Rainfall and parasitic wasp (Hymenoptera: Ichneumonoidea) activity in successional forest stages at Barro Colorado Nature Monument, Panama, and La Selva Biological Station, Costa Rica

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Abstract   1 In 1997, we ran two Malaise insect traps in each of four stands of wet forest in Costa Rica (two old-growth and two 20-year-old stands) and four stands of moist forest in Panama (old-growth, 20, 40 and 120-year-old stands).

2 Wet forest traps caught 2.32 times as many ichneumonoids as moist forest traps. The average catch per old-growth trap was 1.89 times greater than the average catch per second-growth trap.

3 Parasitoids of lepidopteran larvae were caught in higher proportions in the wet forest, while pupal parasitoids were relatively more active in the moist forest.

4 We hypothesize that moisture availability is of key importance in determining parasitoid activity, community composition and trophic interactions.

Keywords Barro Colorado Nature Monument, Ichneumonoidea, La Selva, parasitoids, precipitation, tropical moist forest, tropical wet forest.

Introduction

One of the largest groups of parasitic Hymenoptera is the superfamily Ichneumonoidea, which consists of two families (the Ichneumonidae and the Braconidae), 64 subfamilies and an estimated 100 000 species world-wide (Gauld & Bolton, 1988; Wahl & Sharkey, 1993). The majority of experimental work done with parasitoid wasps focuses on specific strategies of individual species or genera (e.g. Nealis, 1988; Gauld, 1991; Thangavelu, 1993). Relatively little is known about the community structure, geographical range, environmental requirements, host specificity and behaviour of most species, particularly of tropical species (Askew & Shaw, 1986; Gauld & Bolton, 1988; Memmott *et al.*, 1994). The Ichneumonoidea attack a wide variety of holometabolous hosts. They range from highly specialized parasitoids that develop within the bodies of a living host to more generalized ectoparasitoids (Askew & Shaw, 1986). Parasitoids are also characterized as either idiobionts, which kill or paralyse the host immediately after oviposition, or koinobionts, which allow the host to continue to feed and move around, eventually killing it at some later stage of development.

Many factors influence the timing and duration of parasitoid activity, including host phenology, the life history character-istics of each parasitoid species and abiotic factors. Seasonal patterns of insect activity are often correlated with temperature, as processes such as development and diapause are often intimately associated with temperature change (Wolda, 1988). Fink & Völkl (1995) gave several examples of small insects for which low humidity and high temperature have detrimental effects on life expectancy and reproductive success. In tropical forests, temperatures remain practically constant throughout the year, yet most insects still exhibit seasonal patterns of activity. In forests with pronounced dry seasons, periods of peak activity among insects tend to be more pronounced and to continue for shorter periods than in less seasonal forests (Wolda, 1988). Using data from 12 to 13 years of light trapping on Barro Colorado Nature Monument (BCNM), Wolda (1989) found that peaks in insect activity were correlated significantly with either the start or the end of dry seasons, but was unable to explain why this pattern occurred. Smythe (1985) showed that night-flying insects at BCNM have an early wet season peak, followed by a late wet season low. He hypothesized that insect activity peaked when food was most abundant.

Seasonal rainfall patterns are important in influencing fluctuations in foliage condition (Boinski & Fowler, 1989), flowering time (Johnson, 1992) and litterfall (Wright & Cornejo, 1990). Numbers of herbivorous insect populations in general are depressed significantly during the dry season, and then increase with the onset of the wet season (Buskirk & Buskirk, 1976; Wolda, 1978; Janzen, 1993; Kato *et al.*, 1995; Coley & Barone, 1996; Novotny & Basset, 1998). Janzen (1981) suggested that

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annual fluctuations in rainfall may also be a significant driving force of seasonal fluctuation of parasitoid populations. In a study of the ichneumonid community in Georgia's Piedmont, Gaasch *et al.* (1998) found that ichneumonids attacking similar orders of hosts tended to peak synchronously. They predicted that host seasonality was an important factor in determining parasitoid flight phenology. If tropical populations of hosts and parasitoids increase at the beginning of the wet season, we do not know whether the parasitoids are responding to the increase in precipitation, to the increase in potential hosts, or to other factors.

Many factors have been suggested to influence parasitoid activity and diversity, including plant-host–parasitoid interactions (Gauld *et al.*, 1992), resource fragmentation (Janzen & Pond, 1975; Janzen, 1981), competition (Hawkins *et al.*, 1990), predation (Price *et al.*, 1980) and abiotic factors. In an intensive study of the ichneumonines of Florida, Heinrich (1977) found that on sunny days, ichneumonines were active only during the early morning and evening hours, disappearing completely during the majority of the day. Significantly fewer icnheumonoids were caught in Malaise traps in hot, dry, sunny areas, such as field and cleared forest, than in nearby traps not as exposed to the sun (Gauld, 1987).

In this paper, we compare one year (1997) of data from 16 Malaise traps in two tropical forests with distinct annual precipitation patterns and correlate parasitoid flight activity with rainfall. La Selva Biological Station in Costa Rica is a tropical wet forest that is often characterized as aseasonal (but see below). Barro Colorado Nature Monument in Panama is a tropical moist forest with a pronounced dry season annually. Table 1 summarizes the biology of the 18 ichneumonid subfamilies we caught during this study. We focus our analysis first at the level of the superfamily Ichneumonoidea, and then on the seven most commonly caught of the ichneumonid subfamilies.

