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ECOLOGY OF RAGADIA MAKUTA (LEPIDOPTERA:

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SATYRINAE) IN TROPICAL RAINFORESTS OF SABAH,

MALAYSIA

MAHADIMENAKBAR MOHAMED DAWOOD

PRESENTED IN CANDIDATURE FOR THE DEGREE OF

MASTER OF SCIENCE

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UNIVERSITY OF DURHAM

DEPARTMENT OF BIOLOGICAL SCIENCES

2000



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A spectral to

ECOLOGY OF RAGADIA MAKUTA (LEPIDOPTERA: SATYRINAE) IN

TROPICAL RAINFORESTS OF SABAH, MALAYSIA

M.Sc. thesis by Mahadimenakbar Mohamed Dawood

ABSTRACT

The satyrid butterfly, *Ragadia makuta* Horsfield was studied in lowland dipterocarp rainforest in Sabah, Borneo. Data were collected monthly from March 1999 to February 2000 in two habitat types, unlogged forest and forest that had been selectively logged 10 to 11 years previously. The primary aim was to investigate the effects of selective logging on *R.makuta* abundance and distribution. Transect walk-and-count and point sampling techniques were used to record satyrinae, morphinae and riodinidae butterflies plus one species of danaidae (*Idea stolli*). Butterflies were sampled at 80 observation stations along 8 km of transects in unlogged and logged forest.

Measurements of vegetation structure showed that effects of logging were still evident 10 years after logging. Logged forest had lower canopy and understorey cover and fewer large trees but a larger proportion of pioneer *Macarangga* spp. compared with unlogged forest. *R.makuta* abundance was not affected by selective logging. Habitat requirements of *R.makuta* were investigated and in both unlogged and logged forest, *R.makuta* was more abundant in areas with greater cover of its larval host-plant (*Selagenella* spp.). There was some evidence for *R.makuta* changing its habitat requirements from unlogged forest to logged forest but these changes were relatively small.

The distribution and abundance of R.makuta varied from month to month in relation to rainfall. Rainfall one month before surveys was negatively correlated with R.makuta abundance. This indicates that rainfall may affect adult abundance through its impacts on larval development and survival.

The use of R.makuta as biodiversity indicator for other butterflies was examined. R.makuta abundance was positively correlated with diversity of other satyrid and riodinid butterflies. This suggested that R.makuta could be used as indicator of other understorey butterflies and that R.makuta may be an important tool for conservation studies.

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Mahadimenakbar Mohamed Dawood University of Durham Summer 2000

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Chapter 1: Introduction

1.1 Tropical Rainforests

About 28 % (3.6 billion hectares) of the earth's land area is covered with closed-canopy forest (Sharma *et al.* 1992). Around the world, roughly about 3 % of forest occurs in Europe, 15 % in the former Soviet Union, 14 % in Asia and the Pacific, 12 % in North America, 22 % in Latin America and 24 % in Africa (Sharma *et al.* 1992) and about 10 % in Australasia (World Conservation Monitoring Centre 1992). In the tropics, there are four major types of woody vegetation; rainforest, monsoon (seasonal) forest, thorn forest and savanna forest (Whitmore 1990). The first three types of forest are known as tropical moist forest while savanna forest is considered as tropical dry forest. Tropical rainforest occurs in all three tropical land areas: the American rainforest region in the South America continent, which is the largest $(4x10^6 \text{ km}^2)$, the Malesian rainforest region (Southeast Asia and the east coast of tropical Australia; 2.5x10⁶ km²) and the African rainforest region $(1.8x10^6 \text{ km}^2)$ (Whitmore 1990). Rainforest is considered as montane forests.

In 1891, A.F.W. Schimper, a German botanist created the phrase 'tropical rainforest' (Tropische Regenwald) for the forest of the permanently wet tropics (Whitmore 1990). Tropical rainforest occurs near the equator between 23.5°N and 33.5°S where rainfall is high, over 2,000 mm per annum and temperatures are uniformly high (mean greater than 24°C) and frost free.



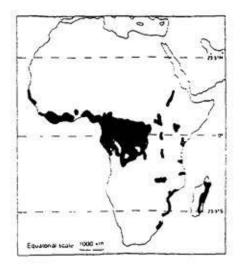
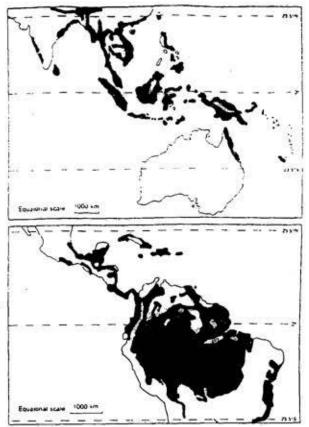


Figure 1.1: Map of major distribution of Tropical Rainforests in the world (shaded areas). Source, Reading *et al.* 1995.



Within tropical rainforest, the tree crowns can be divided into three layers; the lower layer (30 to 40 m above the ground), the middle layer (40 to 50 m), and the emergents, where the crowns of the tallest trees can reach up to 70 m. These emergents produce a very uneven canopy. These three layers form a dense screen of leaves preventing penetration of much sunlight to the forest floor. This results in the undergrowth being comparatively sparse and the microclimate under the canopy being very moist (Jones 1997). Mature trees can have trunk diameters exceeding 3 m and can have crown diameters over 20 m (Jacobs 1988). Trees with tall and heavy trunks usually have buttresses at the base for support. In some trees, the trunk is divided into a collection of thin separate stems. The forest also contains many lianas and woody climbers which climb up the trees into the canopy searching for sunlight. Herbs such as orchids and ferns sometimes occur as epiphytes on tree branches. On the forest floor, growth is sparse due to the dense canopy and low light levels. The forest of western

Malesia is dominated by the Dipterocarpaceae, a family of trees whose name literally means "two winged fruit", although in many species, the fruits have more than two wings.

1.2 Diversity within Tropical Forests

For most groups of terrestrial plants and animals, diversity is lowest near the poles, and increases towards the tropics, especially in tropical rainforest. However, this latitudinal gradient does not occur in all taxa. For example, species diversity for some groups of marine and freshwaters organisms and invertebrates (e.g. seabirds, lichens, marine benthic organisms, parasitic wasps and soil nematodes) are higher at high latitudes that at lower latitudes (Huston 1994).

Tropical rainforests are believed to contain 50-80 % of the world's species even though rainforest covers only 8 % of the land area (Watt *et al.* 1997a). For example, a 10 hectare area of rainforest in Borneo was found to contain approximately 700 tree species which is equal to the number of all tree species found in North America (Botkin & Talbot 1992). The number of plant species with 10 cm girth or greater at breast height in primary lowland forest is often about 60 to 150 per hectare but can exceed 200 to 300 in very species-rich areas such as western South America and parts of Malesia (Richards 1996). The high species richness of tropical forest is illustrated by La Selva forest of Costa Rica. Here, 1,500 species of plant, 388 species of birds, 63 species of bats, 42 fish, 122 reptiles and 143 butterfly species were recorded within a small area of 13.7 km² (Stork 1996).

Many hypotheses attempt to explain high diversity in the tropics but there are three main categories; (1) *in situ* speciation is more frequent in the humid tropics; (2)

rates of extinction are lower in the tropics; (3) many parts of this region are old, so that tropical ecosystems have had more time to develop (Reading *et al.* 1995).

Several factors may lead to more frequent *in situ* speciation in the humid tropics. For instance the structure and topography of tropical forests may lead to geographical isolation whilst low productivity can promote limited dispersal, leading to greater isolation (Huston 1994). Shorter generations and greater productivity may also lead to greater turnover and increased selection (Rohde 1992).

In tropical forest ecosystems, a combination of high temperatures (which increase metabolic energy expenditure disproportionately to photosynthesis) and low nutrient availability (due to leeching of nutrients from the soil) results in low net primary productivity (Huston 1994). As a result, there is no dominance of any tree species and the most common species make up less than 15% of the total (Jacobs 1988). This lack of dominance gives the opportunity for other species to grow in an area with less intense competition than in temperate climates.

The general latitudinal pattern in species numbers must be at least in part related to some climatic factor, or combination of factors mentioned above, that change in a consistent manner with latitude (Ricklefs 1973). Spatial heterogeneity affects the chances of co-existence between potentially competing species and between predators and prey. More types of structural refuges in an area as a result of increased heterogeneity may permit more species to co-exist. Small populations may survive in the tropics because the physical environment is more or less constant, producing a highly stable ecosystem.

Many parts of the tropics are older and more stable than other ecosystems. Fossil evidence shows that rainforest has existed since the Cretaceous and early Tertiary periods some 50 to 80 million years ago (Richards 1996). There have been opportunities

for species to migrate along a variety of routes from Pleistocene refugia in the last 2 million years (Reading et al. 1995)

In summary, there appears to be no single explanation for the latitudinal variation in species richness shown by a particular taxon. Rather, several ecological processes interact to produce the polar/tropical gradient in numbers of species. These processes are in turn affected by a number of factors including average temperature and precipitation, the variability in temperature and precipitation, annual net primary productivity and geological history.

1.3 Threats to Tropical Forests

Forests have been important to humans for a long time. Forests have social and environmental benefits and play an important role in economic development. This gives income, employment and foreign exchange to countries that have large areas of forest. Forests not only provide land for cultivation and a source of wood production, but also other products including firewood and charcoal, poles for thatching, fodder for animals, 'bush-meat' and palm wine, rattans, fruits and medicine. For indigenous people, forests provide food and shelter for them to survive. Forests play an important role for other organisms, as a large fraction of the earth's biological diversity lives in forests or depends on forest, especially tropical rainforests. Many of the endemic species found in tropical rainforests occur only in the small area where they evolved (Botkin & Talbot 1992). For example, in the New Guinean region, 7.2 % of the world's remaining tropical forests support 22% of the world's endemic tropical forest birds (Johns 1997).

