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Rainfall but not selective logging affect changes in abundance of a tropical forest butterfly in Sabah, Borneo

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Abstract: We investigated the effects of rainfall on the distribution and abundance of the satyrine butterfly *Ragadia makuta* in selectively logged and unlogged forest on Borneo. In 1997–98, there was a severe El Niño–Southern Oscillation (ENSO) drought, and annual surveys over a 4-y period showed that abundance of *R. makuta* was greatly reduced during the drought, but that populations quickly recovered after it. Monthly surveys over a 12-mo period of typical rainfall showed that high rainfall in the month preceding surveys significantly reduced butterfly abundance. Butterfly abundance and distribution did not differ between selectively logged and unlogged areas in either monthly or annual surveys and there was no difference between selectively logged and unlogged areas in the pattern of post-drought recovery. These results indicate that the abundance of *R. makuta* was significantly reduced both after high rainfall and during severe drought, but that these impacts were short-lived and were not affected by habitat disturbance. ENSO droughts on Borneo naturally often lead to widespread forest fires and thus impacts of ENSO events for butterflies are more likely to be due to indirect effects of habitat loss, rather than direct effects of drought on butterfly population dynamics.

Key Words: climate change, drought, ENSO, habitat disturbance, Lepidoptera, *Ragadia makuta*, Satyrinae

INTRODUCTION

Throughout tropical regions, rain forests are rapidly being logged (Collins *et al*. 1991). This disturbance to tropical forests and its impact on global biodiversity are areas of current concern (Fimbel *et al*. 2001, Groombridge & Jenkins 2000, Lawton *et al*. 1998). Over half of diversity in terms of number of species is represented by insects (Ødegaard 2000) and within this group, tropical butterfly communities are diverse with many endemic species dependent on closed-canopy forest (Collins & Morris 1985, Sutton & Collins 1991). In temperate regions, year-to-year fluctuations in butterfly populations are well known (Pollard & Yates 1993), and spatial synchrony in these fluctuations over large areas indicates the importance of climate in affecting insect abundance (Hanski & Woiwod 1993, Roy *et al*. 2001, Sutcliffe *et al*. 1996). In contrast to temperate regions, tropical regions experience little variation in either temperature or photoperiod, and changes in rainfall are the most important factors affecting seasonality. Butterflies have been shown to be sensitive to environmental gradients in tropical regions (Kremen 1992) particularly in those parts of the tropics with well-defined wet and dry seasons (Braby 1995, Owen 1971, Spitzer *et al*. 1993). However, it is not known if populations in regions that are generally considered to be aseasonal, such as Borneo (Marsh & Greer 1992), also fluctuate in response to rainfall. In addition, most studies investigating effects of forest disturbance on tropical insect populations have taken place over relatively short periods, during which time environmental conditions have been more or less constant. These studies have not considered the potential interactive effects of forest disturbance and climate on species distributions; for example, whether populations in unlogged and logged forest are equally sensitive to changes in climate.

In 1997–98, an El Niño–Southern Oscillation (ENSO) event occurred which was associated with a widespread and prolonged drought in South-East Asia. This ENSO event was the most severe on record, and future climate-change scenarios predict that these droughts will become more extreme (IPCC 2001). Many satyrine butterfly species of tropical lowlands are known to be particularly sensitive to changes in humidity (Braby 1995). In this paper, we investigate the effects of rainfall on the spatial distribution and abundance of the satyrine butterfly *Ragadia makuta* Horsfield 1829 in lowland dipterocarp forest in Sabah, Borneo. In the absence of ENSO droughts, this

