beating: 2469 individuals; flight-interception traps: 6450 individuals; sticky traps: 5242 individuals). The material collected in the upper canopy included 5148 individuals collected during the day, and 1724 individuals collected at night. Insect herbivores collected in the upper canopy included 1791 individuals representing 187 species. The variable 'time of day' explained 6 to 9% in the total variance in arthropod distribution, depending on the sampling method (strata effects: 40–70% of variance; site effects: 20–40% of variance; Basset *et al.*, 2001a). The salient features and limitations of the sampling programme at La Makandé are detailed and discussed elsewhere (Basset *et al.*, 2001a).

Beating samples

In total, 195 beating samples were obtained from the upper canopy, representing 48.6 m^2 of leaf area sampled. They included 145 and 50 samples obtained during day and night, respectively. Significantly more arthropods were collected per sample during the day than at night (mean per sample was 7.02 ± 0.590 and 2.94 ± 0.279 individuals, respectively; Mann–Whitney $U = 4957.0$, $p < 0.001$; see Fig. 27.2 for the most common taxa). In particular, Formicidae and Apidae were more abundant during the day than at night (Mann–Whitney tests, both with $p < 0.001$; Fig. 27.2; Formicidae not displayed).

The abundance of insect herbivores, however, was not significantly higher during the day than at night (Table 27.1). There was no indication of a large vertical movement of insect herbivores from the understorey to the upper canopy at night ($AC = 0.22$). The Chrysomelidae were more abundant during the night than the day, Curculionidae and Psylloidea showed the reverse trend, and other taxa showed no particular affinity for time of day (Fig. 27.2). Collectively, sap-sucking insects were more abundant during the day than at night in the upper canopy, whereas leaf-chewing insects were not (Mann–Whitney tests with $p < 0.01$ and $p = 0.436$, respectively).

Although many more species of insect herbivores were collected in the upper canopy during the day ($n = 102$) than at night ($n = 25$), this simply reflected the higher sampling effort during the day, particularly with the sledge. Rarefaction estimates calculated with 50 individuals indicated similar species richness in the upper canopy during the day and at night ($n = 27 \pm 4$ (SD) and 25 ± 1 (SD), respectively). The proportion of singleton species collected in the upper canopy during both day and night was high and not significantly different (63% and 76%, respectively; Fisher's exact test, $p = 0.346$). The evenness of herbivore communities in the upper canopy tended to be lower during day than

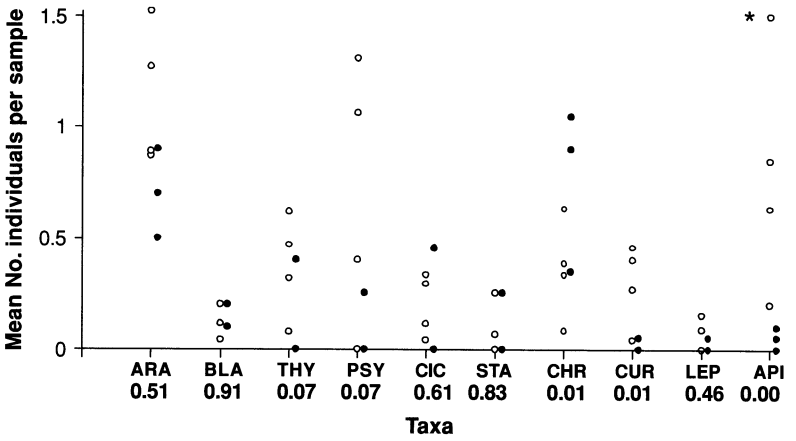


Fig. 27.2. Mean number of individuals collected per beating sample during the day (open circles, four sites) and at night (closed circles, three sites) in the upper canopy for the most common higher arthropod taxa. Numbers below each taxa code refer to the p value of Mann–Whitney tests. ARA, Araneae; BLA, Blattodea; THY, Thysanoptera; PSY, Psylloidea; CIC, Cicadellidae; STA, Staphylinidae; CHR, Chrysomelidae; CUR, Curculionidae; LEP, Lepidoptera; API, Apidae; *out of scale, with 2.92 individuals per sample.