Study sites

Barro Colorado Nature Monument, Panama

Barro Colorado Nature Monument (BCNM) is a moist tropical lowland forest located at 9°9′N, 79°51′W. Barro Colorado Island (BCI) is a ~1500 ha island that was created in 1914 as a result of the flooding of the Chagres River during formation of the Panama Canal (Leigh & Wright, 1990; Dietrich *et al.*, 1996). BCNM encompasses BCI, several smaller islands and surrounding mainland forest. Its dry season is associated with large-scale leaf-fall of tree species, few birds and mammals breeding, less litter decomposition, and a noticeable decrease in insect population densities as compared to the wet season (Leigh *et al.*, 1996). BCI receives approximately 2600 mm of rainfall annually (Dietrich *et al.*, 1996). It has a pronounced dry season, usually from late December to early May, when heavy rains commence. During the dry season, winds increase dramatically and temperatures rise about 1 °C on average as the amount of cloud cover decreases. Over 90% of the rainfall on BCI occurs during the wet season that lasts the remainder of the year.

La Selva Biological Station, Costa Rica

La Selva Biological Station is a tropical lowland wet forest in the province of Heredia, Costa Rica, located at 10°26′N, 83°59′W (McDade *et al.*, 1994). The station encompasses 1536 ha of protected natural reserve, positioned at the foothills of the central

Table 1 Ichneumonid life history and trap catches of the subfamilies in Barro Colorado Nature Monument, Panama and La Selva Biological Station, Costa Rica

| Subfamily | BCNM | | La Selva | | | | | |
	Total no. caught	% of total ichneumonid catch	Total no. caught	% of total ichneumonid catch	K/I	E/L/P	N/C	Primary hosts
Anomaloninae	12	0.3	18	0.2	K	L	N	Lep/Col
Banchinae	62	1.7	303	3.0	K	L	N	Lep
Campopleginae	172	4.6	927	9.1	K	L	N	Lep
Cremastinae	79	2.1	622	6.1	K	L	N	Lep
Cryptinae	1082	29.1	1528	15.0	I	P	C	Lep
Ctenopelmatinae	1	0.03	3	0.0	K	L	N	Sym
Ichneumoninae	815	22.0	987	9.7	I	P	N	Lep
Labeninae	23	0.6	23	0.2	I	P	C	> 2 host orders
Lycorinae	0	0	1	0.0	K(?)	L(?)	N(?)	Lep
Mesochorinae	4	0.1	62	0.6	K	L	N	Hym
Metopiinae	50	1.3	328	3.2	K	L	N	Lep
Ophioninae	7	0.2	38	0.4	K	L	N	Lep
Orthocentrinae	775	20.9	2365	23.3	K	L	N	Dip
Oxytorinae	3	0.1	17	0.2	K	L	N	Dip
Pimplinae	543	14.6	1793	17.6	I/K	E/L/P	N/C	> 2 host orders
Rhyssinae	3	0.1	8	0.1	I	L/P	C	Col/Sym
Tersilochinae	81	2.2	1145	11.3	K	L	N	Col
Tryphoninae	0	0	2	0.0	K	L	C	Sym/Lep

K = koinobionts; I = idiobionts; N = endoparasitic; C = ectoparasitic; E = attacks egg host; L = attacks larval host; P = attacks pupal host

volcanic mountain chain of Costa Rica and just within the Caribbean coastal plain. The majority of the reserve lies within the natural boundaries of the confluence of the Sarapiqui and Puerto Viejo rivers and their tributaries. La Selva receives approximately 4000 mm of rain per year (Sanford *et al.*, 1994). Although La Selva is often cited as an aseasonal wet forest, reports of the average weekly precipitation recorded from 1982 to 1991 show the lowest weekly precipitation near the end of March, and the greatest precipitation near the end of August. For a detailed description and comparison of both sites see Gentry (1990b).

Methods

We ran eight Townes-style Malaise traps (Townes, 1972), at BCNM and eight at La Selva. Traps were purchased from Sante Traps, Lexington, KY. Malaise traps are fine-mesh tent-like structures that intercept flying insects. We orientated each trap along a north–south axis with the collecting jar of 70% ethanol facing south. We placed the traps in areas of different forest stand age, with treatments of 20, 40, 120-year-old and old-growth stands in Panama, and two 20-year and two old-growth sites in Costa Rica. In each forest stand we ran two traps, for a total of eight traps at each site. We emptied and replaced the jars on each trap every 2 weeks for the year beginning January 1997. Each time we emptied the traps, we removed, counted and recorded the total number of Ichneumonoidea from the bulk sample. In addition, we sorted all Ichneumonidae to subfamily. To aid in this process, we gave each individual that we mounted a conventional label and unique barcode in order to facilitate further identification and analysis.

Precipitation was recorded at BCNM by the Smithsonian Tropical Research Institute's Terrestrial – Environmental Sciences Program (T-ESP) (Paton, 1997) and at La Selva Biological Station at the East Bank Meteorological Station by the Organization for Tropical Studies (OTS).

We ran a repeated measures analysis of variance (RM-ANOVA) (SAS – General Linear Models Procedure) to test for variation in parasitoid abundance between La Selva and BCNM and between old and second growth. For the forest-age analysis, we pooled the six second-growth traps at BCNM with the four second-growth traps at La Selva and compared those to the remaining traps. Because insect populations increase at an exponential rate, the natural logarithms of the numbers of individuals caught per sample were used in the analysis.

We used the genmod procedure of SAS for generalized linear models to compare community structure at each site. For the seven most frequently caught ichneumonid subfamilies: the Campopleginae, Cremastinae, Cryptinae, Ichneumoninae, Orthocentrinae, Pimplinae and Tersilochinae, two separate RM-ANOVAS were performed. In the first analysis, we log-transformed the absolute number of individuals in each subfamily that was caught per trap during each sampling period. To factor out differences in between-trap efficiency resulting from microhabitat differences in placement, and assuming that these differences are constant across subfamilies, we then ran the same analysis (RM-ANOVA) using the proportion of the number of individuals caught in that subfamily to the total number of Ichneumonidae caught for that trapping period. As is customary

for proportions, we transformed these data by taking the arcsin square root of the ratio.