Forests are an important component of the biosphere because they help to stabilize natural systems by maintaining air, water and soil quality. Trees in forests help to cool the tropical region (which receives high solar radiation), by pumping enormous

quantities of water into the atmosphere to form clouds, which then reflect sunlight back into outer space. The water vapour generated by tropical forest also carries considerable quantities of energy in the form of latent heat which is released when the vapour condenses as rain. A proportion of this heat is transported by clouds to temperate zones, therefore spreading out solar radiation. Forests also protect watersheds, emit oxygen and play a large role in influencing biogeochemical processes, regulating runoff and groundwater, controlling soil erosion, influencing local climate and reducing downstream sedimentation and flooding. Trees in forests also act as carbon sinks, which are important in eliminating carbon dioxide from the atmosphere, thus reducing the green house effect. In addition, forests have aesthetic value and offer recreational opportunities. In short, tropical rain forest may cover only a small proportion of the earth's surface but they are vital for the global cycling of energy, water and nutrients.

Forests have been disturbed in many different ways since humans started farming. For example, logging, animal ranching, firewood collecting, traditional agriculture, urban development, mining and other developments have been identified as causes of deforestation and forest degradation. In addition, fire and drought have also caused extensive damage to large areas of forests.

Deforestation is the total or nearly total loss of natural forest and it is caused by the conversion of natural forest to another type of vegetation or land use (WWF 1992). 154 million ha of natural rainforest were lost between 1981 to 1990, with 48 % of this deforestation occurring in the Americas, 25 % in Asia and 26 % in Africa (Whitmore 1997). Other less severe forms of disturbance may degrade forests. For example, forest is degraded when a logged forest is left to recover, or forests are felled and the land farmed for a few years and then allowed to regenerate. Damage caused by forest degradation is less severe than complete deforestation, because the forest and its ecological function may more or less recover, although biodiversity, ecosystem functioning, structural complexity and species' interdependencies are likely to have been disturbed and may take several centuries to recover (Sayer & Whitmore 1991).

Logging inevitably changes the physical environment of the forest. Due to canopy loss during logging, the amount of light reaching the forest floor is increased. This can adversely affect phytophobic plants such as some epiphytes and mosses which live in damp environments or may require a high moisture level to reproduce. Daily maximum air temperature will increase, generally by at least by 4°C and also the diurnal range of soil temperature will be up to 14°C in a clearing (Johns 1997). Relative humidity will also change when forest is severely disturbed. These microclimatic changes can directly affect the number and distribution of leaf litter invertebrates which are important to decomposition processes.

One of the ways to reduce disturbance to forests is the practice of selective logging. In this method, 8 to 15 trees are removed per ha (Sabah Forestry Department 1989). This only removes the most valuable timber trees and it aims to improve forest productivity and forest management while harvesting timber. Although impacts of selective logging are less severe than clear felling, it can still cause considerable damage to the forest through changing forest structure and species composition. Logging only removes marketable trees but the extraction techniques may cause high levels of associated damage, and may also destroy fruit trees important to animals. For instance, it was reported that about 40 to 70 % of the residual stand was damaged by selective commercial logging in Sabah, Borneo (Sabah Forestry Department 1989). Moreover, a study by Nussbaum *et al.* (1993) showed that vegetation and topsoil is removed and compacted over large areas after selective logging is intended to be sustainable, but if the

interval between logging events is short, this may cause greater damage and perhaps higher species loss (Whitmore 1997).

Forestry is very important to many tropical countries' economy. In 1990, the World Resources Institute suggested that rates of forest loss were as much as 204,000 km² annually (Colchester 1995) and global consumption of wood products was running at around 3,400 million m³ annually (Johns 1997). About 80 % of wood harvested in the tropics is burnt as fuel or has other domestic uses. In Europe and other developed regions, it is used mainly for structural and decorative purposes and for conversion into pulp for papermaking. In Central America forested areas are cleared for cattle ranching whereas in South East Asia, logging is the main cause of reduction in forested area. Roads built for logging give access to farmers to clear previously inaccessible forest for farming, thus compounding the disturbance. Shifting cultivation in the form of slash and burn cultivation and clearance for grazing land or other agricultural settlement has had a greater impact on forest areas than selective removal of high value hardwood (Sharma *et al.* 1992).

1.4 Effects of Forest Disturbance

The role of forests in maintaining stability in ecosystems is undoubtedly important. Structural changes in the forest are the immediate effects of logging of primary forests. These include a decline in overstorey tree size, increased abundance of small-stemmed species, and a decrease in larger commercial species (Bawa & Seidler 1998). A study in the Brazilian Amazon showed that removal of about 2 % of trees with diameter of 10 cm or more destroyed about 26 % of other trees (Uhl & Vieira 1989). If these forests are disturbed intensively, there may be widespread consequences. For instance, global climates may be affected dramatically by declining forested areas through changes in precipitation patterns. The role of forests as carbon sinks may also be affected and reduction of forested areas may have impacts on the global carbon cycle. It has been estimated that deforestation releases between 1 and 3 billion tones of carbon by increasing the rate of decay of organic matter in trees and soil (Woodwell 1992). Deforestation may thus contribute to global warming. Another consequence of loss of forests is degradation of watersheds, which has serious social, economic and environmental impacts in many countries (Rowe *et al.* 1992). In addition, extensive deforestation disrupts the nutrient cycle and reduces soil fertility. Deforestation also causes soil erosion leading to loss of capacity of soil to retain water. In addition to these effects due to the clearance of forest around the world, loss of forest will also affect the biological diversity dependent on these areas (Sayer & Whitmore 1991).

Many studies have investigated the effects of disturbance in tropical forest on its fauna, and these studies indicate a loss of biological diversity. This is potentially a severe problem given that the rate of habitat loss is about 56,000 hectares a day (Botkin & Talbot 1992). In Borneo, patches of primary forest have retained many mammal and bird species that forage in the surrounding timber tree plantations around these patches (Duff *et al.* 1984). During logging operations, arboreal vertebrates can move to intact forest nearby and then return to their previous areas after logging (Whitmore 1997). Thus, this kind of disturbance might have less of an impact on species richness. However, it may change the proportion and/or composition of the species where edge and gap-favoring species may increase and sensitive species decline (Whitmore 1997). A study conducted in Tanzania showed that birds of the shaded forest understorey and larger insectivores of mixed canopy were affected seriously by human disturbance (Fjeldsa 1999). Other studies in Borneo found that 10 years after selective logging, about 95 % of the bird species were present but some specialist guilds such as groundfeeding insectivores were absent (Lambert 1992). The density of civets in logged forest was also found to be significantly lower than in primary forest (Heydon & Bulloh 1996). However in Uganda, rodents were recorded in increased densities in selectively felled forest than in undisturbed mature forest (Kasenene 1984). Thus some mammal and bird species are sensitive to disturbance while some are able to persist in disturbed forest and forest fragments.

In terms of the number of species contributing to global biodiversity, insects represent over half of all described species (Price 1997). There are currently 900,000 species of insects described and there may be two to ten times as many more still undiscovered (Pedigo 1991). The effects of clear felling on insects have been well documented (Holloway *et al.* 1992; Watt *et al.* 1997) but there are still few data available for effects of less severe small-scale disturbance (Hamer *et al.* 1997). Before any predictions of impacts of disturbance on biodiversity can be made for a tropical country such as Malaysia, it is essential to have an accurate profile of that diversity, including species richness, abundance and distribution. This can then be related to projections of habitat loss due to human activities to provide estimates of potential loss of species (Holloway & Barlow 1992).

Moths (Chey et al. 1997; Willott 1999), dung and carrion beetles, litter arthropods and termites (Watt et al. 1997b, Lawton et al. 1998, Jones & Eggleton 2000) and butterflies (Hill et al. 1995; Hamer et al. 1997) are commonly used in studies on the impact of forest disturbance because they are comparatively easy to sample and study. Insects are known to be sensitive to environmental changes and so can be used as ecological indicators of forest disturbance (McGeoch 1998). This is because insects are sensitive to microclimatic changes such as relative humidity, temperature and light penetration. Logging causes structural changes which lead to these microclimatic changes. Any faunal group used as indicators of environmental change should satisfy some basic criteria (McGeoch 1998). These organisms should be universal in distribution as far as possible. The organisms must be sensitive to changes at an individual and species level in the spatial and temporal pattern in the environment so that they will reflect changes readily and their specific tolerances should be measurable. The use of more than one type of organism, like the simultaneous use of beetles, moths and ants would increase confidence and applicability. The method should also be cost effective, rapid and simple, both for field samplings and subsequent analysis. If a single group is selected it should be a highly diverse one, because the greater the species richness of a species group, the more sensitive they are to habitat change (Johns 1992). Identification should also be relatively simple and quick (Holloway 1980, Lawton *et al.* 1998).

Insects mediate many biological processes such as pollination, seed dispersal and decomposition but forest disturbance and fragmentation can cause disruption to these processes (Didham *et al.* 1996). Fragmentation may change the genetics and demography of the remnant populations and make component populations fragment further. Furthermore, forest fragmentation exposes species assemblages to more edge effects and changes habitat heterogeneity (Klein 1989). For example, pollination has been shown to be directly affected by fragmentation through a reduction in the abundance and species richness of pollinators, and indirectly by the alteration of their behavior and flight patterns (Didham *et al.* 1996). Many studies on the effects of forest fragmentation on insects in the tropics have been conducted using beetles. Studies in Central America showed that dung and carrion beetle communities in forest fragments differed from those in contiguous forest. Forest fragments had fewer species and less dense populations than comparable intact forest areas (Klein 1989) and 47 % of the

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most abundant beetle species were significantly affected by forest fragmentation (Didham *et al.* 1998). However, a study in Southeastern Australia found that habitat fragmentation did not reduce species richness of carabid beetles in remaining forest remnants, and not all populations declined due to forest fragmentation and edge effects. Some beetle species increased in abundance and some were not affected. From this study, it was suggested that the effects of habitat fragmentation might be a consequence of isolation and habitat modification (Davies & Margules 1998).