Table 27.1. *Faunal similarities among the understorey and upper canopy samples, during the day and at night (refer to Fig. 27.1 for similarity codes), for the most common herbivore taxa in samples obtained by beating*

Taxa	Total No. species collected	Morisita–Horn index (Shared Species Estimator)[a]						Change of abundance index[b]	Mann–Whitney test p value[b]	Interpretation[c]
		S1	*S2*	*S3*	*S4*	*S5*	*S6*			
All herbivores	154	0.146 (10)	0.069 (4)	0.750 (12)	0.375 (19)	0.044 (7)	0.307 (6)	0.22	0.231	1, 2 less evident
Psylloidea	4	0.805 (–)	1 (–)	1 (–)	0.805 (–)	0.805 (–)	1 (–)	0.79	0.071	?
Membracidae	14	0 (–)	0 (–)	0 (–)	0.292 (–)	0 (–)	0 (–)	0.24	0.607	?
Cicadellidae	20	0 (–)	0 (–)	0 (–)	0.739 (–)	0 (–)	0 (–)	0.10	0.608	Probably 1
Elateridae	7	0 (–)	0 (–)	0.921 (–)	0 (–)	0 (–)	0 (–)	0.17	0.972	Probably 1
Chrysomelidae	40	0.423 (8)	0.274 (1)	0.397 (2)	0.648 (9)	0.183 (3)	0.649 (6)	−0.09	0.010	2 and 1
Curculionidae	35	0 (–)	0 (–)	0.925 (–)	0 (–)	0.004 (–)	0 (–)	0.89	0.006	Probably 1

[a]Insufficient data for calculation indicated by –.

[b]For differences between day and night in the upper canopy (see Methods).

[c]Whether results are consistent with hypotheses 1 or 2 (see text) or cannot be evaluated (?).

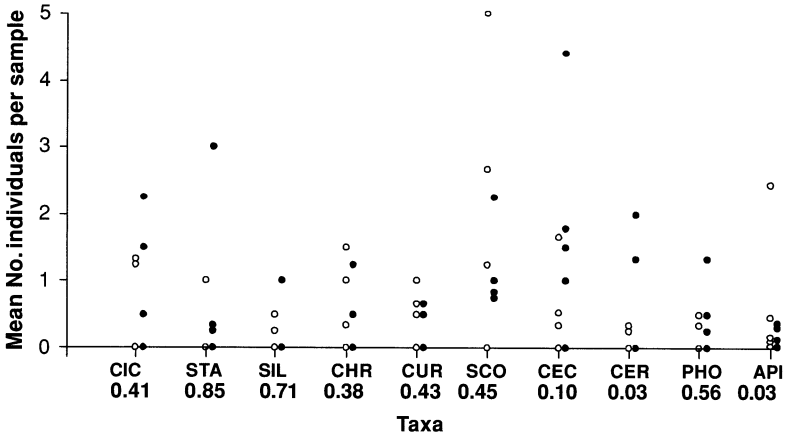


Fig. 27.3. Mean number of individuals collected per flight-interception trap sample during the day (open circles, five sites) and at night (closed circles, five sites) in the upper canopy for the most common higher arthropod taxa. Numbers below each taxa code refer to the p value of Wilcoxon signed-rank tests. CIC, Cicadellidae; STA, Staphylinidae; SIL, Silvanidae; CHR, Chrysomelidae; CUR, Curculionidae; SCO, Scolytinae; CEC, Cecidomyiidae; CER, Ceratopogonidae; PHO, Phoridae; API, Apidae. For the sake of clarity, data for Scolytinae, Cecidomyiidae and Apidae are scaled down by factors 2, 5 and 100, respectively.

during night, but not significantly so ($E = 0.628$ (95% confidence limit (CL) 0.667–0.588) and 0.733 (95% CL 0.822–0.644), respectively).

Most coefficients of similarity calculated for herbivore taxa using the data generated by beating were low (Table 27.1). In many cases, low sample size precluded a clear interpretation of the data. Overall, the similarities of the assemblages of insect herbivores across day and night in either stratum (coefficients *S3* and *S4*) were higher than the similarities between strata at a particular time of day (*S1* and *S2*), favouring hypothesis 1. The coefficient *S6*, however, was also relatively high for all herbivores (Morisita–Horn index = 0.307), indicating that movements of fauna do occur between the understorey during the day and the upper canopy at night. This was evident for the Chrysomelidae (*S6*: Morisita–Horn index = 0.649), which further showed significantly higher abundance in the upper canopy at night than during the day (Table 27.1, Fig. 27.2).

Flight-interception trap samples

During the 16 trapping days at the five sites, the trap set up in the upper canopy provided 28 samples, 14 obtained during the day and 14 at night. Overall, arthropod activity in the upper canopy during the day was high, but not significantly higher than at night (mean number of individuals collected per sample was 105.6 ± 38.6 and 53.08 ± 9.47, respectively; Wilcoxon test, $Z = -0.941$, $p = 0.347$; see Fig. 27.3 for the most common taxa). The Ceratopogonidae, however, were more active at night than during the day and the Apidae showed the reverse trend (Wilcoxon tests, both with $p < 0.05$; Fig. 27.3).