Results

Superfamily analysis

We first analysed our data at the superfamily level, comparing ichneumonoid activity between BCNM and La Selva, and between old- and second-growth forest. Ichneumonoidea were more active at La Selva than at BCNM ($F = 8.83$, d.f. $= 1,12$, $P = 0.0117$) and in old-growth than in second-growth forest ($F = 5.10$, d.f. $= 1,12$, $P = 0.0434$). During the calendar year 1997, the eight traps at La Selva caught a combined 18 696 ichneumonoids, which amounts to a per-trap average 2.32 times greater than the total catch (8049 ichneumonoids) for the BCNM traps. Although the difference observed between sites was independent of forest age, it was dependent on season ($F = 2.42$, d.f. $= 25,300$, $P = 0.0019$), with much higher catches at La Selva during the first months of the year corresponding to BCNM's dry season (Fig. 1). The average trap-catches among the six old-growth traps were 1.89 times greater than the average for the 10 second-growth sites. Although both forests were seasonal, old-growth traps consistently caught more ichneumonoids than did second-growth traps, regardless of season (Fig. 1).

Subfamily analyses

Community structure differed between the two sites (Table 2). We ranked the seven most frequently caught subfamilies from
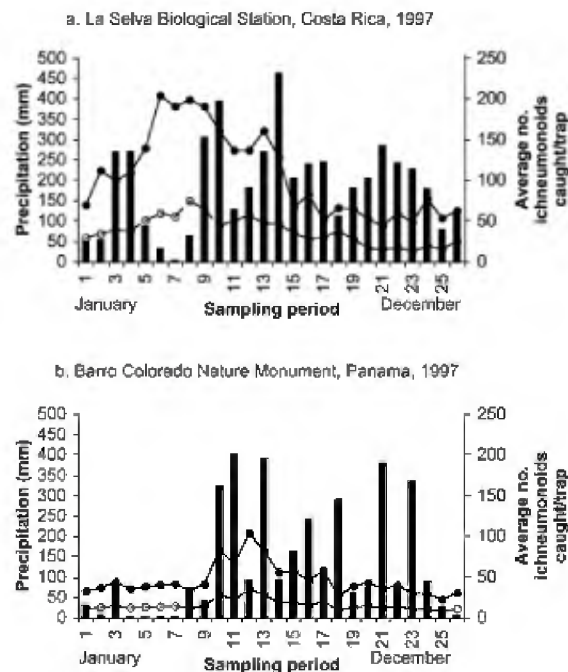

Figure 1 Cumulative precipitation (solid bars) over the 14-day trapping period compared to the average number of Ichneumonoidea caught per trap by forest type for (a) La Selva Biological Station, Costa Rica and (b) Barro Colorado Nature Monument, Panama. Closed circles and solid lines represent old-growth forest catches, while open circles and dashed lines represent second-growth forest catches.

most to least abundant in the total catch for the year and created a log-abundance/rank curve (Southwood, 1978). Using a Poisson distribution with log(log(y))-transformed data, we found a significant interaction between rank and site (Chi-squared = 13.3, d.f. = 1, $P = 0.0002$). We estimated the scale parameter for the model using the square root of Pearson's Chi-Squared divided by the degrees of freedom. The significant interaction suggests that community structure, and not simply absolute numbers of ichneumonids caught, is important in defining the differences we found between La Selva and BCNM.

We then analysed the seven most frequently caught subfamilies with a RM-ANOVA using the absolute number of individuals caught (Table 2). Figure 2 depicts the average monthly catches in old- and second-growth treatments at both sites. Five of the seven commonest subfamilies were statistically more abundant in the trap catches at La Selva than at BCNM: Campopleginae, Cremastinae, Pimplinae, Orthocentrinae and Tersilochinae. For each of these subfamilies, the difference between sites was dependent on date. The Cryptinae were statistically no more active at either site, and the Ichneumoninae were more active at La Selva, but only during the 4 months of the study corresponding to BCNM's dry season. Only two subfamilies, the Orthocentrinae and the Tersilochinae, were more active in old growth forest than in second growth forest.

Considering proportions rather than absolute catches, cryptines and ichneumonines were caught in higher proportions at BCNM, whereas pimplines, campoplegines, cremastines and

tersilochines made up greater proportions of the trap-catch at La Selva. The proportion of orthocentrines caught was also higher at La Selva, but the difference depended on date for each of these subfamilies. Tersilochines and orthocentrines made up more of the old-growth trap catch than the second-growth trap catch. However, the difference in Orthocentrines was largely due to the difference between the forest types at BCNM ($F = 10.56$, d.f. = 1,12, $P = 0.0070$).

While all other subfamilies were less active in the tropical moist forest, two subfamilies, the Cryptinae and the Ichneumoninae, did not differ significantly in abundance between the sites. Both attack Lepidoptera pupae. For each sampling period, we summed the eight subfamilies that exclusively attack Lepidoptera (see Table 1) and ran a RM-ANOVA with the proportion of pupal parasitoids to all Lepidoptera parasitoids, and the proportion of larval parasitoids to all Lepidoptera parasitoids (Table 3). A higher proportion of parasitoids attacking Lepidoptera are larval vs. pupal at La Selva, and pupal vs. larval at BCNM. In addition, we found a higher proportion of parasitoids attacking larval vs. pupal Lepidoptera in old-growth than in second-growth forest. We ran the same analysis dividing the data into four treatments: La Selva old-growth, La Selva second-growth, BCNM old-growth, and BCNM second-growth. Old-growth traps at La Selva caught the highest proportion of parasitoids attacking larvae, while the lowest proportion was caught in second-growth traps at BCNM.