Conversion of forested areas to plantation also affects insects in these areas. Studies in Sabah, Borneo showed that diversity of macrolepidoptera was highest in undisturbed sites compared to plantation sites (Watt *et al.* 1997a). Holloway *et al.* (1992) found that moth diversity was much lower in the early stages of forest regeneration following clearance but beetle diversity showed no significant decline that could be attributed to logging. However, a study by Chey *et al.* (1997) found that moth diversity in forest plantations was high, similar to natural secondary forest. This might have been due to the type of plantation, which had been planted with *Eucalyptus deglupta*, and had a very diverse understorey both in terms of plant species (secondary regrowth species) and architecture, which may have supported a more diverse moth fauna. For leaf litter-ants, studies in Ghana showed that forest clearance and the establishment of cocoa plantation had little or no effect on diversity (Watt *et al.* 1997a).

During commercial selective logging, timbers are extracted selectively to reduce damage to forests but this can still cause considerable impact on the fauna living in these forests. Studies in Sabah, Borneo showed that the proportion of mites and pseudoscorpions was higher in primary forest, while beetles, millipedes and cockroaches were higher in the selectively logged forest (Burghouts *et al.* 1992). For tropical forest butterflies in Buru, Indonesia, species richness, abundance and evenness of butterflies were all significantly lower in selectively logged forest (Hill et al. 1995). Butterfly assemblages are sensitive to even moderate changes in forest structure resulting from human disturbance (Spitzer et al. 1993, Hamer et al. 1997, Lewis et al. 1998).

Ants, diptera, araneae, thysanoptura, homoptera, coleoptera and orthoptera were significantly more abundant in partially manually cleared forest plots rather than in complete clearance plots (Watt *et al.* 1997b). This suggested that arthropod abundance may be affected by the way a forest is managed. In Vietnam, the species composition of butterflies in gaps created by illegal logging and in closed canopy differed significantly (Spitzer *et al.* 1997). Although the species richness and diversity was higher in gaps, the conservation value of closed canopy habitat lay in the presence of species with restricted geographic ranges (Spitzer *et al.* 1997). Species diversity, evenness and richness of butterflies in forested area were significantly higher than in disturbed open areas (Idris *et al.* 1999, Zaidi & Kayau 1995). If the disturbance is small, or the forest is converted to plantation of timber or cocoa, the impact on insects appears less pronounced (Watt *et al.* 1997b).

A forest remnant of Amazonian forest showed that edge effects increased the richness and altered the composition of butterfly communities. This may be due to light penetrating the understorey and other edge effects that initiate the growth of flowers which attract butterflies to this area, increasing their abundance and diversity (Brown & Hutchings 1997). Owen (1971) also suggested that light disturbance will increase the abundance and diversity of tropical butterflies due to edge effects.

It is now clear that extensive human disturbance of forested areas does have a significant impact on insect communities. Some species disappear from disturbed areas. Lack of information on numbers, distribution, status and ecology of tropical forest

species make it important to conserve and manage forests carefully. A more focused approach to the problems of forest disturbance and its effects on insect communities is required to fill the numerous gaps in current knowledge. It is likely that any disturbance of natural forest whether naturally or man-made, will change the relative frequencies of animal and plant species and extinction rates may increase if natural habitats are repeatedly and heavily disturbed (Sayer & Whitmore 1991).

1.5 Sabah Rainforest

Sabah is situated at the northern tip of the island of Borneo, between latitudes 4°8' and 7°22'N and longitudes 115°7' and 119°17'E (Fig. 1.2). It is the second largest state of the 13 states within the Federation of Malaysia with a total area of 73,718.7 km². The climate is marine equatorial, with rainfall ranging from 1,700 to 5,100 mm per annum and greatly influenced by the Northeast monsoon from November to February and the Southwest Monsoon from May to August. Average temperature is between 25-30°C (Marsh & Greer 1992).

The tropical rainforest of Southeast Asia is one of the oldest and most complex ecosystems in the world. Though tropical rainforest generally refers to lowland forests, other forest types such as mangroves, peat swamps and montane forests are also covered by the term, and all these forests occur in Sabah. The total forested area in Malaysia covers about half of the total land area, with 6.4 million hectares in Peninsular Malaysia, 4.7 million hectares in Sabah and 9.4 million hectares in Sarawak (Sabah Forestry Department 1989). By the end of 1997, forest covered 44,487.5 km² or 60.3 % of Sabah's total land area, including plantation forestry (Yasuma & Andau 1999). This includes forest reserves, state land and park forests. Currently about 3.6 million hectares (48.8 %) of Sabah's land area is under forest reserves (WWF 1992). Much of the

forested land has been gazetted as permanent forest estates (which means land reserved by the government for forestry, specifically for permanent timber production), national and state parks, or other similar legally protected forest areas. State and national parks cover all major forest types so that all types of forest are conserved for future generations.

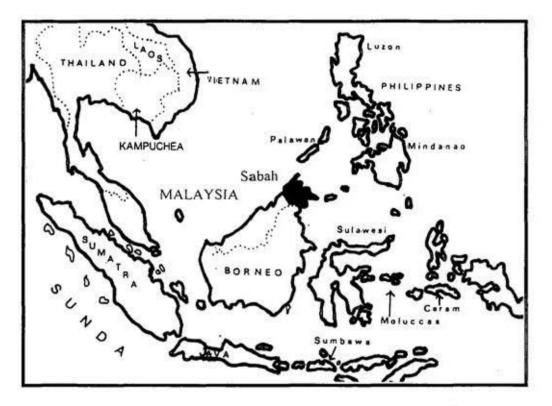


Figure 1.2: Map of Sabah, which is located on the northern tip of Borneo

The island of Borneo is regarded as a major centre of species diversity and is rich in endemic species. For example, a 2 ha area of forest in the Sepilok Forest Reserve in Sabah may contain up to 198 tree species, with 667 trees (diameter at breast height> 9cm) per hectare (Chey *et al.* 1997). In Danum Valley, south east Sabah, 511 species of trees greater than or equal to 10 cm girth at breast height were recorded in two 4 ha plots (Newbery *et al.* 1992). In terms of terrestrial mammals, a total of 222 species have been recorded in Borneo and out of this, 194 species are recorded in Sabah (Yasuma & Andau 1999). There are over 3,000 species of trees native to Sabah (73,719 km²), in comparison to about 30 native tree species in the UK which is several times larger (224,100 km²). In terms of arthropods, out of about 25,000 individuals, more than 4,000 species were collected from the canopy of 10 trees (five species) in Borneo (Watt *et al.* 1997a). The rich diversity of Borneon plant life contributes to the diversity of the insect fauna, much of which feed on plants. There are 973 recorded Bornean butterfly species, of which Kinabalu Park, Sabah alone has 625 species, that is 66.7 % of the total species in Borneo (Hauser *et al.* 1997). According to Otsuka (1988), there are about 850 species of butterflies in Sabah and about 50 of them are endemic to Borneo.

1.6 Forestry in Sabah

Commercial logging in Sabah started around 1879 when a timber concession was granted at Pulau Gaya off the West Coast of Sabah. It was later gazetted as the first Forest Reserve in North Borneo. The British North Borneo Chartered Company formed the Forest Department in 1914. The first "Conservator of Forests", Mr. D.D. Wood was appointed in 1920 to manage the increasing logging activities. This department was responsible for the supervision and monitoring of forest exploitation, revenue collection and the collecting of forest botanical specimens (Sabah Forestry Department 1989). In 1974, large-scale plantation forestry started in Sabah at Brumas near Tawau, in the south east of the country. About 40,000 ha of *Acacia mangium, Gmelina arborea, Paraseranthes falcataria, Pinus caribaea* and *Eucalyptus deglupta* plantation have replaced natural forest (Chey *et al.* 1997) and the state government has planned to expand plantation forestry and monoculture of *Acacia mangium* in Danum Valley in the future.

Forestry is currently very important to Sabah's economy. 70 % of total government revenue comes from forestry (Johns 1997). Sabah forest revenue in 1996 was about US\$ 150 million (Sintoh 1998) and the average revenue from forest resources was about US\$ 188 million per year for the past 17 years (Sabah State Government 1998). Average timber extraction intensity in Sabah for the first cut is 90 m³ per ha where most of the large trees are removed (Blockhus *et al.* 1992). In order to ensure that forestry continues to be an important sector of Sabah's economy, legislation was passed by the State Legislature in 1984 to keep at least 4.2 million hectares of Sabah's forest as permanent forest estates. This was to guarantee the security of tenure of all forested land and ensure forestry as a lasting component of the State's economy. Currently, about 433,534 ha of virgin forest are left in Sabah, that is only 5.4 % of Sabah's land area (WWF 1992).

Selective logging is the extraction of mature commercial trees from areas designated as production forest. There are two systems employed in selective logging, the monocyclic and polycyclic system. In the monocyclic system, all saleable timber trees are harvested in a single operation and relogging may take place only after 60-80 years. The area is then left to regenerate naturally (Whitmore 1984). Non-commercial trees may be eliminated to give way for seedlings of valuable species to grow without competition. The Sabah Foundation, the largest timber concern in Sabah practices this method and the logging operation was designed for a rotation period of 60 years. This is to allow the logged over forest sufficient time to recover and regenerate. In polycyclic systems, selected trees are extracted over a continuous cycle. Only fully mature trees are felled and extracted. Smaller trees are left to grow until mature and then be felled in the next logging operation after 25 to 40 years (Whitmore 1984).

