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# Temporal variation in abundance and diversity of butterflies in Bornean rain forests: opposite impacts of logging recorded in different seasons

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**Abstract:** We used traps baited with fruit to examine how the temporal variation of butterflies within primary forest in Sabah, Borneo differed between species. In addition, we compared patterns of temporal variation in primary and selectively logged forest, and we tested the hypothesis that selective logging has different recorded impacts on species diversity of adults during the wet monsoon period and the drier remaining half of the year. Species of Satyrinae and Morphinae had significantly less-restricted flight periods than did species of Nymphalinae and Charaxinae, which were sampled mainly during the drier season, especially in primary forest. Species diversity of adults was significantly higher during the drier season in primary forest, but did not differ between seasons in logged forest. As a consequence, logging had opposite recorded impacts on diversity during wetter and drier seasons: primary forest had significantly higher diversity than logged forest during the drier season but significantly lower diversity than logged forest during the wetter monsoon season. The results of this study have important implications for the assessment of biodiversity in tropical rain forests, particularly in relation to habitat disturbance: short-term assessments that do not take account of seasonal variation in abundance are likely to produce misleading results, even in regions where the seasonal variation in rainfall is not that great.

**Key Words:** biodiversity, fruit feeding, Lepidoptera, Nymphalidae, seasonality, selective logging

## INTRODUCTION

Herbivorous insects in temperate regions display marked temporal variation in abundance and activity, mainly in response to changes in temperature and photoperiod (Speight *et al.* 1999, Wolda 1988). Such variation also occurs in the tropics but is more complex and less well understood, although it is clear that rainfall rather than temperature or photoperiod is more important (Fensham 1994, Louton *et al.* 1996). In tropical regions with distinct wet and dry seasons, many insect species attain maximum adult abundance during the wet season, probably in response to changes in plant physiology and growth (Didham & Springate 2003, Wolda 1989), in particular

the abundance of new foliage (Fensham 1994, Novotny & Basset 1998, Shapiro 1975). In regions with no distinct dry season, adult abundance and activity are generally less variable (Hebert 1980, Wolda & Galindo 1981), although some species still show clear temporal fluctuations in relation to more subtle variations in rainfall and host-plant dynamics (see Didham & Springate 2003 and Wolda 1988 for reviews, Hill *et al.* 2003).

In addition to being related to ecological characteristics, the degree of temporal variation displayed by species is also likely to be constrained by phylogeny. Within the family Nymphalidae, the subfamilies Satyrinae and Morphinae are regarded as being very closely related, forming a single clade, with the subfamilies Nymphalinae and Charaxinae forming a separate grouping along with the mainly neotropical Heliconiinae and Calinaginae (Ackery 1984, Parsons 1999). Species of Satyrinae and Morphinae have narrower geographical distributions on

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average than species of Nymphalinae and Charaxinae (Hamer *et al.* 2003) and also differ in their host plants (Robinson *et al.* 2001). They may additionally differ in their patterns of temporal variation, for instance as a result of phylogenetic variation in host-plant dynamics (Didham & Springate 2003) but this has not previously been examined.

Differences among species in the pattern of temporal variation in abundance could have important implications for comparisons of the diversity and faunal composition of species assemblages between natural and disturbed habitats in different seasons. This may be a particular problem if habitat disturbance affects patterns of temporal variation, for instance due to changes in host-plant dynamics or species composition (Didham & Springate 2003). Such problems are likely to be especially important in tropical regions, where very high species diversity coupled with practical and financial constraints on biodiversity sampling have resulted in increasing emphasis on short-term rapid surveys (e.g. Jones & Eggleton 2000, Kitching *et al.* 2001). For instance, tropical butterflies have been shown to be sensitive to seasonal changes in rainfall (Braby 1995, Hill *et al.* 2003) but there have been few quantitative descriptions of community-wide patterns of butterfly seasonality in tropical rain forests (DeVries *et al.* 1999, Owen & Chanter 1972) and it is not known whether disturbance has different impacts on butterfly assemblages in different seasons.

Within South-East Asia, the greatest impact of habitat disturbance is on forests in the Malay Archipelago, including the island of Borneo. In the Malaysian state of Sabah (northern Borneo), most remaining forest is reserved as production forest and designated to be selectively logged at regular intervals of 30–60 y (Whitmore 1991). By the end of 2010, all remaining forest that is not within conservation areas is likely to have been selectively logged at least once, and there is increasing pressure on remaining areas of forest as timber resources run out.