Table 2 Results of the RM-ANOVA for differences in (a) total abundance of each subfamily caught per trap and (b) the proportion of each subfamily in the total ichneumonid catch for each trap between sites, between forest types, and the interaction between site and date. Analyses between sites and types each had one degree of freedom, while the date*site analyses had 25 degrees of freedom. Bold lettering represents P-values < 0.05.

Subfamily	BCNM total/ La Selva total	SITE			SITE*DATE			FOREST TYPE		
		F	d.f.	P	F	d.f.	P	F	d.f.	P
(a) Total abundance										
Cryptinae	0.71	0.16	1,12	0.6920	1.47	25,300	0.0720	1.17	1,12	0.3010
Ichneumoninae	0.83	0.45	1,12	0.5134	2.52	25,300	**0.0001**	1.83	1,12	0.2007
Orthocentrinae	0.33	12.33	1,12	**0.0043**	4.48	25,300	**0.0001**	7.41	1,12	**0.0185**
Pimplinae	0.30	15.33	1,12	**0.0021**	1.64	25,300	**0.0296**	0.08	1,12	0.7810
Campopleginae	0.19	13.89	1,12	**0.0029**	1.72	25,300	**0.0196**	0.46	1,12	0.5119
Cremastinae	0.13	32.61	1,12	**0.0001**	1.78	25,300	**0.0139**	3.59	1,12	0.0824
Tersilochinae	0.07	47.94	1,12	**0.0001**	4.55	25,300	**0.0001**	5.99	1,12	**0.0307**
(b) Proportion of the total ichneumonid catch										
Cryptinae	1.94	26.79	1,12	**0.0002**	1.02	25,300	0.4430	4.02	1,12	0.0681
Ichneumoninae	2.27	5.23	1,12	**0.0411**	1.82	25,300	**0.0572**	0.08	1,12	0.7849
Orthocentrinae	0.86	0.09	1,12	0.7716	3.37	25,300	**0.0001**	5.02	1,12	**0.0448**
Pimplinae	0.83	10.01	1,12	**0.0082**	1.83	25,300	**0.0102**	2.73	1,12	0.1244
Campopleginae	0.51	12.56	1,12	**0.0040**	1.12	25,300	0.3135	0.02	1,12	0.8994
Cremastinae	0.34	9.64	1,12	**0.0091**	1.40	25,300	0.0992	2.15	1,12	0.1685
Tersilochinae	0.19	134.32	1,12	**0.0001**	5.18	25,300	**0.0001**	13.06	1,12	**0.0036**

Figure 2 Average monthly catch of (a) Campopleginae, (b) Cremastinae, (c) Cryptinae, (d) Ichneumoninae, (e) Orthocentrinae, (f) Pimplinae and (g) Tersilochinae in old- and second-growth forests at BCNM, Panama and La Selva, Costa Rica, during 1997. Average catches at La Selva are designated by squares, while catches at BCNM are designated by circles. Symbols representing old-growth catches are solid and connected by a solid line. Second-growth symbols are clear and connected by dashed lines. Because the study began in mid-January, monthly averages for that month are artificially low.
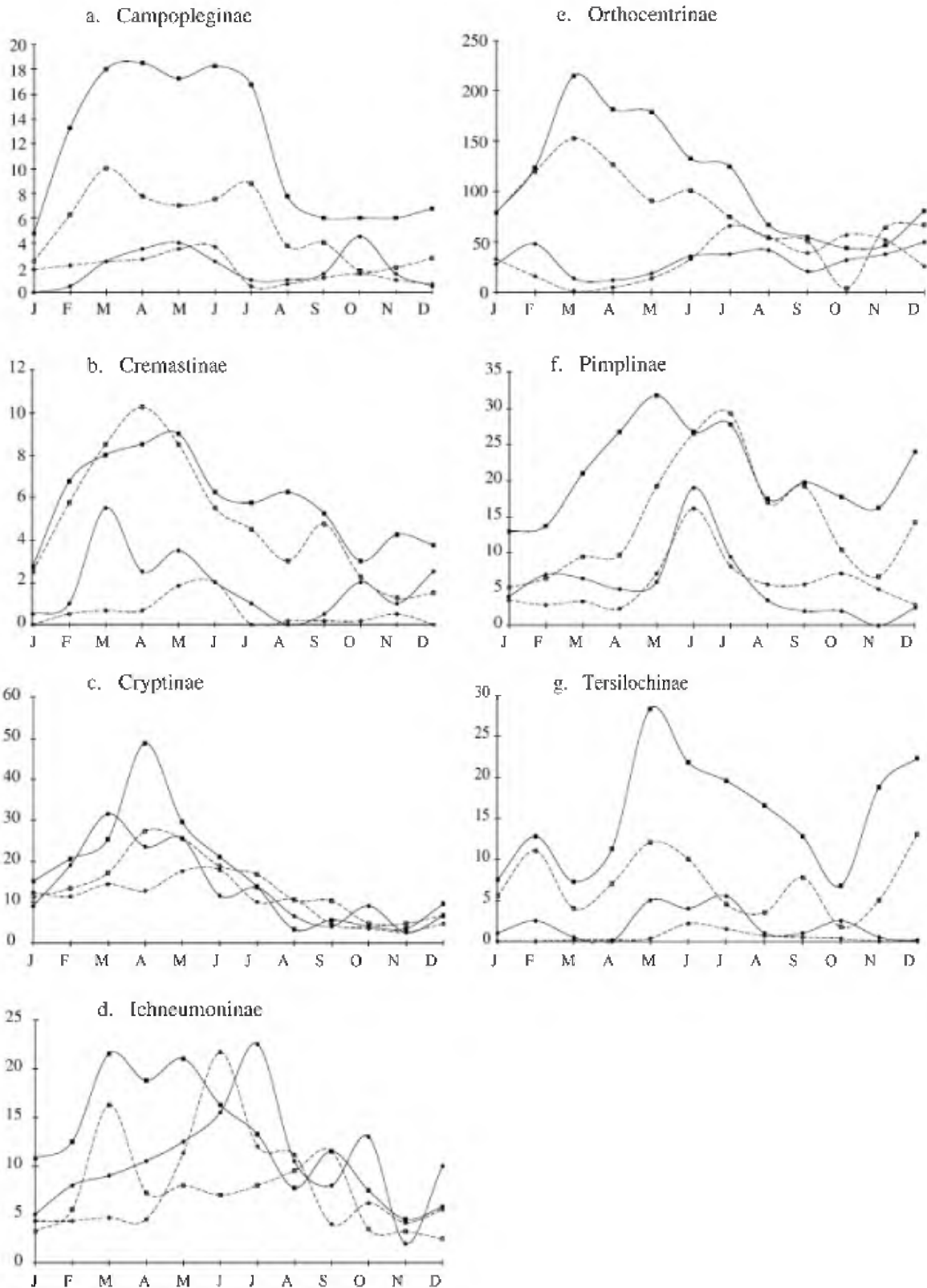
a. Campopleginae
b. Cremastinae
c. Cryptinae
d. Ichneumoninae
e. Orthocentrinae
f. Pimplinae
g. Tersilochinae