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region experiences relatively little variation in rainfall and rainfall is consistently high (generally >100 mm mo^{-1}), typical of the moist 'aseasonal' tropics (Marsh & Greer 1992). Few butterfly species are present in large enough numbers for the type of study described here; most common species are either widespread 'weedy' species of low conservation value, or migrants. *Ragadia makuta* is an exception to this pattern; it is relatively abundant but its geographical distribution is restricted to Sundaland (Java, Borneo, Sumatra, Malay Peninsula) and thus it has relatively high conservation value. In addition, this species is confined to the forest understorey (Corbet & Pendlebury 1992, Hill 1999, Hill *et al.* 2001), suggesting that it may be particularly vulnerable to habitat disturbance which opens up the canopy. A previous study on *R. makuta* carried out during the 1997 drought indicated a reliance on damp micro-habitats (Hill 1999) where its larval host plant *Selaginella* spp. occurs (Igarashi & Fukuda 1997, 2000). This suggests that populations may be sensitive to changes in rainfall and that they may have difficulty recovering from drought, particularly in more open forest. In this paper, we study annual changes in the distribution and abundance of *R. makuta* over a 4-y period (1996–1999) spanning the ENSO drought. We also investigate monthly changes in butterfly distribution and abundance in relation to rainfall over a period (March 1999–February 2000) of typical rainfall. We investigate impacts of selective logging on the recovery of populations from the effects of a severe drought and the sensitivity of populations to short-term changes in rainfall by comparing populations in unlogged forest with those in forest selectively logged during 1988–1989.

MATERIALS AND METHODS

Study site

Fieldwork took place at Danum Valley Field Centre, adjacent to the Danum Valley Conservation Area (DVCA) and the Ulu Segama Forest Reserve, Sabah, Borneo (5°N, 117°50′E). The study area is within lowland evergreen dipterocarp rain forest (see Marsh & Greer (1992) for a detailed description of the site), and average rainfall (2822 mm y^{-1}) is typically high. The Danum Valley Conservation Area covers approximately 428 km^2 of protected unlogged forest (Collins *et al.* 1991), 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 cables and tractors. Rainfall data from May 1996–February 2000 were obtained from a meteorological station at the Danum Valley Field Centre.

Survey techniques

Butterflies were sampled at 81 observation stations along existing trails in two areas of forest: undisturbed forest in DVCA and forest that had been selectively logged in 1988–1989. Observation stations were marked at 100-m intervals along transects and there were two transects in each habitat (unlogged forest: 41 stations, transects 1 and 2, total length 4.3 km; logged forest: 40 stations, transects 3 and 4, total length 4.2 km). Butterflies were surveyed along transects using a combination of point-count techniques and walk-and-count techniques modified from methods developed in temperate regions by Pollard (1977), and were similar to methods used in previous tropical studies (Hamer *et al.* 1997, Hill 1999, Hill *et al.* 1995). All butterflies observed during a 5-min period were recorded within a 10-m radius of stations, and all butterflies seen within 5 m either side of the path were also recorded while a single observer was walking between stations. Surveys were carried out between 10h00 and 14h00 (corresponding with peak flight activity), and only during sunny weather. In all analyses, data were analysed on a station-by-station basis; total numbers of butterflies recorded at each station also included butterflies seen within 5 m of paths either side of each station. Care was taken to avoid recording the same individual more than once. However, it is possible that abundance data may include multiple sightings, but these will occur similarly across habitats and years and so are unlikely to affect interpretation of results. In highly heterogeneous landscapes, as occur at the study site, it is essential to have good spatial and temporal replication. In this study, 81 observation stations covering an area of > 10 ha were surveyed intensively over a 12-mo period and annually over a 4-y period. This ensured that a wide range of microhabitats and environmental conditions was sampled.

Survey periods

Annual surveys In order to investigate the impacts of the ENSO drought, butterfly data were collected at all 81 observation stations by JKH from August to October 1997, 1998 and 1999. Fieldwork in 1997 coincided with a severe drought associated with the 1997–98 ENSO event, and the drought persisted at the study site until the beginning of May 1998. Fieldwork in 1998 and 1999 took place approximately 4 mo and 17 mo, respectively, after the drought had ended. Abundance of *R. makuta* was also measured before the drought during a period of normal rainfall in September 1996, at 65 of the 81 observation stations used in 1997–1999. All surveys were repeated four times in each year, and data for each year were then combined for analysis. Vegetation data (see below) were collected only in 1997, and so habitat quality for *R. makuta* was determined using data from 1997. Most of the year-by-year analyses are carried out using the main dataset from 1997–1999 from 81 observation stations.