Butterfly assemblages on Borneo are diverse (*c.* 1000 species; Otsuka 1988) with many endemic species dependent on closed-canopy forest (Beck & Schulze 2000, Collins & Morris 1985, Sutton & Collins 1991). Previous studies of impacts of selective logging on Bornean butterflies have provided conflicting results, reporting both increased and decreased diversity in logged forest (review by Hamer & Hill 2000 for butterflies and moths; Beck & Schulze 2000, Willott *et al.* 2000). This lack of consensus was due mainly to differences in the spatial scale at which studies were carried out (Hamer & Hill 2000, Hill & Hamer 2004), but may also have been due in part to confounding effects of temporal variation in species abundance in different habitats. Hamer *et al.* (2003) showed that butterfly species' associations with

light in primary forest could be used to predict responses to selective logging and thus explain changes in species diversity within rain forest in relation to habitat disturbance. However it was not known how temporal variation in abundance differed between species, or whether responses of species to selective logging differed between seasons.

In this paper we examine the temporal variation in adult abundance of butterfly species, we compare patterns of temporal variation in primary and selectively logged forest, and we test the hypothesis that selective logging has different impacts on species diversity during different seasons of the year.

## METHODS

### Study site and butterfly sampling

Fieldwork took place within the Danum Valley Conservation Area (DVCA) and the Ulu Segama Forest Reserve, Sabah (5°N, 117°50' E; details of sites in Marsh & Greer 1992). The DVCA covers approximately 428 km<sup>2</sup> of unlogged lowland evergreen rain forest and is surrounded by extensive areas of production forest, most of which have been selectively logged. During the 1980s, logging methods in the study area followed a modified uniform system (Whitmore 1984) in which all commercial stems > 0.6 m diameter were removed using high lead cable and tractor extraction methods. Temperature at the study area (annual mean = 26.7 °C) is typical of the moist tropics (Walsh & Newbery 1999). Rainfall is usually > 100 mm every month (as is typical of evergreen rain forest; Whitmore 1991) but there is nonetheless regular seasonal variation, with significantly higher rainfall occurring during the northerly monsoon period (October–January, in some years extending into September and February; mean = 255.1 mm mo<sup>-1</sup>, SD ± 40.5, n = 6 mo), than during the remaining half of the year (March–August; mean = 189.7 mm mo<sup>-1</sup>, SD ± 38.0, n = 6 mo; t-test using equal variance estimate;  $t_{10} = 2.88$ ,  $P = 0.02$ ; data are monthly means for the period 1985 to 1998, from Table 2 in Walsh & Newbery 1999).

It is difficult to identify butterflies reliably when they are in flight in species-rich areas such as Borneo (Walpole & Sheldon 1999), and so we focused on the guild of fruit-feeding nymphalid butterflies that can be caught in traps baited with rotting fruit (this guild comprises approximately 75% of all nymphalid butterflies recorded on Borneo; Hamer *et al.* 2003, Hill *et al.* 2001). In this study we used traps baited with rotting banana (see Daily & Ehrlich 1995 and DeVries 1987 for details of trap design). Two fresh bananas were placed in each trap on the day prior to the first sampling day, and were left in the trap for the rest of the sampling period; a fresh

piece of banana was then added to each trap every second day. This ensured that all traps contained a mixture from fresh to well-rotted bait. During each sampling period, traps were emptied daily, and all trapped butterflies were identified (following Otsuka 1988 and Tsukada 1982), marked with a felt-tipped pen and released. All recaptures were excluded from statistical analyses. Individuals of the genera *Euthalia* and *Tanaecia* cannot be identified reliably in the field and were killed by thoracic compression, collected and identified in the laboratory using keys and figures in Corbet & Pendlebury (1992) and Otsuka (1988); where necessary, this included dissection of male genitalia. Mounted specimens and dissected genitalia are housed in the Institute of Tropical Biology and Conservation, Universiti Malaysia Sabah.