Historically, two methods of logging extraction were employed in Sabah, which are tractor and cable yarding. Conventional tractor logging methods were used on moderate terrain while on slopes more than 20°, cable yarding or 'highlead' was used

(Marsh & Greer 1992). Cable varding is a method where logs are hauled to a landing site which is usually located at the top of a hill by using a system of cables powered by a stationary engine, while tractor logging method uses moving machines (tractors), to drag the logs. These two methods have significant impacts on the forest as both techniques require clearing of forests for skid trails and roads that causes damage to non-commercial trees. Cable yarding has now been stopped because this method is considered destructive because a large area (c. 20 ha) has to be completely flattened around the spar tree and heavy damage is more localized on the ridgetop where the hauling machinery is sited. A spar tree is a tree or steel tower which is used to suspend operating cables above the ground located near the winching machine (Dykstra & Heinrich 1995). It is also reported that damage also occurs along radial corridors corresponding to the main winch line position (Marsh & Greer 1992). This method can cause damage that is greater than using tractors (Johns 1997). Tractor logging methods, on the other hand cause a mosaic of skid tracks, broken trees and undamaged patches. This method is still being practice in Sabah.

Reduced impact logging (RIL) techniques are increasingly being practiced in Sabah since 1992. Guidelines have been implemented for pre-felling vine cutting, 100% stock mapping, directional felling, marking potential crop trees that are likely to be damaged during felling and skidding, and substantial planning and supervision of bulldozer-yarding operations (Putz *et al.* 1998). The aim of RIL is to reduce damage to residual forest during selective logging (Pinard & Putz 1996, Pinard & Putz 1997).

In Sabah, forest reserves have been divided into 7 different classes (WWF 1992) to make it easier to manage and control. These forest reserves are as follow:

• Class I - Protection Forest. Forest conserved for the maintenance of the stability of essential climatic, watershed and other environmental factors. There are 283,376

hectares of this forest in 43 locations throughout Sabah. These areas cannot be logged.

- Class II Commercial Forest. Forest can be logged to supply timber and other products. There are 2,743,959 hectares of Commercial Forest Reserves in 28 locations throughout Sabah.
- Class III Domestic Forest. Forest for supplying timber and other forest products for local consumption only. There are 7,355 hectares of Domestic Forest Reserves in 10 locations throughout Sabah.
- Class IV Amenity Forest. Forest providing amenity and arboretum works to local inhabitants. There are 20,767 hectares of Amenity Forest Reserves in 11 locations throughout Sabah.
- Class V Mangrove Forest. Forest supplying mangrove timber and other products to meet the general demands of trade. *Rhizophora sp.* are most commonly harvested, and products range from firewood to fishing stakes. Collectively, there are 316,024 hectares of Mangrove Forest Reserves in 17 locations throughout Sabah.
- Class VI Virgin Jungle Forest. Forest conserved intact strictly for forestry research purposes. Logging is strictly prohibited in these forest reserves. The Sepilok Virgin Jungle Reserve, in Sandakan, at 4000 hectares is one of the largest tracts of undisturbed lowland dipterocarp forests in Sabah. Collectively, there are 90,386 hectares of Virgin Forest Reserves in 50 locations throughout Sabah.
- Class VII Wildlife Reserve. Forest conserved primarily for the protection and research of wild animal species. There are 132,652 hectares of Wildlife Reserves in two locations. They are Tabin Wildlife Reserve and Kulamba Wildlife Reserve.

1.7 Diversity Measurements

Species diversity is one important dimension of any ecological community. The simplest measure of species diversity is to count the number of species present in an area. This concept is known as species richness. One problem with this concept is that it treats rare species and common species as equals (Magurran 1988). There are two components of diversity in any community, first the total number of species it contains, (species richness), and second, the distribution of individuals among those species (equitability or evenness; Putman 1994). Diversity is higher in a community when there are more species and when the species are equally abundant. Diversity can be measured by recording the number of species, by describing their relative abundance or by using a measure which combines the two components.

At a local scale, at least two types of diversity measure can be distinguished. Firstly, cardinal diversity measures; those that treat each species as equal and then create the index by adding the species in some way. Examples are Williams alpha, Shannon H', species richness and species density indices. Secondly, ordinal diversity measures, those that treat each species as essentially different and create a representation of diversity by ranking each species in an order of some kind such as species abundance distributions (Cousin 1991). Cardinal indices are suitable for describing the diversity of a guild of species but are unsuitable for description of communities where ranking the very different species found in a community is the better option.

Biodiversity can be considered at a range of spatial scales. An increase of sampling area will consequently increase the number of distinct habitats and their biological communities encountered. In this case, the number of species within a sampled community and the degree to which species are common to adjacent communities will both influence estimates of biodiversity (Southwood & Henderson

2000). There are thus a number of different spatial scales for the assessment of biodiversity. Firstly, α -diversity is the biodiversity within a particular site, habitat, community, or biotope. Secondly, β -diversity, measured at the same spatial scale as alpha diversity, is a comparison of the similarity between sites. Thirdly, γ -diversity, is the biodiversity within a particular geographical area or landscape. Thus γ -diversity is a combination of β and α diversities of a group of communities within a geographic area (Southwood & Henderson 2000).

Butterflies, which are very diverse on Borneo and have many endemic species (Otsuka 1988) are ideal organisms to be used for biological indication purposes (Kremen 1992). Furthermore, butterflies have also been suggested as good environmental indicators due to their common dependence on particular food plants, their sensitivity to microenvironment variations, and their often wide geographical ranges (Pollard 1977, Thomas & Mallorie 1985). Butterflies are a suitable group for ecological studies for the following reasons; their taxonomy is well known (in comparison with other tropical insect groups; Otsuka 1988) and there are some data available on their geographic distribution and for some species also on their life history (Corbet & Pendlebury 1992, Kremen 1992). This is in contrast with other insects group in the tropics, where one is often limited to working with morphospecies. Besides, butterflies occur at moderate levels of species richness, and are quite relatively to sample. These characteristics have made tropical butterflies a popular group for investigations into the effects of small-scale disturbance, selective logging and forest fragmentation (Hill et al. 1995, Hamer et al. 1997, Spitzer et al. 1993, 1997, Lewis et al. 1998, Willott et al. 2000).

1.8 The study species Ragadia makuta

Commonly known as the striped ringlet, *Ragadia makuta umbrata* Fruhstorfer is one of the 72 species of sub-family Satyrinae recorded in Sabah. It is normally seen flying close to the ground in the undergrowth of closed-canopy forests at most elevations (Cobert & Pendlebury 1992). The size of forewing is 25 to 30 mm and both sexes are similar morphologically (Otsuka 1988). Usually it flies singly but sometimes can be seen flying in pairs. The underside of this butterfly is striped dark and light brown with a series of submarginal silver eyespots (see fig. 1.3). The upper side is pale brown in colour. The larvae feed on the herb *Selagenella* spp. (Cobert & Pendlebury 1992). These herbs are commonly found in closed-canopy forests, usually close to streams. At Danum Valley, at least 8 species of this plant have been recorded (Parris 1997). Another *Ragadia* species which can be found in Borneo is *Ragadia annulata* Grose-Smith, which is confined to high elevations around 4,000 to 5,000 feet a.s.l. (Otsuka 1988). Throughout Oriental region, nine species of *Ragadia* have been recorded (D'Abrera 1985).

There are several reasons why *R.makuta* is useful for autecological studies investigating habitat requirements of species in tropical forest. This species occurs at high abundance compared to other forest species but it is not a 'weedy' species and its distribution is restricted to Sundaland (West Malaysia, Borneo, Sumatra and Java) and so it has considerable conservation value. The adults have conspicuous wing colours making them easily seen even under dense canopy. Although the wing size is relatively small compared with other tropical butterflies, it is a low-flying species with slow flapping flight making it easy to spot and therefore it is easily and reliably recorded from ground-based surveys without having to gain access the canopy. Being a poor flier, it has been suggested that it might be vulnerable to forest disturbance since this species

is confined in closed-canopy forest (Hill 1999). In addition, the food plants for this butterfly (*Selagenella* spp.) can be readily recorded from ground-based survey making it possible to quantify habitat habitat requirements (Hill 1999).



Figure 1.3: R.makuta perching on Selagenella sp.

This thesis investigates the distribution and abundance of *R.makuta* in unlogged and logged forest selectively logged 10 to11 years previously. Chapter two describes the study site and general materials and methods used to survey butterflies. Chapter three investigates habitat requirements of *R.makuta* and the effects of habitat modification on distribution and abundance of *R.makuta*. Chapter three also describes the methods used to measure and analyze vegetation structure at the study sites. Chapter four investigates seasonal effects of rainfall and sunshine on *R.makuta* abundance and chapter five discusses the use of *R.makuta* as a bioindicator for other forest butterflies.

2.1 Aims of Study

The aims of this study were: (1) To investigate the impacts of selective logging on abundance of *R.makuta*, (2) To investigate habitat requirements of *R.makuta*, (3) To investigate whether *R.makuta* is a suitable species to be used as biological indicator of forest disturbance (objectives 1 to 3 are all in chapter 3), (4) To investigate seasonal changes in the distribution and abundance of *R.makuta* (chapter 4), and (5) To investigate whether *R.makuta* can be used as an indicator of the distribution and abundance of other butterflies (chapter 5).

2.2 Study Site

The study sites were located near the Danum Valley Field Centre (DVFC), in the Ulu Segama Forest Reserve (117°35'E and 5°49'N) in South-eastern Sabah, Malaysia (Fig. 2.1). The nearest town is Lahad Datu, which is about 85 km to the east. Most of the area is covered with lowland mixed dipterocarp forest. Only 9 % of the area is above 760 m a.s.l and considered as montane forest. The Danum Valley Conservation Area (DVCA) covers an area of 438 km² and lies within a 97,300 km² area of the Yayasan Sabah (Sabah Foundation) timber concession area (Marsh & Greer 1992).

The purposes of DVCA are mainly for conservation, education and nature tourism. It was redesignated as a class I (protected) forest reserve in 1995 to remain undisturbed forever as a wildlife sanctuary. This area is important for populations of almost all of Borneo's large land mammals such as Sumatran rhinoceros (*Dicerorhinus sumatrensis*), sun bear (*Helarctos malayanus*), clouded leopard (*Neofelis nebulosa*) and orang utan (*Pongo pygmaeus*) (Yasuma & Andau 1999). In 1986, the research centre at DVFC was officially opened at an elevation of 150 m a.s.l. adjacent to the Segama River.