Table 3 Results of the RM-ANOVA for differences in the proportion of parasitoids of pupal lepidoptera and larval Lepidoptera to total Lepidopteran parasitoids. Bold lettering represents *P*-values < 0.05. Statements in parentheses indicate the site or forest type in which proportions are significantly higher.

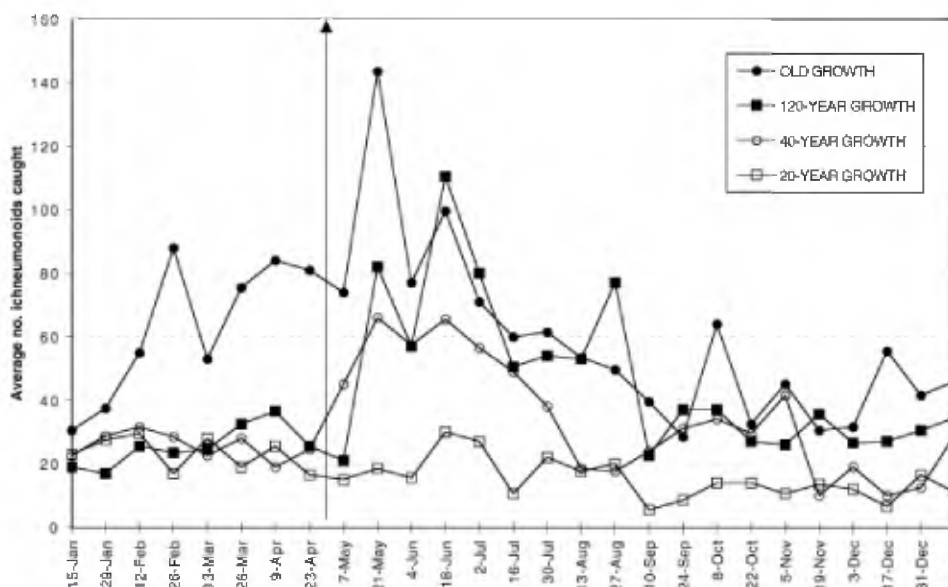|	BCNM	La Selva	SITE			FOREST TYPE			SITE*FOREST TYPE		
			F	d.f.	*P*	*F*	d.f.	*P*	*F*	d.f.	*P*
Parasitoids of pupal Leipdoptera/ total Lepidoptera parasitoids	0.84	0.53	23.81 (BCNM)	1,12	**0.0004**	0.74	1,12	0.4054	9.79 (BCNM second-growth)	3,12	**0.0015**
Parasitoids of larval Leipdoptera/ total Lepidoptera parasitoids	0.16	0.47	92.81 (La Selva)	1,12	**0.0001**	5.88 (old-growth)	1,12	**0.0320**	43.79 (La Selva old-growth)	3,12	**0.0001**

Figure 3 Average catch by 14-day sampling period for the four forest-age treatments at BCNM, Panama 1997. The solid arrow represents the first rain following the dry season.

Dry season refugia

Evidence from BCNM suggests that there may be a dry-season refuge in old-growth forest. Figure 3 depicts the average trap-catches of Ichneumonoidea for each of the four forest-age classes at BCNM. We ran a RM-ANOVA for differences in trap-catches among the forest age classes at each site. We found a significant difference between the number of ichneumonoids caught by forest age/site ($F = 7.61$, d.f. $= 3,12$, $P = 0.0041$) and that the difference was date-dependent ($F = 1.77$, d.f. $= 75,100$, $P = 0.0030$). A Tukey's Studentized Range Test for each sampling period showed that catches were lowest in BCNM second-growth than all other forest age classes or sites throughout 1997. The difference between BCNM second-growth and all of La Selva was statistically significant from the beginning of the study through the 8th sampling period, and from BCNM old-growth catches during the 6th and 8th sampling periods. Figure 3 shows an increase in the old growth catches at BCNM from the beginning of the study through the 8th sampling period. After the first rain of the wet season in Panama, BCNM second-growth traps continued to catch the least number of

ichneumonoids, but the difference between the treatments was no longer statistically significant.