Monthly surveys In order to investigate short-term changes in butterfly distribution and abundance, data were collected monthly at 80 of the 81 observation stations from March 1999 to February 2000 during a period of normal rainfall. Each survey was repeated twice by MMD and JT in each month (total of four surveys per month), and data for each month were then combined for analysis. Forward stepwise multiple regression was used to investigate the relationship between butterfly abundance and six rainfall variables; rainfall during the month of the survey, rainfall during the previous month, and rainfall 2 mo, 3 mo, 4 mo and 5 mo previously. These periods were chosen to cover the survey periods as well as the likely duration of the development period of the generation giving rise to adults recorded on surveys.

Determining the distribution of suitable habitat

Hill (1999) quantified the habitat requirements of *R. makuta* at the study site in 1997, and we will only briefly describe the methods here. Habitat requirements of *R. makuta* were quantified in unlogged forest (41 stations). The following vegetation data were recorded within a 30-m radius of every observation station: number, circumference at breast height, and distance from station of 10 nearest trees (excluding trees with circumference less than 0.6 m at breast height); estimated vegetation cover (%) at ground, low (2 m above ground), understorey and canopy levels. Because these measurements are highly correlated, they were analysed by a principal components analysis (PCA; Norusis 1992). Percentage cover of larval host plant (*Selaginella* spp., Fukuda 1983) within 10 m of every station and distance (m) to nearest stream were also measured at every station. Hill (1999) used forward, stepwise logistic regression to relate presence/absence of *R. makuta* in unlogged forest (41 stations) to five independent habitat variables; the first three factor scores from the PCA (which accounted for 75% of the variability in the data set), distance to nearest stream and percentage cover of larval host plant, *Selaginella* spp.

In this paper, we use the regression equation from the logistic model derived in unlogged forest in 1997 to calculate the predicted probability of *R. makuta* being present at each of the 81 stations in both selectively logged and unlogged forest in 1998 and 1999. Habitat data were collected only in 1997 but it is unlikely that the habitat variables measured in this study differ markedly among years, and so we use this probability of occurrence in 1997 as an index of habitat quality for *R. makuta* at each station. We then investigate changes in the post-drought distribution of *R. makuta* in logged and unlogged habitats in relation to the availability of suitable breeding habitat as measured by the index of habitat quality. Unless otherwise stated, we only present significant results.

RESULTS

Rainfall

Table 1 shows rainfall for 5 mo each year (May to September) from 1996 to 1999. This 5-mo period was chosen to cover the survey period as well as the development time of the generation giving rise to adults present during the surveys. In Sabah, drought months have been defined as those with < 100 mm rain (Walsh 1996). The exact start of the drought period at Danum Valley was not clear, but rainfall data show that between March 1997 and May 1998, there were 5 mo with < 100 mm of rain (March, June and September 1997, March and April 1998), and all but 1 mo during this period had < 70% of normal monthly rainfall. During the study period in 1997, there were 36–43% fewer raindays each month, and 29–45% less rainfall compared with other years. The number of consecutive days without rain was also significantly greater in 1997 (maximum of nine consecutive days without rain in May 1997), than in other years. Rainfall during 1998 and 1999 was similar to that in 1996, before the drought (Table 1). During the monthly surveys (March 1999 to February 2000), total monthly rainfall at the study site ranged from 144.8 mm (September 1999) to 489.4 mm (January 2000; 12-monthly mean = 288.7, SD = 100.0). Rainfall during this period was typically high and similar to the normal average of 233 mm mo^{-1} (Douglas *et al.* 1992).