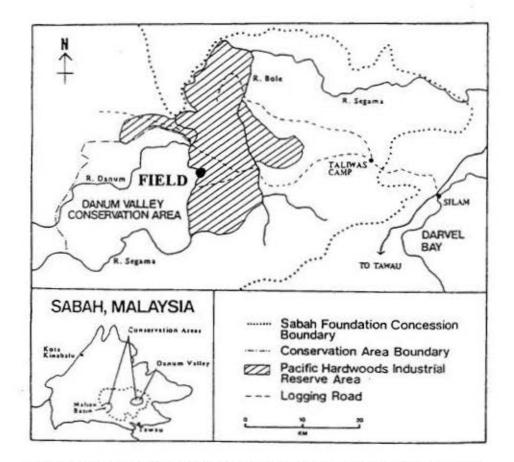


Figure 2.1: Location of DVFC in Sabah. Source, Marsh & Greer 1992.

2.2.1 Forest structure of the study area

Study sites were located in primary forest and selectively logged forest. In primary forest, trees in the family Dipterocarpaceae dominate the area. According to a survey conducted in 1969-72, 88 % of the large trees in the conservation area were dipterocarps (Marsh & Greer 1992). Common large dipterocarp species that can be found dominating the upper canopy area are species of *Parashorea* spp. and *Shorea* spp. and other *l Rubrushorea* spp. In the selectively logged forest, most of the large dipterocarps (d.b.h.> 60 cm) have been extracted. Pioneer tree species such as *Macarangga* spp. are common along skid trails and the understorey contains a high density of vines and few large trees. These areas have been left to regenerate naturally and contain many species typical of regeneration and succession. The study areas in selectively logged forest were logged in 1988 and 1989 using tractor and high methods described in chapter 1.

2.3 Sampling Techniques

2.3.1 About the transects

Four transects were set up along existing paths in undisturbed forest (2 transects) and forest selectively logged 10 to 11 years previously (2 transects; figure 2.2). Each transect was 2 km long (total 8 km). The first two transects were located in undisturbed primary forest were T1 (West Transect) and T2 (Rhino Transect). Transect 3 (T3; in coupe 89) and T4 (in coupe 88) were located in selectively logged forests. The nearest point between these two transects was approximately 500 m (Hill 1999). Observation stations were set up every 100 m along all transects (80 stations altogether). This study was conducted over a period of one year from March 1999 to February 2000.

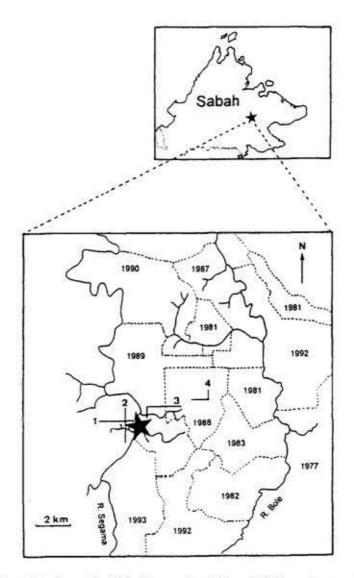


Figure 2.2: Map showing all of the transects; T1 and T2 in primary forest. T3 and T4 in logged forest. ★ is DVFC. All forest west of Segama River lies in DVCA. Years on map refer to date of selective logging. Source, Hill 1999.

2.3.2 Vegetation analysis

Vegetation structure was measured at all 80 stations in March 1999. Distribution of larval host-plant, *Selagenella* spp. was also measured. The following vegetation variables were measured at every station within a 30 m radius of the station: height of trees, distance of trees from the station, girth of trees, distance of station to nearest stream, type of trees, point of inversion of trees, percentage cover of ground vegetation, low vegetation, understorey vegetation, canopy cover and canopy openness. Chapter 3 discusses vegetation measures in more detail.

2.3.3 Butterfly data

The sampling technique was a combination of transect walk-and-count and point sampling (Hill 1999). Recording took place only between 10:00 and 14:00h, which is the time of peak flight activity for butterflies and recording took place only on sunny days. The recorder walked at a uniform pace of ca. 1 km hour⁻¹ along the transects and recorded all butterflies from the sub families Satyrinae and Morphinae and family Riodinidae. One species of Danaidae (Idea stolli) was also recorded. All butterflies seen within 5 m to the left and right of the recorder and 5 m ahead were recorded while the recorder walked between observation stations. At every station, the recorder additionally observed butterflies within a radius of 10 m of the station during a period of 5 minutes. A maximum of one transect was surveyed per person per day. Care was taken not to record the same individual twice. An individual butterfly flying in and out of the transect was recorded only once. Each transect was surveyed twice each month by two recorders (J. Tangah and myself), giving a total of four surveys per month. Data for the four surveys each month were summed for analysis. Data were analysed on a station by station basis combining data for each station with data recorded on paths up to 50 m sided each station.

Before this work was carried out, recorders were trained to identify all satyrinae, moephinae and riodinididae sighted on trails. An identification manual was carried along during the surveys to help identify difficult species. An effort was also made to catch these species with a hand net to be identified. Identification of butterflies was based on Otsuka (1988). All unidentified individuals were noted.

Chapter 3: Habitat Requirements of *Ragadia makuta* and Effects of Habitat Modification on Distribution and Abundance

3.1 Introduction

Lowland tropical rainforests are rapidly being converted to other land uses or deforested. Ecological disturbance in these areas is becoming increasingly evident (Sayer & Whitmore 1991, Rowe *et al.* 1992). There are six major causes of direct habitat disturbance that can be identified around the world, especially in the tropics; 1) conversion to permanent agricultural land, 2) large scale commercial timber extraction, 3) shifting cultivation, 4) infrastructure development 5) charcoal production and 6) small scale removal by local inhabitants of forest resources such as fuelwood (Reading *et al.* 1995).

In Southeast Asia, closed-canopy forest destruction is mainly caused by land clearance for plantation, agriculture, resettlement projects and commercial logging. Selective logging is widespread in Sabah where 3.5 % of forest (about 1,557 km²) is selectively logged annually (Lambert 1992). Large commercial trees with girths 60 cm or greater are extracted while smaller trees are left to grow naturally until they are suitable to be extracted in the subsequent harvesting period, which is after 60 years in Sabah (Whitmore 1997). Although it does not generally decrease the total forested areas, this technique modifies the forest ecosystem since removal of large trees causes considerable damage to remaining trees (Lambert 1992). After selective logging has been carried out, the remaining forest occurs as a mosaic of vegetation types ranging from patches of exposed mineral soil without vegetation along skid trails and log landings, to patches of undisturbed forest on steep slopes (more than 20°) that are not suitable to be logged, or in water catchment areas, or in areas with no commercial timbers. Canopy cover will slowly change during the regeneration period after logging

where pioneer tree species such as *Macarangga* sp. grow along the skid trails and large gaps caused by logging and rapidly colonize and dominate these heavily disturbed areas (Lambert 1992).

Selective logging also results in considerable changes in the output of sediment and water within the logged area where construction of logging roads and skid trails causes large increases in sediment yield in rivers (Douglas *et al.* 1992, Douglas 1999). Microclimates within forests are very different from the non-forested areas in terms of the amount of light penetration, air temperature and moisture and these abiotic factors directly affect most plant and animal activities (Reading *et al.* 1995). Selective logging decreases canopy cover due to the removal of large timber trees and few remnant trees remain. As a result, incoming solar radiation to the ground increases the air temperature and reduces the moisture level, affecting the activity of many organisms including arthropods (Ewel & Bigelow 1996).

Although species diversity is high in the tropics, it has generally been difficult to study habitat requirements of tropical butterflies because few species are present in large numbers. Most common species are usually either widespread generalist species of low conservation value or migrants (Hill 1999). *Ragadia makuta* is however, amenable to autecological studies because it is relatively common and is dependent on closedcanopy forest but also has a relatively restricted distribution confined to Sundaland (Hill 1999). In addition, the larval host-plant of *R.makuta* is known (*Selagenella* spp.) and can be recorded from the ground. Knowledge of the habitat requirements of an organism is important to its conservation in disturbed environments, so that conservation efforts can be concentrated where suitable habitat is present. There is little point in trying to conserve species where their environment is no longer suitable (Speight *et al.* 1999).

The aims of this chapter are:

- To quantify forest structure in unlogged and logged forest, in order to investigate the effects of selective logging on forest structure.
- To investigate the effects of selective logging on *R.makuta* in term of changes in distribution and abundance.
- To describe habitats requirements of *R.makuta* in its natural habitat (unlogged forest) and in disturbed habitat (logged forest).
- To investigate if any changes in distribution and abundance were due to *R.makuta* changing its habitat requirements in response to disturbance. Knowledge of an ability for a species to change its requirements in disturbed habitat may be important for its conservation in the future.