Overall, insect herbivores were not significantly more active during the day than at night in the upper canopy and this was also true of the particular herbivore taxa that were well sampled with flight-interception traps (Table 27.2, Fig. 27.3). There was no indication of a large vertical migration of insect herbivores from the understorey to the upper canopy at night ($AC = 0.15$). The number of herbivore species collected in the upper canopy during the day and at night was similar ($n = 47$ and 44, respectively) and so were the rarefactions calculated to 50 individuals (day: $n = 182 \pm 151$ (SD); night: 120 ± 67 (SD)). The proportion of singleton species collected in the upper canopy during the day and at night was high and not significantly different (83% and 75%, respectively; Fisher's exact test, $p = 0.441$). The evenness of herbivore communities in the upper canopy tended to be lower during the day than at night, but not significantly so ($E = 0.703$ (95% CL 0.769–0.638) and 0.783 (95% CL 0.853–0.714), respectively).

Scolytinae, the most abundant herbivore group in flight-interception traps, greatly influenced the similarity values across the assemblages of insect herbivores (Table 27.2). Several species of Scolytinae appeared indiscriminantly with regard to either stratum or time

Table 27.2. *Faunal similarities between the understorey and upper canopy, during the day and night (refer to Fig. 27.1 for similarity codes), for the most common herbivore taxa collected using flight-interception traps*

Taxa	Total No. species collected	Morisita–Horn index (Shared Species Estimator)[a]						Change of abundance index[b]	Mann–Whitney test p value[b]	Interpretation[c]
		S1	*S2*	*S3*	*S4*	*S5*	*S6*			
All herbivores	158	0.758 (0)	0.601 (15)	0.748 (20)	0.752 (13)	0.699 (119)	0.586 (0)	0.15	0.528	Neither 1 nor 2
Psylloidea	7	0 (–)	0.571 (–)	0 (–)	0.333 (–)	0.400 (–)	0 (–)	0.33	0.480	?
Cicadellidae	33	0.284 (–)	0.241 (1)	0.746 (1)	0.550 (1)	0.442 (5)	0 (–)	−0.15	0.414	1
Derbidae	11	0 (–)	0 (–)	0.396 (–)	0 (–)	0 (–)	0 (–)	−0.30	0.564	Probably 1
Elateridae	9	0 (–)	0 (–)	0 (–)	0 (–)	0 (–)	0 (–)	−0.30	0.705	?
Chrysomelidae	15	0.063 (–)	0.133 (–)	0.800 (1)	0.520 (2)	0 (–)	0.158 (–)	0.21	0.380	1
Curculionidae	20	0 (–)	0 (–)	0 (–)	0 (–)	0 (–)	0 (–)	0.43	0.429	?
Scolytinae	23	0.884 (–)	0.842 (4)	0.979 (–)	0.900 (8)	0.881 (–)	0.813 (–)	0.32	0.447	Neither 1 nor 2

[a]Insufficient data for calculation indicated by –.

[b]For differences between day and night in the upper canopy (see Methods).

[c]Whether results are consistent with hypotheses 1 or 2 (see text) or cannot be evaluated (?).

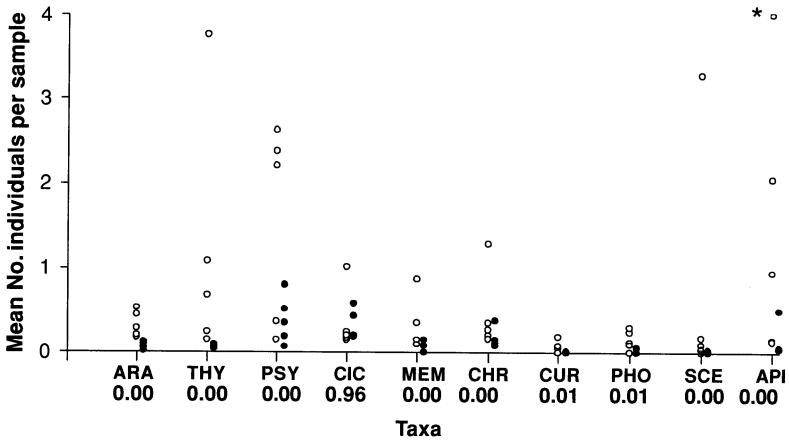


Fig. 27.4. Mean number of individuals collected per sticky trap sample during the day (open circles, five sites) and at night (closed circles, five sites) in the upper canopy for the most common higher arthropod taxa. Numbers below each taxa code refer to the p value of Wilcoxon signed-rank tests. ARA, Araneae; THY, Thysanoptera; PSY, Psylloidea; CIC, Cicadellidae; MEM, Membracidae; CHR, Chrysomelidae; CUR, Curculionidae; PHO, Phoridae; SCE, Scelionidae; API, Apidae; *out of scale, with 18.5 individuals per sample.