Drought and yearly butterfly abundance

Coinciding with the drought in 1997, the distribution and abundance of *R. makuta* was significantly reduced in 1997, compared with other years (Wilcoxon matched-pairs, signed-ranks test; 1998 vs. 1997, $Z = -5.88$, $P < 0.001$; 1999 vs. 1997, $Z = -5.36$, $P < 0.001$). After the drought, *R. makuta* was between 2.5 times (1999) and 4.3 times (1998) more abundant than in 1997 (1997, mean = 0.7 individuals per station, SD = 1.1, total recorded = 60 individuals; 1998, mean = 3.2, SD = 4.2, total recorded = 260; 1999, mean = 1.9, SD = 1.7, total recorded = 153). There was no difference in abundance before and after the drought (comparing 1998 with 1996; Wilcoxon matched-pairs, signed-ranks test, $Z = -1.32$, $N = 65$, $P = 0.19$), or in the number of stations occupied ($\chi^2 = 1.52$, 1 df, $P = 0.22$), indicating that 4 mo after the end of the drought, the distribution and abundance of *R. makuta* had returned to pre-drought levels.

The distribution of *R. makuta* increased after the drought, with 28 stations colonized between 1997 and 1998. In our analyses, we use the terms colonization and

Table 1. Rainfall data from Danum Valley Field Centre during May–September from 1996 to 1999. 'Drought days' = number of consecutive days without rain (mean and maximum over the 5-mo period). Means followed by a different superscript letter are significantly different at the 5% level.

	Monthly rainfall (mm)		Number of raindays per month		Drought days	
Year	Mean (SD)	Total	Mean (SD)	Total	Mean (SD)	Max.
1996	186.9 (49.5)	934.6	21.2 (2.9)[a]	106	1.5 (0.9)[a]	5
1997	132.7 (75.0)	663.4	12.0 (4.0)[b]	60	2.8 (2.2)[b]	9
1998	215.1 (60.6)	1075.3	19.0 (2.6)[a]	95	1.8 (1.1)[a]	5
1999	241.4 (69.2)	1206.9	18.6 (4.4)[a]	93	1.9 (1.4)[a]	7

extinction to refer to stations where *R. makuta* appeared or disappeared during the study. Because we can never be certain that a species is absent from a site, these terms refer to *apparent* colonizations or extinctions. Changes in butterfly presence/absence at stations from 1997 to 1998 were related to habitat quality (Table 2; ANOVA of habitat quality by forest type (logged or unlogged) and butterfly presence/absence, with transect nested within forest type; butterfly presence/absence $F_{3,71} = 9.38$, $P < 0.001$). Stations that were colonized in 1998 had higher habitat quality (mean = 0.37, SD = 0.20) compared with stations that were vacant in 1997 and 1998 (mean = 0.18, SD = 0.19; t-test, t = –3.41, 47 df, P = 0.001).

Approximately 17 mo after the end of the drought in 1999, the distribution of *R. makuta* was as extensive as in 1998 (57 stations occupied in both years). Nineteen (68%) of the stations that were colonized in 1998 were still occupied in 1999, although there was considerable turnover among stations in terms of butterfly presence/absence (Table 2). As in the previous year, changes in butterfly presence/absence at stations from 1998 to 1999 were related to habitat quality (Table 2; ANOVA of habitat quality by forest type and butterfly presence/absence, with transect nested within forest type; butterfly presence/absence $F_{3,71} = 4.64$, $P = 0.005$).

There were no effects of isolation in relation to whether a station was colonized or not immediately after the drought; stations that were vacant in 1997 and 1998 were no further from the nearest occupied station (mean = 200.0 m, SD = 126.5) than were stations that were colonized in 1998 (mean = 178.6 m, SD = 91.7; Mann–Whitney Z = –0.36, N = 49, P = 0.7). Over the 3-y period, stations that were vacant in all years were no further from an occupied station than were stations that were continuously occupied (Z = –1.45, N = 42, P = 0.15).