### Temporal variation in abundance within primary forest

To examine the temporal variation in abundance of individual species in primary forest, we hung 40 traps at 100-m intervals along 4 km of transects (see Hill 1999 for map showing locations). These were set up along straight lines on cardinal compass directions (N–S and E–W) irrespective of topography and sampled a representative range of variation in forest structure and vegetation (Hamer *et al.* 2003). We sampled butterflies on 12 successive days per mo for 12 mo (October 1999 to September 2000 inclusive) and we used monthly abundance data to calculate two indices of temporal variation in abundance. Firstly, following recommendations of Batschelet (1981) and Zar (1999) for analysing data with circular distributions (because the first and last months of the year are consecutive), the abundance of each species each month was converted into polar coordinates and these were used to calculate a mean vector for each species (using equations 26.6–26.8 in Zar 1999; hereafter termed temporal clumping index), which varied from 0 (when individuals of a species were dispersed evenly across the year) to 1.0 (when all individuals of a species were sampled in a single month). This index allowed us to quantify the degree of temporal variation in flight periods of each species during the year of study, but provided no information on the type of variation with respect to rainfall. To provide this information, for every species we calculated the proportion of individuals recorded during the wetter half of the year (September–February) and used this as an index of each species' wet-season preference. These months were chosen a priori on the basis of long-term rainfall data from DVFC (see above) and moving the boundaries between wet and dry seasons by a month in either direction did not qualitatively affect the results. All analysis of temporal variation was restricted to species where  $N \geq 12$  (i.e. one or more individuals sampled per month on average).

### Impacts of selective logging

To examine the impacts of selective logging on species diversity during different seasons, we hung an additional 40 traps at 100-m intervals along 4 km of transects in forest selectively logged 10–12 y previously. These were sampled on the same days as the 40 traps in primary forest. Primary and logged forest were at similar altitudes within the same river catchment and the maximum distance between traps in primary and logged forest was < 10 km. Thus there was likely to have been little difference between habitats in species diversity or faunal composition prior to logging. In logged areas, we avoided logging roads, which we considered to be non-forest habitats, but we included skid trails (formed by bulldozers pulling out logs) where transects crossed them.

Following recommendations and formulae in Magurran (1988) and Lande (1996), we examined species diversity using Simpson's and Shannon's diversity indices ( $\lambda$  and  $H$  respectively). These both combine species richness and relative abundance into a single index: Simpson's index, expressed as  $1-\lambda$ , measures the probability that two randomly chosen individuals from a given community are different species, and is weighted towards the most abundant species in the sample; Shannon's index places greater emphasis on species richness and is less strongly affected by the most abundant species (Hurlbert 1971, Magurran 1988). Both indices are largely independent of species abundance distributions and are unaffected by variation in sample size provided  $2N$  greatly exceeds the total number of species present (Lande 1996), as was the case for all analyses in this study ( $N > 900$  for all diversity analyses whereas the total number of species of Nymphalidae on Borneo  $\approx 210$ ; Otsuka 1988; see Appendix 1 for values of  $N$ ).

In order to test for differences in diversity between primary and logged forest during wet and dry periods, we used two-way analysis of variance of diversity each month, including a term for the interaction between habitat and time of year (wet or dry period). The same transects were used repeatedly in this study but there were very few between-month recaptures and so each month's data could be considered independent of those for previous or subsequent months. Nonetheless, to check that repeated sampling was not a problem, we also used a repeated-measures general linear model to examine the interaction between habitat and time of year: this analysis used within-subjects contrasts to account for temporal pseudoreplication. In addition, to examine whether or not the results obtained depended on the temporal scale at which the data were analysed, we also calculated total diversity over each 6-mo period, used bootstrap methods to calculate standard errors for each index (Sokal & Rohlf 1995) and compared between habitats using pair-wise randomization tests

based on 10 000 re-samples of species abundance data, following Solow (1993). This test calculates the observed difference in diversity between samples ( $\delta$ ) and assesses the significance of this value from its position among the ordered values of  $\delta$  found by randomization. Specifically, for a two-tailed test, the estimated P-value is given by the proportion of re-samples with values of  $\delta$  greater than the observed value (Solow 1993). This is an exact test, in that the nominal significance level is equal to the actual rate of false rejection of the null hypothesis.

## RESULTS

### Temporal variation in abundance within primary forest

Excluding recaptures, we sampled 2061 individuals of 55 species from 40 sampling stations in primary forest (Appendix 1). The most abundant species (*Mycalesis orontis*) comprised 18.6% of individuals and 11 species (20%) were represented by a single individual. The number of months in which each species was sampled was strongly correlated with its abundance (Spearman correlation;  $r_s = 0.98$ ,  $n = 54$ ,  $P < 0.001$ ). Thus although the median cumulative sum of species' presence was only 4.5 mo, all of the commonest species ( $N \geq 12$  within primary forest) were present for most of the year (median = 11 mo,  $n = 21$  species, interquartile range = 4.0).