of day. The percentage of individuals, for example, of one undetermined species of *Xyleborus* collected in the understorey during day and night, and in the upper canopy during day and night, were 17, 35, 33 and 15%, respectively. In this case, neither hypothesis 1 nor 2 pertains. More individuals of Cicadellidae, Derbidae and Elateridae were collected in the upper canopy at night than during the day, but differences were not statistically significant (Table 27.2). Further, similarities calculated for these groups were not consistent with hypothesis 2. Similarities for Cicadellidae, Chrysomelidae and, possibly, Derbidae were more consistent with hypothesis 1.

Sticky-trap samples

A total of 192 sticky traps were recovered from the upper canopy at five sites, with 100 traps operating during the day and 92 at night. On average and correcting for longer exposure at sites C and E, 10.8 ± 0.78 arthropods were caught per trap during 3 hours of exposure in the upper canopy (day and night data pooled). This corresponded to catch rates of about 3.6 arthropods per trap per hour, or of 2.5 arthropods per 500 cm^2 per hour. Overall, sticky traps set in the upper canopy collected significantly more arthropods during the day than at night (mean 17.7 ± 1.10 individuals and 3.4 ± 0.29, respectively; Wilcoxon rank test, $Z = -8.09$, $p < 0.001$). The pattern was similar for insect herbivores (day: 4.5 ± 0.51 individuals, night: 1.12 ± 0.12 individuals, $Z = -6.92$, $p < 0.001$). The overall levels of activity of many taxa were higher during the day than at night, including those of the Araneae, Phoridae, Brachycera, Scelionidae, Apidae and, among herbivorous taxa, Thysanoptera, Psylloidea, Membracidae, Chrysomelidae and Curculionidae (Fig. 27.4). Catches of herbivores did not increase notably in the upper canopy at night ($AC = 0.60$), suggesting that no strong influx of herbivores from lower strata occurred at that time.

DISCUSSION

Each of the sampling methods used in this study has limitations and these are discussed in Basset *et al.* (2001a). In particular, the reflectance of yellow sticky traps and their efficiency may be higher during the day than at night. In addition, their efficiency may be higher in the canopy than it is in the understorey, although the reverse is also plausible. Other factors, such as wind speed and air temperature, may further complicate the interpretation of levels of arthropod occurrence as measured by flight-interception and sticky traps. Overall, beating data indicated real differences in the occurrence of sedentary taxa from site to site. Data from the flight-interception traps reflect the flight activity of larger, heavier arthropods,

whereas sticky-trap data reflect the flight activity of smaller arthropods, perhaps increasing the magnitude of the differences observed here, although to what extent is not clear.

Our sampling methods were also less efficient for larger herbivores, such as certain Orthoptera and Phasmoptera. It is well known that the activity of these taxa tend to segregate between day and night (e.g. Lockwood *et al.*, 1996). It is probable that more efficient collection of these taxa would have resulted in more contrast in overall arthropod activity between day and night.

Beating data identified significant differences in the abundance of certain taxa between day and night. These differences were often higher when estimated with sticky traps – which are commonly used in economic entomology to monitor the diel activity of particular herbivore pests (e.g. Johnson & Mueller, 1990; Weintraub & Horowitz, 1996). In contrast, flight-interception traps showed few differences in arthropod activity between day and night. This result may reflect the different sampling regime represented by the three methods. Whereas collecting using beating or sticky traps occurred for 3 hours in the middle of the afternoon or of the night, flight-interception traps ran continuously from 06:00 to 18:00 and from 18:00 to 06:00, respectively. A simple segregation of flight-interception trap material into day and night catches may have resulted in fewer differences between day and night, particularly if a high proportion of catches occurred either at dusk or dawn. Data from the flight-interception traps were also influenced by abundant catches of Scolytinae, of which several species showed no clear preferences for either strata or time of day. Some of these beetle species may well forage preferentially at dawn or dusk.