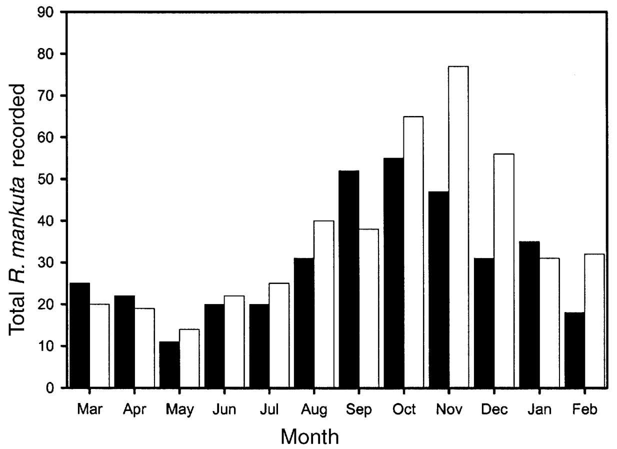

Figure 1. Total numbers of *Ragadia makuta* recorded at 80 observation stations on four transects in unlogged (solid bars) and selectively logged (hollow bars) forest from March 1999 until February 2000.

Monthly changes in butterfly distribution and abundance

A total of 806 *R. makuta* (367 in unlogged forest, 439 in logged forest) was recorded during the 12-mo survey period from March 1999 to February 2000 (Figure 1). Mean abundance of *R. makuta* at stations (excluding zeros) was lowest in May and highest in October (ANOVA of butterfly abundance by month, nesting transect within logged/unlogged forest type, month $F_{11,378} =$

Table 2. Changes in presence/absence of *R. makuta* at 81 stations in logged and unlogged forest between 1997 and 1998, and 1998 and 1999, in relation to habitat quality (mean and SD). n = number of stations.

	Habitat quality			
Butterfly presence/absence	n	Unlogged	n	Logged
1997–98				
Present both years	12	0.57 (0.26)	17	0.58 (0.25)
Colonized by 1998	15	0.34 (0.19)	13	0.40 (0.21)
Extinct by 1998	2	0.76 (0.17)	1	0.30
Absent both years	12	0.10 (0.08)	9	0.28 (0.26)
1998–99				
Present both years	20	0.49 (0.26)	27	0.51 (0.25)
Colonized by 1999	6	0.33 (0.36)	4	0.28 (0.09)
Extinct by 1999	7	0.31 (0.17)	3	0.40 (0.25)
Absent both years	8	0.09 (0.03)	6	0.28 (0.32)

4.20, P = 0.013). There were also significant differences between months in the proportion of stations where *R. makuta* was recorded present or absent ($\chi^2 = 48.9$, 11 df, $P < 0.001$). Twofold variation in abundance was observed over the 12-mo period but monthly mean abundance (range 1.32 (SD = 0.48) to 2.55 (SD = 1.99) was similar to that observed in the post-drought surveys of 1998 and 1999.

None of the six rainfall variables investigated (rainfall during survey, rainfall during previous month, rainfall 2 mo previously, rainfall 3 mo previously, rainfall 4 mo previously, rainfall 5 mo previously) were correlated with any other (Pearson correlation, $P > 0.09$ in all cases). Forward, stepwise multiple regression showed that numbers of butterflies recorded each month were significantly and negatively related to rainfall in the month before the survey, but not to any other rainfall variables (unlogged forest, $F_{1,10} = 17.4$, $P = 0.002$, regression slope = –0.11 (SE = 0.03), $R^2 = 0.64$; logged forest, $F_{1,10} = 17.4$, $P = 0.008$, slope = –0.14 (SE = 0.04), $R^2 = 0.52$; Figure 2). Butterfly distribution (number of stations with records) was also negatively related to rainfall in the previous month (unlogged forest, $F_{1,10} = 21.2$, $P = 0.008$, regression slope = –0.035 (SE = 0.008), $R^2 = 0.68$; logged forest, $F_{1,10} = 6.4$, $P = 0.03$, slope = –0.031 (SE = 0.012), $R^2 = 0.39$). There were no significant differences between logged and unlogged forest in either the slopes or elevations of the relationships between numbers of *R. makuta* recorded or butterfly distribution and rainfall in the previous month (ANCOVA of butterfly abundance in logged and unlogged forest, with rainfall as a covariate; forest type × rainfall interaction, $P > 0.6$ in both cases, forest type $P > 0.4$ in both cases). Comparison of R^2 values showed that in unlogged forest, more of the variation in butterfly abundance and distribution was explained by rainfall compared with logged forest.