Even though there were only few months when the commonest species were not recorded, there was nonetheless substantial variation between months in the abundance of these species within primary forest (mean coefficient of variation [ $SD \times 100/\text{mean}$ ] = 93.1%,  $n = 21$ ,  $SD \pm 48.9$ ). This variation ranged from species being spread more or less evenly across the year to species having highly clumped occurrence (mean temporal clumping index = 0.31,  $n = 21$ ,  $SD \pm 0.23$ , range = 0.01–0.84). Species of Satyrinae and Morphinae had significantly lower variation in abundance than did Nymphalinae and Charaxinae (Table 1; t-test for arcsine-transformed data;  $t_{19} = 2.9$ ,  $P < 0.05$ ). In terms of rainfall preference, there was a highly significant difference between taxa in the proportion of individuals recorded during the wet season (Table 1; t-test for arcsine-transformed data;  $t_{19} = 5.4$ ,  $P < 0.001$ ): Nymphalinae

and Charaxinae were much more abundant during the drier half of the year (March–August) than the wetter half (September–February) whereas Satyrinae and Morphinae had slightly higher abundance during the wetter half of the year (Table 1).

### Impacts of logging on seasonality

We recorded 1019 individuals of 41 species in primary forest plus 920 individuals of 43 species in logged forest during the wetter half of the year, and we recorded 1042 individuals of 48 species in primary forest plus 980 individuals of 50 species in logged forest during the drier half of the year (Appendix 1). There was a significant positive relationship between temporal clumping index in natural and logged forest both for Satyrinae and Morphinae (stepwise linear regression with index in logged forest as the dependent variable, for species where  $N \geq 12$  in both habitats, using arcsine-transformed data with constant of zero;  $F_{1,9} = 19.7$ ,  $P < 0.01$ ) and for Nymphalinae and Charaxinae ( $F_{1,6} = 403$ ,  $P < 0.001$ ). For Nymphalinae and Charaxinae, the slope of this relationship (0.72,  $SE \pm 0.036$ ) was significantly lower than 1 ( $t_5 = 7.8$ ,  $P < 0.01$ ), indicating significantly greater temporal clumping in primary forest. For Satyrinae and Morphinae, however, the slope (1.5,  $SE \pm 0.34$ ) was not different to 1 ( $t_9 = 1.5$ ,  $P > 0.1$ ), indicating the same pattern of temporal variation in the two habitats.

### Seasonal impacts of logging on species diversity

There was no overall difference in diversity between habitats ( $P > 0.3$  for Simpson's and Shannon's diversity indices). However both indices were significantly higher during months in the drier half of the year (Table 2; two-way ANOVA by time-of-year and habitat; Simpson's index,  $F_{1,20} = 5.2$ ,  $P < 0.05$ ; Shannon's index,  $F_{1,20} = 5.4$ ,  $P < 0.05$ ). There was also a significant time-of-year by habitat interaction ( $F_{1,20} = 4.8$ ,  $P < 0.05$  and  $F_{1,20} = 5.1$ ,  $P < 0.05$  respectively); primary forest was more diverse than logged forest during months in the drier season whereas logged forest was more diverse than primary forest during months in the wetter season (Table 2). This interaction was confirmed by a repeated-measures general linear model (within-subjects contrast for habit by time-of-year interaction:  $F_{1,10} = 24.9$ ,  $P = 0.001$  and  $F_{1,10} = 24.4$ ,  $P = 0.001$  for Simpson's index and Shannon's index respectively).

Combined diversity over each half of the year showed a similar pattern to diversity each month (Table 2): both indices were significantly higher in primary forest over the drier season ( $\delta = -2.47$ ,  $P = 0.001$  and  $\delta = -0.19$ ,  $P < 0.001$  for Simpson's and Shannon's index respectively) but significantly higher in selectively logged

**Table 1.** Indices of temporal clumping and wet-season preference for butterflies in primary forest in Sabah, Borneo.

	Satyrinae and Morphinae		Nymphalinae and Charaxinae	
	mean $\pm$ SD	n	mean $\pm$ SD	n
Temporal clumping	0.24 $\pm$ 0.18	12	0.47 $\pm$ 0.31	9
Wet season preference	0.57 $\pm$ 0.10	12	0.28 $\pm$ 0.15	9

n is the number of species in each case.