Discussion

Based on our findings, we suggest that rainfall (moisture) is a key to understanding tropical parasitoid activity and community structure. First, let us consider the limitations of our data. Our study's design is pseudoreplicated in that it includes only one wet and one moist site (Hurlbert, 1984). As a result we cannot strictly conclude whether the observed between-site differences are caused by rainfall patterns or other factors. Nevertheless, we can still gain understanding from such regional comparisons (Hargrove & Pickering, 1992) and feel that our findings corroborate our hypothesis and conclusion that rainfall patterns are important in determining parasitoid community activity.

Malaise traps are commonly used to sample insect communities and effectively sample flying insects in many habitats (Matthews & Matthews, 1970; Darling & Packer, 1988; Noyes, 1988). Malaise trap catches depend on adult abundance, flight activity, propensity to be captured, and trap design and

condition. As with all insect-trapping studies, our sampling is biased with respect to true community structure because trap efficiency depends on taxon and individual behaviours. Nevertheless, we believe that Malaise traps are an excellent quantitative tool to measure changes in relative abundance in time and space. Although they do not collect inactive individuals within a population and thus cannot be used to measure absolute densities, they allow relative comparisons of activity between samples.

A further limitation of our study is that it spans only a single year – a year complicated by an El Niño/Southern Oscillation event (ENSO) that brought about abnormal weather conditions at both BCNM and La Selva. At BCNM, 1997 was the driest year since record taking began in 1925 (Paton, 1997). OTS reports that 1997 precipitation at La Selva was about 800 mm above the average for the years 1985–91. However, because the ENSO event only exacerbated the difference in precipitation between the sites, it perhaps allowed us to see more clearly the effects of moisture on the parasitoid community.

Despite these limitations, our data show a strong correlation of moisture with parasitoid wasp activity, supporting the hypothesis that abiotic factors are important in influencing parasitoid activity (Heinrich, 1977; Gauld, 1987). During 1997, ichneumonoid activity was much higher at La Selva, where 4843 mm of rain fell, than at BCNM, which received 1714 mm of rainfall (Paton, 1997). Moisture levels may also have contributed to the higher ichneumonoid activity recorded in the old-growth than second-growth forest. From 1972 to 1997, the Smithsonian's T-ESP measured both temperature and relative humidity on BCI in old-growth forest (Lutz Tower) and in a clearing (El Claro) (Windsor, 1990; Paton, 1997). Monthly temperatures were on average 3 °C higher and relative humidity approximately 10% lower in the clearing than in old-growth forest. Although we did not measure these variables at our second-growth sites, we expect measurements from second-growth to fall somewhere between those of the clearing and old-growth forest. Thus, assuming that moisture stress reduces flight activity, moisture is one factor that may explain the higher levels of activity that we observed in old-growth vs. second-growth forests.

Old-growth refuges may be crucial to the ability of many insects to survive periods of climatic stress. Janzen (1973) found that in the dry forest, insect activity increased during the dry season in areas where the effects of the drought were especially mild. During the dry season, parasitoid wasps appear to leave second-growth for old-growth forest. Figure 3 shows an increase (relative and absolute) in old-growth trap catches at BCNM during the dry season. I. D. Gauld (personal communication) recorded a similar phenomenon in his Malaise traps in old- and second-growth dry forest in Guanacaste, Costa Rica. During the dry season, his old-growth traps caught more ichneumonids than his second-growth traps. Schowalter *et al.* (1986) suggested that structurally more complex older forest may provide herbivores with a refuge from unfavourable conditions in drier, younger stands. If parasitoids use old-growth forest as a refuge from drought conditions, conserving old-growth forest becomes more important as human activity increases forest fragmentation and global warming increases physiological stress.

Clearly, moisture is just one factor influencing the parasitoid community. Differences between sites in floral composition,

potential hosts and forest structure may be important in determining parasitoid activity and community structure. For example, recent surveys of floral composition report a total of 121 plant families (1668 species) at La Selva and 118 families (1320 species) at BCNM (Gentry, 1990a). Such differences may affect plant-host–parasitoid interactions by providing a greater variety of available niches or a more fragmented resource base.

Whatever the cause, it is most interesting that we caught fewer parasitoids of larval Lepidoptera at BCNM compared to La Selva, while parasitoids of pupal Lepidoptera were caught in approximately equal proportions. This difference could again be due to differences in moisture levels. We assume that foliar hunting parasitoids are more exposed to desiccation than those hunting for pupae on the ground. For example, the Smithsonian's T-ESP recorded relative humidity approximately 10–15% higher near the forest floor than above the canopy (Windsor, 1990). In a study comparing parasitoids caught in the canopy vs. ground Malaise traps on BCI, Ayoub *et al.* (unpublished study) found that diurnal parasitoids were active only in the understory, yet nocturnal parasitoids were active throughout the forest. They surmised that while diurnal parasitoids are spatially limited in their activity by the threat of desiccation, nocturnal parasitoids avoid the threat by being active at night. Parasitoids attacking larval Lepidoptera must search for their hosts feeding on the leaves in the canopy, thus exposing themselves to more intense desiccation stress than ground foraging species. Because La Selva is wetter than BCNM, the activity of parasitoids attacking larval Lepidoptera may be less constrained.