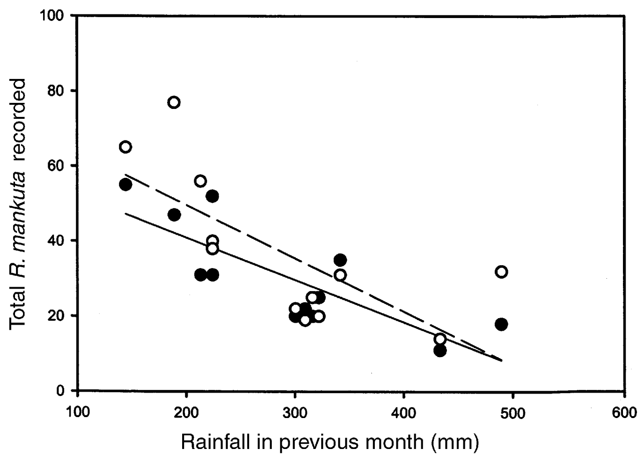

Figure 2. Relationship between numbers of butterflies recorded each month in unlogged (solid circles and line) and selectively logged forest (hollow circles and dashed line) and rainfall in the month before surveys.

Selective logging and butterfly distribution

There was no difference between selectively logged and unlogged forest in the number of stations where *R. makuta* was recorded in either 1997, 1998 or 1999 (χ^2 test, $P > 0.2$ in all years), or between months ($\chi^2 = 1.39$, 1 df, $P = 0.3$). There were also no significant differences between logged and unlogged forest in butterfly abundance in either annual or monthly surveys (ANOVA of *R. makuta* abundance when present, with year/month and forest type (logged or unlogged) as factors, and transect nested within forest type; among years, forest type $F_{1,138} = 0.33$, $P = 0.6$; among months, forest type $F_{1,378} = 0.007$, $P = 0.9$). Data from monthly surveys showed that butterfly abundance was more variable in logged than in unlogged forest (Levene's test for equal variance, $F = 3.76$, $P = 0.05$), although this was not observed in the annual data. There was no difference between selectively logged and unlogged forest in the availability of suitable habitat for *R. makuta* (ANOVA of habitat quality index by forest type, with transect nested within site; habitat quality, $F_{1,77} = 0.35$, $P = 0.6$).

There were, however, significant differences among transects in butterfly abundance (ANOVA of *R. makuta* abundance when present, with year/month and forest type as factors, and transect nested within forest type; annual data, transect $F_{2,138} = 6.55$, $P = 0.002$; monthly data, transect $F_{2,378} = 12.2$, $P < 0.001$), and also in the number of stations where *R. makuta* was recorded (1997, $\chi^2 = 9.0$, 3 df, $P = 0.03$; 1998, $\chi^2 = 9.1$, 3 df, $P = 0.03$; 1999, $\chi^2 = 11.6$, 3 df, $P = 0.009$; monthly data, $\chi^2 = 37.4$, $P < 0.001$). In all surveys, *R. makuta* was present at most stations on transect 3 in logged forest and present at fewest stations on transect 4 in logged forest, with transects in unlogged forest having intermediate values. There were also significant differences among transects in habitat quality (ANOVA of habitat quality by forest type, with transect nested within site; transect, $F_{2,77} = 4.75$, $P = 0.01$), with transect 3 in logged forest having the highest habitat quality, and transect 4 (also in logged forest) having the lowest.