**Table 2.** Species diversity of butterflies in primary and selectively logged forest during wet and dry seasons in Sabah, Borneo. See text for rainfall during the two seasons.

Temporal scale	Season	Simpson's index		Shannon's index	
		Primary	Logged	Primary	Logged
		Mean $\pm$ SE	Mean $\pm$ SE	Mean $\pm$ SE	Mean $\pm$ SE
Monthly	wet	0.87 $\pm$ 0.011	0.89 $\pm$ 0.017	2.41 $\pm$ 0.08	2.57 $\pm$ 1.04
	dry	0.92 $\pm$ 0.007	0.89 $\pm$ 0.009	2.77 $\pm$ 1.12	2.57 $\pm$ 1.05
6-monthly	wet	0.89 $\pm$ 0.005	0.91 $\pm$ 0.005	2.64 $\pm$ 0.08	2.80 $\pm$ 0.07
	dry	0.93 $\pm$ 0.003	0.91 $\pm$ 0.005	3.01 $\pm$ 0.07	2.82 $\pm$ 0.08

forest over the wetter season ( $\delta = 1.53$ ,  $P = 0.01$  and  $\delta = 0.16$ ,  $P < 0.01$  respectively). Hence the results were not qualitatively affected by the temporal scale at which the data were analysed or by the different weighting given by Simpson's and Shannon's indices to the commonest species in the sample.

Seasonal differences in impacts of logging on species diversity were accompanied by seasonal differences in faunal composition in the two habitats. Within primary forest, Satyrinae and Morphinae comprised 56% of species and 79% of individuals during the wet season but only 50% of species and 59% of individuals during the dry season ( $\chi^2$  test for number of individuals;  $\chi^2_1 = 95.1$ ,  $P < 0.001$ ) whilst in logged forest, they comprised 54% of species and 74% of individuals during the wet season but only 44% of species and 62% of individuals during the dry season ( $\chi^2_1 = 30.8$ ,  $P < 0.001$ ; Appendix 1). Hence Nymphalinae and Charaxinae comprised a greater proportion of species and individuals during the drier season than during the wet season, especially in primary forest.

## DISCUSSION

### Collection of data

During the study, we caught a total of 3961 individuals from 62 species, which represents  $> 80\%$  of the fruit-feeding species that have been recorded at the study site. This species richness is similar to that recorded using similar methods at other sites in Sabah (Schulze & Fiedler 1998, Schulze *et al.* 2001). Although traps catch only one guild of butterflies, and species in other guilds may have different patterns of temporal variation (Orr & Häuser 1996), traps avoid the problems of species identification that can be encountered using walk-and-count transect techniques in highly diverse regions (Walpole & Sheldon 1999). As in previous studies (DeVries *et al.* 1999, Novotny & Basset 1998, Schulze & Fiedler 2003), we have assumed that temporal variation in adult abundance reflects similar variation (though not necessarily the same timing of peak abundance) for all developmental stages of species. There are currently few data available to confirm this, but support comes from studies showing

that changes in adult abundance are related to climate variables affecting immature stages (Hill *et al.* 2003), and thus we are confident that our results for adults reflect the phenology of species during the study.

Observed differences in relative abundance among species could in part have reflected differences in attraction to traps (Davis & Sutton 1997, Hughes *et al.* 1998) but this is unlikely to have affected the relative abundance of individual species in different months. Nor were our data affected by variation in the availability of natural fruit within the forest, because this did not differ between months in either habitat during the sampling period (Mustaffa 2001). Observed patterns of temporal variation could nonetheless have reflected variation in adult activity in addition to abundance, because rainfall suppresses the flight activity of most species. However this was unlikely to have been a marked effect because rain was generally restricted to the second half of the afternoon during even the wettest months, and traps were left open continuously. Some species of Satyrinae and Morphinae have a peak in flight activity during the late afternoon, but these are generally strong flyers and are active even in heavy rain (Schulze & Fiedler 1998; pers. obs.).