Based on our results, we hypothesize that rainfall synchronizes a taxonomically broad community of parasitoids and is an important driving force of trophic interactions in tropical forests. If, as we suspect, desiccation limits the activity of parasitoids that attack larval Lepidoptera, we predict increasing levels of larval parasitism along a gradient from dry to wet forests, from young to old forest, from the understory to the canopy, from dry to rainy seasons, and from drier to wetter years. If decreased larval parasitism translates into higher host populations, then we subsequently predict higher levels of herbivory in dry forests, second-growth, the canopy, drier months, and El Niño years. Other interactions beyond the scope of this study may mask these broad generalizations. For example, bottom-up effects such as water stress on plants may determine plant phenology and herbivore activity and performance, and thus influence when parasitoids search for hosts (Price *et al.*, 1980; Wright & Cornejo, 1990; Hunter & Price, 1992; Power, 1992; Gutierrez *et al.*, 1994; Hartvigsen *et al.*, 1995; Polis *et al.*, 1997; Gaasch *et al.*, 1998). While dry conditions and consequent lower larval parasitism may lead to increased numbers of hosts for pupal parasitoids, how density-dependent and abiotic factors interact over generations and across entire communities is unclear. Answers to these questions will emerge only with long-term, cross-community comparisons documenting interactions between climate, plants, herbivores and their many parasitoids and predators.

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References

Askew, R.R. & Shaw, M.R. (1986) Parasitoid communities: their size, structure, and development. *Insect Parasitoids* (ed. by K. Waage and D. Greathead), pp. 225-264. Academic Press, London.

Boinski, S. & Fowler, N.L. (1989) Seasonal patterns in a tropical lowland forest. *Biotropica*, **21**, 223-233.

Buskirk, R.E. & Buskirk, W.H. (1976) Changes in arthropod abundance in a highland Costa Rican rainforest. *American Midland Naturalist*, **95**, 288-298.

Coley, P.D. & Barone, J.A. (1996) Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics*, **27**, 305-322.

Darling, D.C. & Packer, L. (1988) Effectiveness of Malaise traps in collecting Hymenoptera: the influence of trap design, mesh size and location. *Canadian Entomologist*, **120**, 787-796.

Dietrich, W.E., Windsor, D.M. & Dunn, T. (1996) Geology, climate, and hydrology of Barro Colorado Island. *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-Term Changes* (ed. by E. G. Leigh, A. S. Rand and D. M. Windsor), pp. 21-46. Smithsonian Institution Press, Washington DC.

Fink, U. & Völkl, W. (1995) The effect of abiotic factors on foraging and oviposition success of the aphid parasitoid, *Aphidius rosae*. *Oecologia*, **103**, 371-378.

Gaasch, C.M., Pickering, J. & Moore, C.T. (1998) Flight phenology of parasitic wasps (Hymenoptera: Ichneumonidae) in Georgia's piedmont. *Environmental Entomology*, **27**, 606-614.

Gauld, I.D. (1987) Some factors affecting the composition of tropical ichneumonid faunas. *Biological Journal of the Linnean Society*, **30**, 299-312.

Gauld, I.D. (1991) The Ichneumonidae of Costa Rica, 1. *Memoirs of the American Entomological Institute*, **47**, 1-589.

Gauld, I.D. & Bolton, B. (1988) *The Hymenoptera*. British Museum (Natural History) and Oxford University Press, Oxford.

Gauld, I.D., Gaston, K.J. & Janzen, D.H. (1992) Plant allelochemicals, tritrophic interactions and the anomalous diversity of tropical parasitoids: the 'nasty' host hypothesis. *Oikos*, **65**, 353-357.

Gentry, A.H. (1990a) Floristic similarities and differences between southern Central American and upper and central Amazonia. *Four Neotropical Rainforests* (ed. by A. H. Gentry), pp. 141-157. Yale University Press, New Haven.

Gentry, A.H. (1990b) *Four Neotropical Rainforests*. Yale University Press, New Haven.

Gutierrez, A.P., Mills, N.J., Schreiber, S.J. & Ellis, C.K. (1994) A physiologically based tritrophic perspective on bottom-up-top-down regulation of populations. *Ecology*, **75**, 2227-2242.

Hartvigsen, G., Wait, D.A. & Coleman, J.S. (1995) Tri-trophic interactions influenced by resource availability: predator effects on plant performance depend on plant resources. *Oikos*, **74**, 463-468.

Hargrove, W.W. & Pickering, J. (1992) Pseudorplication: a *sine qua non* for regional ecology. *Landscape Ecology*, **6**, 251-258.

Hawkins, B.A., Askew, R.R. & Shaw, M.R. (1990) Influences of host feeding-niche and foodplant type on generalist and specialist parasitoids. *Ecological Entomology*, **15**, 275-280.

Heinrich, G.H. (1977) Ichneumonidae of Florida and neighboring states (Hymenoptera: Ichneumonidae, subfamily Ichneumoninae). *Arthropods of Florida and Neighboring Land Areas*, **9**, 1-350.

Hunter, M.D. & Price, P.W. (1992) Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology*, **73**, 724-732.

Hurlbert, S.H. (1984) Pseudoreplication and the design of ecological field experiments. *Ecological Monographs*, **54**, 187-211.

Janzen, D.H. (1973) Sweep samples of tropical foliage insects: Effects of seasons, vegetation types, elevation, time of day, and insularity. *Ecology*, **54**, 687-708.

Janzen, D.H. (1981) The peak in North American ichneumonid species riches lies between 38° and 42°N. *Ecology*, **62**, 532-537.

Janzen, D.H. (1993) Caterpillar seasonality in a Costa Rican dry forest. *Caterpillars: Ecological and Evolutionary Constraints on Foraging* (ed. by N. E. Stamp and T. M. Casey), pp. 448-477. Chapman & Hall, New York.