Impacts of selective logging on post-drought recovery

There was no difference between selectively logged and unlogged forest in changes in butterfly presence/absence at stations between 1997–98 ($\chi^2 = 1.8$, 3 df, $P = 0.6$) or 1998–99 ($\chi^2 = 3.3$, 3 df, $P = 0.4$). In particular, there was no difference in the number of stations being colonized between selectively logged and unlogged forest ($\chi^2 = 0.06$, 1 df, $P = 0.8$), or among transects ($\chi^2 = 3.14$, 3 df, $P = 0.4$). There was no difference between forest types in turnover rates (number of stations continuously occupied or vacant compared with number of stations becoming colonized or extinct) over the 3-y period ($\chi^2 = 1.0$, 1 df, P = 0.3). There was also no difference between selectively logged and unlogged forest, or among transects, in habitat quality of stations in relation to these changes in butterfly presence/absence (Table 2; ANOVA of habitat quality by forest type and butterfly presence/absence, with transects nested within forest type; 1997–98, forest type $F_{1,71}$ = 0.06, P = 0.82; transect, $F_{2,71}$ = 2.40, P = 0.10; 1998–99, forest type, $F_{1,71}$ = 0.83, P = 0.45; transect, $F_{2,71}$ = 2.66, P = 0.08). There was also no difference in colonization distance between logged and unlogged forest (1997–98, Mann–Whitney Z = –0.95, N = 28, P = 0.3) or among transects (1997–98, Kruskal–Wallis χ^2 = 1.20, N = 28, P = 0.8). These results indicate that selective logging did not affect the expansion of *R. makuta* after the drought.

DISCUSSION

Effects of rainfall on butterfly abundance

This study took place in an area of South-East Asia which is considered to be aseasonal and where there are no well-defined wet and dry seasons (Walsh 1996). Rainfall was typically high during the monthly survey period, although there was a fivefold difference in rainfall which was associated with marked fluctuations in *R. makuta* abundance during this period. *Ragadia makuta* probably breeds continuously at the study site, and although there are no data on adult longevity, data from temperate species suggest it is likely to be approximately 1–2 wk; thus adults recorded on surveys in one month were unlikely to have been alive in subsequent months. Therefore, lower butterfly abundance in months following high rainfall was probably due to high rainfall adversely affecting larval and pupal survival. The relationships between rainfall and butterfly abundance were similar in logged and unlogged habitats, although there was significantly greater variation in butterfly abundance in logged habitats over the 12-mo survey. This suggests that butterflies in modified habitats were more affected by factors other than rainfall not measured in this study, although the similarity in butterfly distribution and abundance in logged and unlogged forest indicates that these effects had little overall impact on *R. makuta*.

Impacts of drought and rates of recovery

Coinciding with the ENSO event in 1997 there was approximately 30% less rainfall during the study period in 1997, compared with years of more normal rainfall. Associated with this reduced rainfall, *R. makuta* was 2–4 times less abundant and occurred at only half as many observation stations in 1997. This contrasts with the monthly data and indicates that the relationship between butterfly abundance and rainfall is not linear and that *R. makuta* is adversely affected by both high rainfall and drought. Data from before the drought in 1996 indicated that the abundance of *R. makuta* had returned to pre-drought levels approximately 4 mo after the end of the drought. Although we have no information on the abundance of *R. makuta* at the end of the drought in May 1998, our data indicate that populations can fluctuate quite markedly over relatively short time periods. *Ragadia makuta* is reported to be a poor flier (Corbet & Pendlebury 1992), and so these rapid changes in abundance are unlikely to have been due to dispersal. In addition, the widespread nature of the drought and its severity indicate that changes in abundance were most likely to have been due to changes in local birth and death rates. There is no information on fecundity or development time of *R. makuta* at the study site, but a development time of 2–3 mo per generation would result in 1–2 generations between the end of the drought and the 1998 study period. This suggests 2–4-fold increases in population size each generation, in broad agreement with short-term population increases in temperate butterflies (Pollard & Yates 1993).

Patterns of population expansion immediately after the drought showed that butterflies colonized areas with higher habitat quality. Between 1997 and 1998, there were no differences in colonization distance between stations that were vacant and those that were colonized, suggesting that dispersal ability was not a significant factor limiting population expansion after the drought. There are no data on dispersal rates for *R. makuta*. However, potential colonization distances were low in this study, and the maximum distance between vacant and nearest occupied stations in 1997 was only 500 m, indicating that any isolation effects in this study were weak. Thus at the scale of the study, habitat quality rather than dispersal ability was more important in determining post-drought distribution. However, high rates of turnover in terms of butterfly presence/absence at stations in years with normal rainfall show the importance of dispersal in allowing *R. makuta* to track suitable habitat at local scales.