We sampled over an entire year, but our results should nonetheless be viewed with some caution, because we could not account for possible variation between years in the pattern of temporal variation displayed by individual species. For instance, there may be different patterns of variation in years with prolonged droughts associated with El Niño events (Hill 1999, Hill *et al.* 2003). However we sampled during a period of typically high rainfall (annual total = 3399 mm, compared with a long-term average of 2669 mm  $y^{-1}$ ; Walsh & Newbery 1999). Moreover our results were qualitatively independent of the temporal scale at which the data were analysed, indicating that species were responding more to the general pattern of seasonality of rainfall and host-plant dynamics than to the particular weather conditions during each month of sampling.

### Temporal variation in abundance

Compared with temperate species, tropical insects tend to have longer activity periods with less well defined

seasonal peaks and a higher proportion of species active throughout the year, particularly in areas lacking a pronounced dry season (Orr & Häuser 1996, Wolda 1988). Our data were consistent with this pattern: most species that were sampled in adequate numbers ( $N \geq 12$ ) were present as adults for most of the year, and the mean index of temporal clumping was relatively low (see Results). There was, however, substantial variation, with some species having highly clumped occurrence, as was also found for other taxa in relatively non-seasonal tropical climates (Wolda & Broadhead 1985, Wolda & Fisk 1981). There were few recaptures of individuals between months in our study, which suggests that long activity periods resulted mainly from overlapping of successive generations rather than long adult life spans, although data concerning life spans of tropical butterflies are lacking (Beck & Schulze 2000).

Species of Satyrinae and Morphinae had less-restricted flight periods than did species of Nymphalinae and Charaxinae, which were sampled mainly during the drier half of the year (Table 1) and had significantly more clumped occurrence in primary forest than in logged forest. These patterns may be explained by differences in the usage of rain forest microhabitats by species in different taxa: species of Satyrinae and Morphinae have a strong preference for dense shade at ground level (Hamer *et al.* 2003, Hill *et al.* 2001) and such species included in this study primarily feed as larvae on shade-tolerant grasses and bamboos (Poaceae), gingers (Zingiberaceae) and Selaginellaceae (Robinson *et al.* 2001). Conversely, species of Nymphalinae and Charaxinae occur more often in the canopy or at ground level in gaps, and exploit a wider variety of relatively shade-intolerant vines, trees and shrubs. The different patterns of temporal variation in the two butterfly taxa could therefore have resulted from differences in host-plant dynamics and in the impact of logging on the dynamics and species composition of host-plants in different microhabitats (Hamer *et al.* 2003). The different patterns could also have arisen from seasonal variation in larval mortality in different microhabitats (D'Amico & Elkington 1995) and further data are needed to address this question.

### Seasonal variation in species diversity and faunal composition

Community-wide patterns of diversity and faunal composition differed significantly between seasons, even though the seasonal variation in rainfall was not that great: species diversity was significantly higher during the drier season within primary forest (Table 2), primarily due to a greater abundance of Nymphalinae and Charaxinae (Table 1), whereas there was no difference between seasons in logged forest (Table 2). As a consequence, selective logging had opposite effects on diversity in

different seasons (Table 2). This emphasizes the need for biodiversity assessments to cover a sufficiently long period to account for seasonal variation in species abundance in different habitats.

The difference in diversity between wet and dry seasons was evident only in primary forest (Table 2). Previous studies have indicated that one of the main impacts of habitat modification such as selective logging is to reduce the spatial heterogeneity within forests (Hamer & Hill 2000, Hamer *et al.* 2003), and the results of this study indicate a similar effect on temporal heterogeneity.

In the face of rapid and widespread habitat modification, emphasis increasingly is being placed on rapid assessments of biodiversity in natural and managed tropical forests, where a lack of resources combined with exceptionally high diversity make full species inventories difficult to achieve (Jones & Eggleton 2000, Kitching *et al.* 2001). Such assessments have typically focused on insects and other invertebrates, which respond more rapidly than vertebrates to disturbance and may be much more important than vertebrates for the maintenance of vital ecosystem processes (Liow *et al.* 2001, Wilson 1987). However our findings suggest that short-term assessments that do not take account of temporal variation in abundance will be misleading, even in regions where there is no pronounced dry season, and so reliable rapid assessment techniques may prove elusive.

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**Appendix 1.** Butterfly species sampled in fruit-baited traps in primary and selectively logged forest during wet and dry seasons in Sabah, Borneo. Data are numbers of individuals of each species, excluding recaptures, in taxonomic order following Otsuka (1988).