Janzen, D.H. & Pond, C. (1975) A comparison, by sweeping, of the arthropod fauna of secondary vegetation in Michigan, England, and Costa Rica. *Transactions of the Royal Entomological Society of London*, **127**, 33-50.

Johnson, S.D. (1992) Climatic and phylogenetic determinants of flowering seasonality in the Cape flora. *Journal of Ecology*, **81**, 56-572.

Kato, M., Inou, T., Hamid, A.A., Nagamitsu, T., Merdek, M.B., Nona, A.R., Itino, T., Yamane, S. & Yumoto, T. (1995) Seasonality and vertical structure of light-attracted insect communities in a dipterocarp forest in Sarawak. *Researches on Population Ecology*, **37**, 59-79.

Leigh, E.G. Jr, Rand, A.S. & Windsor, D.M. (1996) *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-Term Changes*. Smithsonian Institution Press, Washington DC.

Leigh, E.G. & Wright, S.J. (1990) Barro Colorado Island and Tropical Biology. *Four Neotropical Forests* (ed. by A. H. Gentry), pp. 28-47. Yale University Press, New Haven, CT.

Matthews, R.W. & Matthews, J.R. (1970) Malaise trap studies of flying insects in a New York mesic forest. I. Ordinal composition and seasonal abundance. *Journal of the New York Entomological Society*, **78**, 52-59.

McDade, L.A., Bawa, K.S., Hespenheide, H.A. & Hartshorn, G.S. (1994) *La Selva: Ecology and Natural History of a Neotropical Rain Forest*. University of Chicago Press, Chicago.

Memmott, J., Godfray, H.C.J. & Gauld, I.D. (1994) The structure of a tropical host-parasitoid community. *Journal of Animal Ecology*, **63**, 521-540.

Nealis, V.G. (1988) Weather and the ecology of *Apanteles fumiferanae* Viereck (Hymenoptera: Braconidae). *Memoirs of the Entomological Society of Canada*, **146**, 57-70.

Novotny, V. & Basset, Y. (1998) Seasonality of sap-sucking insects (Auchenottyncha, Hemiptera) feeding on *Ficus* (Moraceae) in a lowland rain forest in New Guinea. *Oecologia*, **115**, 514-522.

Noyes, J.S. (1988) A study of five methods of sampling Hymenoptera (Insecta) in a tropical rainforest, with special reference to the Parasitica. *Journal of Natural History*, **23**, 299-310.

Paton, S. (1997) *1997 Meteorological and Hydrological Summary for Barro Colorado Island*. Smithsonian Tropical Research Institute, Balboa, Panama.

Polis, G.A., Hurd, S.D., Jackson, T. & Piñero, F.S. (1997) El Niño effects on the dynamics and control of an island ecosystem in the Gulf of California. *Ecology*, **78**, 1884–1897.

Power, M.E. (1992) Top-down and bottom-up forces in food webs: do plants have primacy?. *Ecology*, **73**, 733–746.

Price, P.W., Bouton, C.E., Gross, P., McPheron, B.A., Thompson, J.N. & Weiss, A.E. (1980) Interactions among three trophic levels: Influence of plants on interactions between insect herbivores and natural enemies. *Annual Review of Ecology and Systematics*, **11**, 41–65.

Sanford, R.L., Paaby, P., LuVall, J.C. & Phillips, E. (1994) Climate, geomorphology, and aquatic systems. *La Selva: Ecology and Natural History of a Neotropical Rain Forest* (ed. by L. A. McDade, K. S. Bawa, H. A. Hespenheide and G. S. Hartshorn), pp. 19–33. University of Chicago Press, Chicago.

Schowalter, T.D., Hargrove, W.W. & Crossley, D.A. (1986) Herbivory in forested ecosystems. *Annual Review of Entomology*, **31**, 177–196.

Smythe, N. (1985) The seasonal abundance of night-flying insects in a neotropical forest. *The Ecology of a Tropical Forest. Seasonal Rhythms and Long-Term Changes* (ed. by E. G. Leigh, A. S. Rand and D. W. Windsor), pp. 309–318. Smithsonian Institution Press, Washington, DC.

Southwood, T.R.E. (1978) *Ecological Methods*. Chapman & Hall, London.

Thangavelu, K. (1993) Natural enemies of muga silkworm *Antheraea assama* Westwood (Lepidoptera: Saturniidae). *Journal of Insect Science*, **6**, 57–69.

Townes, H. (1972) A light-weight Malaise trap. *Entomological News*, **18**, 239–247.

Wahl, D.B. & Sharkey, M. (1993) Superfamily Ichneumonoidea. *Hymenoptera of the World: an Identification Guide to Families* (ed. by H. Goulet and J. T. Huber). Canada Communications Group, Ottawa, Canada.

Windsor, D.M. (1990) Climate and moisture variability in a tropical forest: long-term records from Barro Colorado Island, Panama. *Smithsonian Contributions to the Earth Sciences*, **29**, 145.

Wolda, H. (1978) Seasonal fluctuations in rainfall, food, and abundance of tropical insects. *Journal of Animal Ecology*, **47**, 369–381.

Wolda, H. (1988) Insect seasonality: why? *Annual Review of Ecology and Systematics*, **19**, 1–18.

Wolda, H. (1989) Seasonal cues in tropical organisms: Rainfall? Not necessarily! *Oecologia*, **80**, 437–442.

Wright, S.J. & Cornejo, F.H. (1990) Seasonal drought and the timing of flowering and leaf fall in a neotropical forest. *Reproductive Ecology of Tropical Plants* (ed. by K. S. Bawa and M. Hadley). Parthenon Publishing, Cranforth, U.K.