3.2 Materials and Methods

3.2.1 Vegetation data and analysis

Vegetation data were collected in March 1999, during the first month of fieldwork Vegetation data were recorded within a 30 m radius of all 80 stations on transects (see chapter 2). Every station was divided into 4 quadrants and in each quadrant, two large trees (circumference 60 cm or greater at breast height) and two small trees (circumference greater than 10 cm at breast height) nearest to the station were measured as described in table 3.1. Table 3.1: Variables recorded at every station

Variables recorded	Technique/equipment	Precision	
Height of trees (m)	Visual estimation by two observers	2 m	
Distance of trees from the centre of station (m)	Measured using a tape-measure	0.1 m	
Girth of trees (measured 1.5m above ground; cm)	Measured using a tape-measure	1 cm	
Distance of station to nearest stream (m)	Measured using a tape-measure	0.1 m	
Type of trees (dipterocarps, non-dip. or <i>Macarangga</i> sp.)	Field identification by experienced staff from the Forest Research Centre		
Point of inversion of trees	Visual estimation by two observers	Above or below mid-point	
% cover of ground vegetation (<2 m)	Visual estimation by two observers	5%	
% cover of low vegetation (2 to 5 m above ground)	Visual estimation by two observers	5 %	
% cover of understorey vegetation (5 to 20 m above ground)	Visual estimation by two observers	5 %	
% cover of canopy layer (>20 m)	r of canopy layer Visual estimation by two observers		
% of canopy openness	penness Spherical densiometer (see text for details; fig.3.3)		
% cover of food plant (Selagenella spp.)	4X10m transects (see text for details)	5 %	

Canopy openness was measured using a spherical densiometer (figure 3.1). This is a handheld device comprising a convex mirror with 25 squares marked on its surface. The densiometer is held in front of the body and at elbow height by the recorder standing at the station. Four readings were taken, facing north, east, south and west by counting areas which are not occupied by canopy and the readings were combined for analysis. Two people took readings at every station and the mean value was used in the analysis.



Figure 3.1: Densiometer used to measure canopy openness.

Abundance of *Selagenella* spp. was recorded at each station because this herb is the larval food-plant of *Ragadia makuta*. Abundance of *Selagenella* spp. was measured along 10 m transects running north, south, east and west from the centre of the station. Each transect was divided into 20 cm sections using a tape measure and the number of sections (200 per station) where a *Selagenella* plant touched the tape was recorded. The distance of each station to the nearest stream was also recorded because this is likely to determine the probability of *R.makuta* presence. Meteorological data (temperature, monthly rainfall and sunshine) were obtained from the meteorological station at the field centre.

Vegetation variables measured in this study are likely to be closely correlated and were analysed by principle component analysis (PCA). PCA is a data reduction technique used to reduce a large number of closely related variables to a smaller set of independent factors that summarize the essential information contained in the variables (Child 1969, Norusis 1994, Coakes & Steed 1999).

All variables which were recorded as percentages or proportions were normalized using arc-sine transformation. These variables include canopy, low-level and understorey cover, proportion of large and small *Macarangga* sp. and dipterocarps, *Selagenella* cover and canopy openness. The percentage cover of *Selagenella* spp. at each section was calculated as the mean number of 20 cm transect sections (total 200 sections) with *Selagenella* spp. Canopy openness was calculated from densiometer readings by taking the mean of the two values from two recorders to obtain the percentage of canopy openness at every station.

The distance of stations from the nearest stream was normalised by taking logs (log₁₀). All habitat measurements collected were then incorporated into the factor analysis except for distance to nearest stream and *Selagenella* cover as these two measurements were not direct measures of forest structure (Hill 1999) and were not closely correlated with other variables. Differences between unlogged and selectively logged forest in mean values of vegetation variables listed in table 3.2 were analysed using nested ANOVA (nesting transect within habitat type).

3.2.2 Effects of habitat modification on R.makuta

The frequency distribution of *R.makuta* in unlogged and selectively logged habitat was compared to a Poisson distribution, in which expected if individuals are distributed at random. The variance : mean ratio was then calculated to investigate if distributions were clumped (ratio>1) or regular (ratio<1)

To investigate the impacts of selective logging, mean abundance of *R.makuta* at stations in logged and unlogged forest was compared using nested ANOVA (nesting transects within habitats). Habitat types (unlogged and logged forest) were the main

effect and there were two transects in each habitat. Nested ANOVA was used to test whether there was a difference between habitats after taking account of differences between transects. Following a significant transect effect, a one-way ANOVA was also conducted to compare mean abundance of *R.makuta* on each transect to see which transect was significantly different.

3.2.3 Butterfly data

R. makuta was surveyed along transects T1, T2, T3 and T4 (see chapter 2) each month from March 1999 to February 2000 using a method modified from Pollard (1977). The modification from the original transect technique was due to the differences in habitat structure between tropical rainforest and temperate habitat. Adult *R.makuta* seen within 5 m in front of the recorder and within 5 m to the left and right of the transect were recorded while the observer was walking at a constant pace between stations. In addition, *R.makuta* was also recorded within a 10 m radius at each station for 5 minutes. Surveys were conducted during good weather between 10.00 to 14.00 h, corresponding with peak flight activity (Hill 1999). Data were collected by two recorders (J. Tangah and myself) surveying different transects on different days. Each transect was walked twice each month by each recorder. Data from two recorders was combined for analysis.

3.2.4 Habitat requirements of R.makuta

Habitat requirements of *R.makuta* in unlogged forest (40 stations) were analysed using stepwise multiple regression. Total number $(\log_{10} \text{ number} + 1)$ of *R.makuta* at each station in unlogged forest was related to five vegetation variables; three factor scores from PCA, percentage cover of *Selagenella* plus distance to nearest stream.

Two methods were used to investigate changes in habitat requirements of *R.makuta* in logged forest. First, stepwise multiple regression was used as above to relate the total number of *R.makuta* seen in logged forest (40 stations) to the above five vegetation variables. Equations generated in unlogged and logged forest were then compared to see if the habitat requirements of *R.makuta* changed between unlogged and logged forest.

The second method was to compare observed numbers of *R.makuta* recorded at all stations with those predicted from the regression equation describing habitat requirements in unlogged forest. The equation describing *R.makuta* abundance in unlogged forest was used to predict abundance at all stations in both unlogged and logged forest. The difference between observed and predicted abundance was then calculated. Nested ANOVA, nesting transect within habitat was used to examine whether there were significant differences between predicted and observed abundance of *R.makuta* between habitats and between transects. I also investigated relationships among the five vegetation variables above and between each vegetation variable plus *R.makuta* abundance using Pearson correlations.

3.3 Results

3.3.1 Vegetation analysis

In total, ten variables (50 %) differed significantly between unlogged and logged forest (table 3.2). From these variables, PCA extracted 5 components of variation which accounted for 66.6 % of the variability in the data set (table 3.3). Subsequent analyses considered only the first three of these factors because factors 4 and 5 only accounted for an additional 13 % of the variance in the data set. The weightings of variables contributing to each of the factors are shown in table 3.4.

Variable	Unlo	gged	Logged	
	mean	SD	mean	SD
Point of inversion	1.18	0.37	1.05	0.36
% Canopy cover ***	0.41	0.17	0.15	0.12
% Understorey cover	0.69	0.24	0.66	0.001
% Mid-level cover	0.61	0.19	0.70	0.19
% Ground level cover	0.40	0.23	0.45	0.29
Prop. large dipterocarps*	0.63	0.38	0.46	0.31
Prop. small dipterocarps*	0.18	0.28	0.08	0.15
Prop. large Macarangga sp. ***	-		0.26	0.32
Prop. small Macarangga sp. ***	-	-	0.12	0.23
% Canopy openness	0.03	0.04	0.03	0.03
Girth large trees	32.18	4.87	27.57	5.10
Girth small trees	8.57	2.03	9.81	1.87
Height large trees***	32.18	4.87	27.57	5.10
Height small trees	8.57	2.03	9.81	1.89
Number of large trees	7.82	0.59	7.97	0.16
Number of small trees	8.00	0.00	8.00	0.00
Mean distance to large trees*	0.10	0.04	0.12	0.03
Mean distance to small trees	0.29	0.07	0.30	0.09
% Selagenella cover	0.001	0.001	0.001	0.002
Distance to stream	60.14	54.65	74.22	73.88
Factor 1 (primariness) ***	0.51	0.77	-0.51	0.95
Factor 2 (secondary growth)	-0.08	1.08	0.08	0.92
Factor 3 (heavily disturbed)	-0.007	0.87	0.007	1.13

Table 3.2: Mean scores for variables relating to vegetation structure and distribution of *Selagenella* spp., and mean scores of factor 1, 2 and 3 from PCA in unlogged and logged forest.

Means followed by ^{*} are significantly different at the 5% level, ^{**} are significantly different at 1% level and ^{***} are significantly different at 0.1% level. Large trees are trees with girth at breast height (GBH) greater than 0.6m and small trees are trees with GBH greater than 0.1m.

Factor	Eigenvalue	Percent of Variance	Cumulative percent of variation explained
1	4.35	25.6	25.6
2	2.71	15.9	41.5
3	2.06	12.1	53.6
4	1.19	7.0	60.6
5	1.01	6.0	66.6

Table 3.3: Percentage of variation explained by five factors extracted by PCA

Variables	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
Point of inversion	0.43873	0.05509	0.37347	-0.00761	0.03258
% Canopy cover	0.77900	0.04580	0.10109	0.09459	0.01881
Prop. large dipterocarps	0.75184	-0.12784	0.22451	0.19134	-0.14544
Prop. small dipterocarps	0.30241	0.25486	0.18093	0.42455	-0.66946
% canopy openness	-0.39919	-0.23987	0.08524	0.62677	0.35236
% ground level cover	-0.72208	-0.35486	0.16756	0.06910	-0.27431
Prop. large Macarangga sp.	-0.69039	0.35875	0.20769	0.02620	-0.21686
Prop. small Macarangga sp.	-0.59014	0.18086	0.51227	0.01294	0.15449
% mid-level cover	-0.23448	-0.41433	-0.49507	0.00477	-0.02779
% understorey cover	0.39911	0.74315	0.16455	0.00813	0.00311
Girth large trees	0.54956	-0.52735	0.20530	0.11840	0.17607
Girth small trees	-0.17032	-0.19025	0.78042	-0.26393	0.14289
Height large trees	0.79746	-0.34646	0.18198	-0.04826	-0.05302
Height small trees	0.08137	0.54896	0.40689	-0.27308	0.18103
Number of large trees	0.14866	0.56694	-0.19228	0.51749	0.40625
Mean distance to large trees	-0.15619	0.67680	-0.21536	-0.00444	-0.10934
Mean distance to small trees	0.39405	0.19874	-0.53378	-0.37012	0.09338

Table 3.4: Weightings of variables contributing to factors which have eigenvalues > 1:

Values in bold highlight variables having largest contributions to factors 1 to 3.