	Wet season		Dry season			Wet season		Dry season	
	Primary	Logged	Primary	Logged		Primary	Logged	Primary	Logged
Satyrinae					32. <i>Thaumantis noureddin</i> West.	0	1	1	2
1. <i>Melanitis leda</i> L.	15	33	10	6	33. <i>Discophora necho</i> Felder	16	21	29	36
2. <i>M. zitenius</i> Herbst	0	0	3	1	Nymphalinae				
3. <i>Elymnias panthera</i> Fabricius	0	2	1	0	34. <i>Cupha erymanthis</i> Drury	1	0	1	1
4. <i>E. dara</i> Distant and Pryer	0	0	0	2	35. <i>Cirrochroa emalea</i> Guerin	2	0	14	2
5. <i>Neorina lowii</i> Doub.	133	133	92	154	36. <i>Paduca fasciata</i> Felder	0	4	2	3
6. <i>Lethe dora</i> Staudinger	1	0	0	0	37. <i>Terinos clarissa</i> Boisduval	1	0	0	0
7. <i>Mycalesis anapita</i> Moore	21	60	26	22	38. <i>Kallima limborgi</i> Moore	3	7	2	11
8. <i>M. patiana</i> Eliot	10	8	4	2	39. <i>Rhinopalpa polynice</i> Cram.	4	1	7	1
9. <i>M. fusca</i> Felder	0	3	1	2	40. <i>Neptis hylas</i> L.	0	0	1	0
10. <i>M. kina</i> Staudinger	39	27	35	12	41. <i>N. harita</i> Moore	0	0	1	0
11. <i>M. janardana</i> Moore	0	0	0	6	42. <i>Athyma pravara</i> Moore	2	1	0	1
12. <i>M. dohertyi</i> Elwes	37	9	29	17	43. <i>A. reta</i> Moore	0	1	1	0
13. <i>M. mineus</i> L.	2	1	0	0	44. <i>Parthenos sylvia</i> Cramer	0	1	0	0
14. <i>M. horsfieldi</i> Moore	1	5	0	1	45. <i>Tanaecia pelea</i> Fabric.	0	1	4	0
15. <i>M. orseis</i> Hewit.	74	109	42	110	46. <i>T. clathrata</i> Vollenhoven	1	1	2	1
16. <i>M. maianae</i> Hewit.	51	72	45	72	47. <i>T. aruna</i> Felder	19	26	37	44
17. <i>M. oroatis</i> Hewit.	229	1	154	0	48. <i>Euthalia iapis</i> Godart	0	2	3	4
18. <i>Erites argentina</i> Butler	1	0	1	2	49. <i>E. monina</i> Fabric.	0	3	1	1
19. <i>E. elegans</i> Butler	7	7	0	5	50. <i>Dophla evelina</i> Stoll	20	7	25	9
20. <i>Ragadia makuta</i> Horsfield	144	149	106	126	51. <i>Bassarona teuta</i> Doub.	14	21	24	13
21. <i>Ypthima pandocus</i> Moore	0	0	0	1	52. <i>B. dunya</i> Doub.	79	103	102	128
Morphinae					53. <i>Lexias dirtea</i> Fabricius	2	3	25	14
22. <i>Faunis gracilis</i> Butler	0	0	1	0	54. <i>L. pardalis</i> Moore	2	14	38	63
23. <i>F. canens</i> Hubner	0	0	0	2	55. <i>L. canescens</i> Butler	0	0	10	3
24. <i>F. kirata</i> de Niceville	0	0	0	3	56. <i>Amnosia decora</i> Doub.	4	10	5	12
25. <i>F. stomphax</i> West.	1	0	2	1	57. <i>Dichorragia nesimachus</i> Do.	2	5	3	1
26. <i>Xanthotaenia busiris</i> West.	1	2	7	2	Charaxinae				
27. <i>Amathusia phiddippus</i> L.	2	6	4	5	58. <i>Prothoe franck</i> Godart	51	30	103	54
28. <i>Amathuxidia amythaon</i> Doub.	2	1	5	3	59. <i>Agatasa calydonia</i> Hewit.	0	3	3	6
29. <i>Zeuxidia aurelius</i> Cramer	13	9	7	4	60. <i>Polyura athamas</i> Drury	0	0	0	1
30. <i>Z. amethystus</i> Butler	3	10	8	3	61. <i>Charaxes bernardus</i> Fabric.	6	0	12	4
31. <i>Z. doubledayi</i> West.	2	7	3	1	62. <i>C. durnfordi</i> Distant	1	0	0	0