Selective logging and butterfly distribution

Recent studies have reported both increased and decreased butterfly diversity in response to habitat disturbance (review in Hamer & Hill 2001). What appears more certain is that species with restricted distributions are particularly vulnerable to habitat disturbance (Hamer *et al.* 1997, Hill *et al.* 1995). *Ragadia makuta* has a relatively restricted geographic distribution (Borneo, Sumatra, Java and Malay Peninsula), and is dependent on forest, suggesting that it might be vulnerable to selective logging. Although there were significant differences in vegetation structure between the logged and unlogged study sites 8–9 y after selective logging (Hill 1999), there were no differences between selectively logged and unlogged forest in *R. makuta* distribution or abundance either during or following the drought, or during the monthly surveys. Results from this study support other studies in the same area showing little effects of selective logging on butterflies (Willott *et al*. 2000). In this study there were, however, significant differences in butterfly abundance among transects in all surveys; transect 4 in selectively logged forest had lowest abundance, and transect 3 (also in logged forest) had highest abundance. Differences in butterfly abundance between transects in logged forest may have been due to differences in severity of logging; transect 3 included areas close to a water catchment area that would not have been logged (Hill 1999). High habitat heterogeneity is typical of selectively logged areas throughout the tropics (Whitmore 1998) and our results stress the importance of sampling widely to take account of this heterogeneity (Sparrow *et al*. 1994). Our results also indicate how crucial it is to quantify vegetation structure and availability of larval resources in order to understand responses of forest butterflies to habitat disturbance.

Both selectively logged and unlogged forest were highly heterogeneous in terms of availability of suitable habitat for *R. makuta*. Both forest types contained at least some areas of high quality habitat, and populations contracted into these refuge areas during the drought. Habitat heterogeneity has been implicated in the persistence of temperate butterfly populations during droughts (Ehrlich *et al*. 1980) and results from this study suggest that it is also important in persistence of tropical populations. Habitat heterogeneity which provides populations with refuge areas may explain why extreme climatic events rarely eliminate all populations from a region (Kindvall 1996, Thomas *et al*. 1998).

Interactive effects of drought and habitat disturbance

Tropical butterfly assemblages are diverse but typically contain few species present in large enough numbers for the type of study described here; relatively abundant species are often migrants or widespread generalist species of low conservation value. By contrast, *R. makuta* occurs at relatively high densities but also has a comparatively restricted distribution. Results from this study show that although *R. makuta* populations were significantly reduced during the drought, populations quickly re-expanded after the drought. There was no difference between selectively logged and unlogged forest in either the pattern or rate of recovery of populations from drought. Thus results from this study indicate that there were no interactive effects between habitat disturbance and climate on *R. makuta* distributions. However, these results may not be typical of other species, and more data are required to see whether species with contrasting habitat specificities and/or relative abundances are equally able to withstand extreme climatic events.

Wider conservation impacts of drought

Droughts are relatively frequent on Borneo, and are often associated with ENSO events. For example, the 1982–3 ENSO event was also associated with a severe drought on Borneo (Walsh 1996). The predictions of future climate scenarios for ENSO-associated droughts to be more extreme in tropical regions could have wider implications for tropical forest ecosystems given that droughts in this region usually lead either directly or indirectly to fire and destruction of forest (Guhardja *et al*. 2000). Approximately 50% of Sabah was estimated to be covered by rain forest in 1985, of which 15% is under some sort of protection (Collins *et al*. 1991). In the future, these remaining areas of forest may be threatened not only from increasing demand for timber but also by increasing risk of fire. Predicted impacts of climate change for tropical butterflies are thus more likely to be due to indirect effects of drought on habitat loss, rather than to direct effects on population dynamics.

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