Factor 1 explained more than 25 % of variance in the data set, and increased with increasing canopy cover, proportion of large dipterocarps, mean height and girth of large trees. Factor 1 also increased with the decreasing numbers of *Macarangga* sp. and low ground cover. A high score for Factor 1 thus represented a vegetation structure characteristic of primary forest. Factor 2 explained 15.9 % of variance and increased with increasing understorey cover, height of small trees, number and distance to large trees, and decreasing girth of large trees. A high score for factor 2 could thus be considered to represent a vegetation structure characteristic of secondary growth. Factor 3 explained 12.1 % of the variance in the data set and increased with increasing proportion of small *Macarangga* trees and increasing girth of small trees and with decreasing distance to small trees. A high score for factor 3 thus represented a vegetation structure characteristic of secondary growth.

3.3.2 Effects of habitat modification

3.3. 2.1 Effects of habitat modification on forest structure

Table 3.2 shows the mean scores for 23 variables relating to forest structure, larval host plant cover and three main factors from the PCA. Unlogged forest had significantly higher canopy and understorey cover, a higher proportion of dipterocarps, and significantly taller large trees and shorter small trees. Factor 1 was also significantly higher in unlogged forest. By contrast, logged forest had significantly higher middle-level cover, a higher proportion of *Macarangga* spp. and a larger mean distance to large trees than unlogged forest.

3.3.2.2 Effects of habitat modification on R.makuta

In both habitats, the distribution of *R.makuta* differed significantly from a Poisson distribution (Kolmogorov-Smirnov one-sample tests; unlogged forests, z = 2.50, n = 40, P = 0.001; logged forest, z = 2.14, n = 40, P = 0.001). The variance/mean ratio in both habitats was much greater than 1 (unlogged forest, V / x = 8.17; logged forest, V / x = 8.90) indicating a clumped distribution in both habitats.

A total of 806 individuals of *R.makuta* were recorded in both habitats (Table 3.5). Of these, 367 individuals were recorded at 38 stations (95 %) in unlogged forest and 439 individuals were recorded at 39 stations (97.5 %) in logged forest (table 3.5). Out of 80 stations, only 3 stations were not occupied by *R.makuta*.

Habitat	Station occupied	Total individual seen	
Unlogged forest	38 (95 %)	367	
Logged forest	39 (97.5 %)	439	
Total	77 (96.3 %)	806	

Table 3.5: Total number of *R.makuta* seen in unlogged and logged forest and number of stations occupied during the whole study

Results from nested ANOVA showed that there were no significant differences in *R.makuta* abundance at stations between logged and unlogged forest (ANOVA nesting transects within habitats; habitat $F_{1,76} = 0.89$, P = 0.35; mean abundance of *R.makuta* in unlogged forest = 9.18 per station, SD = 8.7; mean abundance in logged forest = 10.98 per station, SD = 9.9). However, there was a significant difference in abundance among transects (transect effect; $F_{1,76} = 5.58$, P = 0.01). Figure 3.2 shows the mean abundance of *R.makuta* at stations on the four transects. *R.makuta* occurred most frequently on transect 3 (Coupe 89, logged forest; total 320 individuals, mean abundance at stations = 16.00, SD = 11.23) and was least frequently recorded on transect 4 (Coupe 88, also in logged forest) with only 119 individuals recorded (mean abundance = 5.95, SD = 4.60). Intermediate values were recorded in unlogged forest; mean abundance of *R.makuta* on T1 and T2 were 6.08 and 11.50 respectively.

Factor 2 was negatively correlated with mean abundance of *R.makuta* (Pearson correlation; r = -0.22, n = 80, P = 0.05; fig. 3.3b). However there was no significant correlation with factors 1 or 3 (r = -0.07, n = 80, P = 0.56 and r = 0.01, n = 80, P = 0.96 respectively; fig. 3.3a and c).

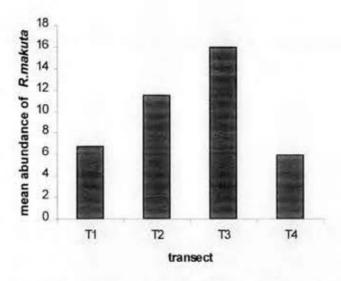


Figure 3.2: Mean abundance of *R.makuta* at stations on each transect

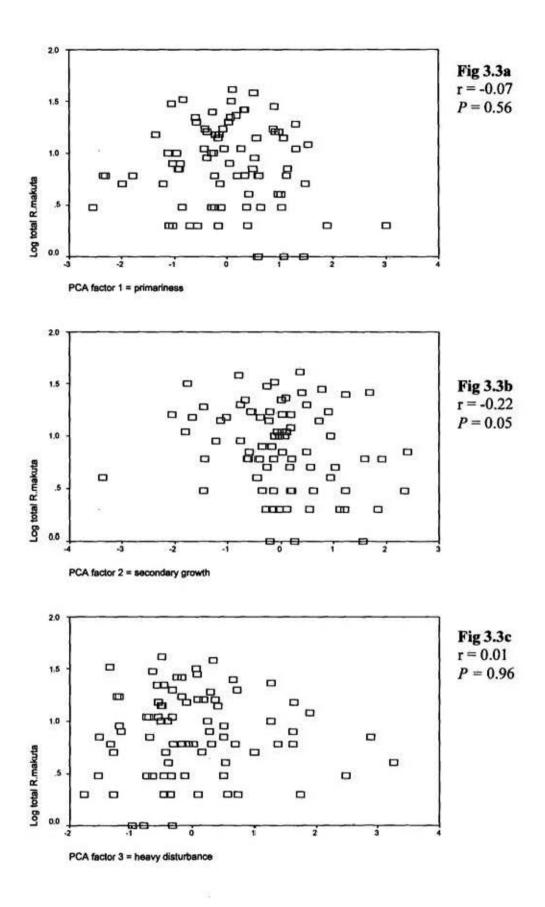


Figure 3.3 a, b and c: R. makuta abundance plotted against PCA factor 1, 2 and 3

3.3.3 Habitat requirements of R.makuta

Stepwise multiple regression described habitat suitability of *R.makuta* at each station in unlogged forest (T1 and T2 only) as follows:

Log₁₀ total *R.makuta* (+1) = 2.85 *Selagenella* (SE = 0.53) - 0.13 Factor 2 (SE = 0.04) + 0.69 (SE = 0.05) Equation 3.1

Factor 2 is a measure of secondary growth from the PCA and Selagenella is the percentage cover of larval host-plant. Factors 1 and 3 and distance to stream were not included in the equation (P>0.05). Thus, in unlogged forest, *R.makuta* habitat requirements can be described as areas with high Selagenella cover with low factor 2 scores (ie. low level of secondary growth).

3.3.4 Impacts of selective logging on habitat requirements of R.makuta

Stepwise multiple regression was used to described habitat requirements of *R.makuta* in logged forest (T3 and T4 only) as follows:

$$Log_{10}$$
 total R.makuta (+1) = 1.81 Selagenella (SE = 0.42) - 0.39 Stream (SE =

0.90) + 1.42(SE = 0.16). Equation 3.2

Where *Selagenella* is percentage cover of larval host-plant and Stream is log_{10} distance (m) of stations from nearest stream. Thus in logged forest, *R.makuta* habitat requirements can be described as areas with high *Selagenella* cover close to streams.

Comparing these two equations, we can see that there was some evidence for *R.makuta* changing its habitat requirements from unlogged to logged forest. In both habitats, *Selagenella* availability was most important in determining *R.makuta* abundance. However factor 2 was also important in determining *R.makuta* abundance in unlogged whereas distance to nearest stream was important in logged forest. Factor 2 and distance to nearest stream were significantly correlated with each other (Pearson

correlation; r = 0.28, P = 0.012), indicating that although *R.makuta* did change its habitat requirements in different habitats, these changes were relatively small.

Results from nested ANOVA showed that there was no difference between habitats in the match between observed and predicted abundance of *R.makuta* ($F_{1,76} =$ 0.11, *P* = 0.80). Furthermore, there were also no differences between transects ($F_{2,76} =$ 2.52, *P* = 0.09). Correlation analysis between predicted and observed *R.makuta* abundance also supports this finding (r = 0.60, *P* < 0.0001, 80 cases; figure 3.4). These results showed that the differences in habitat requirements of *R.makuta* between unlogged and logged forest were small and *Selagenella* availability was most important in determining *R.makuta* abundance in both habitats.

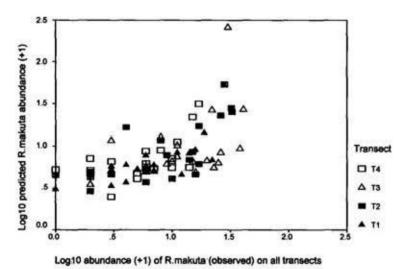


Figure 3.4: Relation between predicted and observed abundance of *R.makuta*. Data are shown separately for each transect.

In order to investigate habitat requirements of *R.makuta* in more detail, correlation analyses were carried out. There was no significant relation between *Selagenella* cover and distance to stream (r = -0.12, P = 0.27; fig. 3.5a). *R.makuta* abundance was negatively correlated with factor 2 (r = -0.22, P = 0.05; fig. 3.3b) and with distance to stream (r = -0.45, P < 0.01; fig. 3.5c). There was a significant positive correlation between *Selagenella* cover and *R.makuta* abundance (r = 0.55, P < 0.01; fig.

3.5b). From figure 3.5b, we can see that there was in fact a non-linear relationship between *Selagenella* cover and abundance of *R.makuta*.