We conclude, therefore, that arthropod activity is indeed higher during the day than at night in the upper canopy. This parallels the outcomes of other studies elsewhere in the tropics, as indicated in the Introduction to this chapter. In particular, taxa such as the Thysanoptera, Psylloidea, Membracidae, Curculionidae, Scelionidae and Apidae were notably more active during the day than at night in the upper canopy. Many Brachycera (Diptera) that were not sorted to family level appeared also to be particularly active during the day in the upper canopy.

Referring back to hypotheses 1 and 2, it is inevitable that a low sample size (with regard to particular herbivore species) will result in low similarities of herbivore faunas, as in the present study. However, it is instructive to compare relative similarity values obtained with comparable sampling effort. Similarity values between day and night faunas in particular strata (*S3* and *S4*) were often higher than between faunas of the understorey and the upper canopy at a particular time of the day (*S1* and *S2*). This suggests that there are rather distinct herbivore faunas foraging in each stratum, an observation consistent with hypothesis 1.

Assemblages of insect herbivores in the upper canopy during the day were species rich but unevenly distributed, with just a few species dominating the communities there. In addition, similarities in *S3* (understorey, similarity between day and night) were often higher than *S4* (upper canopy, similarity between day and night). In particular, the data obtained by beating suggested that faunal turnover between day and night was higher in the upper canopy compared with that in the understorey. This suggests that the magnitude of changes in the microclimatic conditions between day and night in the upper canopy may be more severe than in the understorey, and that only a well-adapted fauna may be able to cope with these changes. It is well known that many insect taxa of tropical rainforests show behavioural and physiological adaptations that result in thermal guilds, such as 'light-seeking' or 'shade-seeking' insects (e.g. Shelly, 1985; Hood & Tschinkel, 1990; Roubik, 1993). Further, it is known that certain insect pests show a positive correlation between activity and air temperature, others a negative one (e.g. Johnson & Mueller, 1990; Weintraub & Horowitz, 1996). All of these behavioural differences may be important in shaping the different assemblages of insect herbivores in different forest strata at different times of the day. In contrast, arthropod diel activity in the understorey may be less clearly differentiated on a day/night basis (Davis, 1999a; Basset, 2000).

The present data also indicate that certain groups, notably the Chrysomelidae, may move at night from the understorey to the upper canopy (evidenced by high values of *S6*), which is also consistent with hypothesis 2. This observation may reflect the activities of just a few species, since none of the sampling methods showed evidence of mass migration from the understorey to the

upper canopy at night. As stressed by Compton *et al.* (2000), however, insect flight in the overstorey (i.e. above the canopy) for dispersal may be significant, especially at night. Future work should determine the ecological characteristics of *resident* species in the upper canopy, of migrating species from the understorey to the overstorey, as well as of species foraging indiscriminately in these different layers.

There are two obvious implications of the present results. First, if faunal turnover is high in the upper canopy between day and night, comprehensive entomological surveys should ensure that arthropods are sampled during the full daily cycle. A popular sampling method such as pyrethrum knockdown is usually performed early in the morning when airflow is reduced (e.g. Adis *et al.*, 1998b). It would be advisable to assess the efficiency of this method for the collection of taxa active predominantly in either the day or the night. Second, our data suggest that many insect herbivores of the upper canopy may be resident and well adapted to environmental conditions there. Since faunal stratification in tropical rainforests may be at an optimum, leading to a diverse fauna in the upper canopy only in closed and undisturbed lowland rainforests, the implications for the conservation of tropical rainforest arthropods are also significant.

ACKNOWLEDGEMENTS

We thank the support teams of Océan Vert, Pro Natura International and Les Accro-Branchés: Francis Hallé, Gilles Ebersolt, Dany Cleyet-Marrel, François Collignon, Laurent Pyot, Olivier Pascal, Roland Fourcaud, Carole Megevand, Thierry Aubert, Lionel Picart and Jean-Yves Serein. Jean-Michel Bérenger, Jean-Pierre Vesco, Philippe Causse, Andréa Haug, Anne-Sophie Hennion, Loïc Lesobre, Florent Marquès and Robert O'Meara helped with insect collecting. Enrique Medianero and Anayansi Valderrama helped to sort the insect samples. Neil Springate commented on the manuscript. Financial help was provided by a Tupper fellowship at the Smithsonian Tropical Research Institute in Panama (Y. B.), Bayer-Agro (H.-P. A.), Secretaria Nacional de Ciencia y Tecnología (H. B.), and Dr Franco Tassi of the Parco Nazionale d'Abruzzo and 'Progetto Biodiversità' (G. C.).