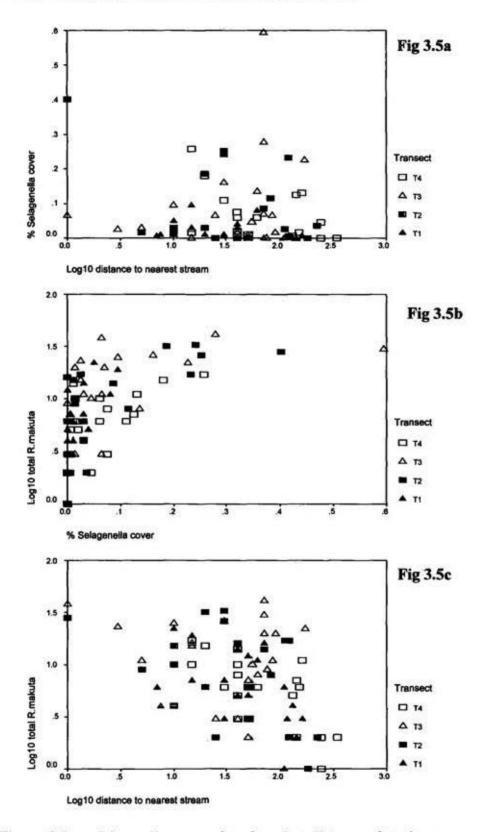


Figure 3.5 a; Selagenella cover plotted against distance of station to nearest stream, b; relationship between *R.makuta* abundance and *Selagenella* cover and c; relation between *R.makuta* abundance to the nearest stream.

3.4 Discussion

3.4.1 Sampling techniques

Many different methods can be used to monitor butterfly communities. One commonly used method is hand-netting. This technique is popular because collection of butterflies can also be made. However, this method has the drawback that many butterflies are difficult to catch due to their rapid flight and because they occur in the canopy. The method used in this study was a modified version of the transect method described by Pollard (1977). Modification was necessary because the original method was developed in temperate regions where the number of butterfly species is relatively low and the vegetation structure is very different compared to tropical rainforest. Many studies conducted in tropical regions have used this technique (Hill *et al.* 1995, Hamer *et al.* 1997, Spitzer *et al.* 1997, Hill 1999). A combination of walking and stopping was used because of the difficulties of sampling butterflies whilst walking along forest trails.

In terms of the rate of individuals seen and species accumulation, transects are highly efficient (Walpole & Sheldon 1999). In addition, this method allows a large area to be surveyed in a wide variety of habitats and microclimates.

Although the are many advantages of using this method, there are some limitations. The major problem is that identification of some species is difficult in flight. On Borneo, 973 species of butterflies have been recorded (Otsuka 1988), making identification of every species in the field impossible. For example, Walpole and Sheldon (1999) could only identify less than 50 % of individuals seen on transects to species. Canopy species are also difficult to survey. One way to overcome this problem is to choose families that are easy to identify on wing. Thus in the study, I only surveyed satyrinae, morphinae and riodinidae. These species fly close to the ground and can be reliably surveyed from ground-level.

3.4.2 Measurements of vegetation variables

The primary aim in collecting vegetation data in this study was to investigate impacts of selective logging and to analyze habitat requirements of *R.makuta*. Output from the PCA showed that more than half (53.6 %) of the total variance in the data set was explained by the first three factors. Points of inversion of trees were recorded because trees which grow in closed-canopy forest usually have their first major branch above midway. Size of trees is also important because large trees usually have large canopy areas and the number and size of trees can determine the upper vegetation covers (canopy, understorey and middle level). Vegetation cover is likely to affect butterfly distribution.

The technique used to record larval host-plant (*Selagenella* spp.) was based on the presence or absence of the plant over an area of 40 m² at every station. The importance of *Selagenella* spp. to abundance of *R.makuta* is shown in Equation 3.1 and 3.2 (see section 3.2.2). The use of quadrats to measure vegetation is not practical in tropical rainforest because there are too many seedlings and dense undergrowth. The method used here can be unreliable where plants are small and intermingled but allows a simple and reliable estimation of cover for species such as *Selagenella* that form distinct clumps (Bullock 1996).

Not all tree species can be readily identified in the field. Many of them need to be carefully identified by comparing leaves and flowers with herbarium specimens. Since the forest of western Malesia is dominated by the Dipterocarpaceae, and pioneer species in disturbed forests are usually *Macarangga* spp., it was adequate to record the tree types either as dipterocarps, non-dipterocarpss or *Macarangga* sp.

It is difficult to carry out accurate quantitative analysis of vegetation cover in tropical forest, especially quantifying upper level vegetation cover. In many cases, visual estimation (as used in this study) is the best method because it can be done quickly (Causton 1988, Bullock 1996) compared with more complicated techniques (e.g. hemi photographs using a fisheye lens). In order to standardize the estimation of the vegetation cover, the same two people did the estimates and they were always in close estimation (estimates differed by less than 10 %). In addition to visual estimation of vegetation cover, spherical densiometer readings were also used to measure canopy openness. These readings were also taken by two people and were also in close agreement.

Heights of trees were also estimated. The commonly used method to measure tree heights with a clinometer was impossible in the forest because of the density of other vegetation obstructing the trees being measured. The differences between the estimates of the two observers were always less than 10 %.

3.4.3 Effects of habitat modification on forest structure and R.makuta abundance

From section 3.3.2.1, we know that there were still significant differences in vegetation structure between unlogged and logged forest 10 to 11 years after logging showing that effects of disturbance persist for a long time. Heydon and Bulloh (1997) reported that 25 % of the logged areas at their study site were still dominated by pioneer vegetation 12 years after logging. In my study, unlogged forest had significantly taller trees plus greater canopy and understorey layer which were associated with a high factor 1 score (primariness).

The proportion of dipterocarps was also significantly higher in undisturbed forest, while in disturbed forest, there were higher numbers of pioneer *Macarangga* spp. Selective logging affects the structure of the forest primarily by removing large dipterocarps. In Sabah, average timber extraction volumes are about 118m³ per ha (Marsh & Greer 1992). However, the degree and impacts of selective logging vary from place to place. From this study, middle level cover was significantly higher, and canopy and understorey covers were significantly lower in logged forest suggesting that the removal of large trees gives an opportunity to the middle sized trees to develop vigorously.

Abundance of *R.makuta* was similar in unlogged and logged forest. However, there was a significant difference in abundance among transects and *R.makuta* abundance was highest on transect 3 and was least abundant in transect 4 (both in logged forest). Differences between T3 and T4 may be due to differences in logging intensity. Transect 3 passed through a river catchment area which was less severely logged (Hill 1999). Streams that passed through the transect make the area high in habitat heterogeneity because it contained patches of logged and intact forest and provided large numbers of microhabitats which were suitable for *R.makuta*.

Recolonization of logged habitat can occur from the small unlogged patches on steep slopes and along watercourse such as areas along transect 3. Areas around transect 4, in the other hand, were logged more severely (Hill 1999) and selective logging had more impacts on *R.makuta* on T4. However, overall, there were no impacts of selective logging on *R.makuta* abundance and distribution.

Previous studies have shown that moderately disturbed forest had more butterfly species than undisturbed forest (Spitzer *et al.* 1993, Spitzer *et al.* 1997, Hamer *et al.* 1997, Lewis *et al.* 1998). Other studies showed that moderately disturbed areas had no difference in species diversity compared with undisturbed primary forest (Willott *et al.* 2000). Lawton *et al.* (1998) found that butterfly species richness increased in old-growth secondary forest but decreased in more disturbed areas. Other lepidoptera, such as moths also showed no significance differences in diversity between unlogged and selectively logged forest (Willott 1999). From here we can say that moderate human disturbance to forests may have little or no effect on insect diversity. However, more severe disturbance generally decreases species richness of insect fauna (Wolda 1987).

Selagenella cover, which was the most important factor that determined the occurrence of *R.makuta*, did not differ between habitats. This probably explains why there were no significant differences in *R.makuta* distribution and abundance between habitats. *R.makuta* is a widespread species in closed-canopy forest. This study has shown that moderate disturbance does not effect *R.makuta*.

There was a significant positive correlation between Selagenella and R.makuta as shown in Figure 3.5b but R.makuta abundance did not increase linearly with Selagenella cover. This indicates that above a critical threshold, increasing Selagenella cover has no effect on R.makuta abundance.

In both habitats, *R.makuta* had a clumped distribution. Organisms tend to aggregate when and where they find resources and conditions that favour reproduction and survival (Begon *et al.* 1996). Butterfly distributions have been reported to have a close association with their larval host plants in many species and habitats (Thomas 1991, Braby 1995) but this has rarely been reported for tropical species.

Host plant quality was not investigated but *R.makuta* may aggregate in areas with high quality *Selagenella* available in the forest. This might also explain why the quantity of *Selagenella* spp. did not affect *R.makuta* abundance after *Selagenella* spp. reached a certain density. Areas close to streams with low secondary growth (factor 2) may favour growth of *Selagenella* spp. thus attracting *R.makuta* to these areas, especially since young vigorous plants may be preferred by insects as oviposition sites (Price 1997).

3.4.4 Impacts of selective logging on habitat requirements of R.makuta

Selagenella cover was important for *R.makuta* presence. This was shown by Equations 3.1 and 3.2 Equation 3.1 also showed that *R.makuta* abundance had a negative relation with secondary growth (factor 2) and in Equation 3.2, a negative relation with distance

to stream. This suggested that in unlogged forest, *R.makuta* preferred less dense areas with high *Selagenella* cover and in logged forest, it preferred areas close to streams with high *Selagenella* cover. A study conducted by Hill (1999) showed that *R.makuta* was more likely to occur at stations close to streams in less dense forest. This was true in this study (Equation 3.1 and 3.2). However, in Hill's (1999) study, *Selagenella* cover was not included as an important factor that determined *R.makuta* occurrence. This might be due to the different method used in measuring *Selagenella* cover in the two studies.

Factor 2 and stream were significantly correlated to each other in this study, meaning that although factor 2 was in Equation 3.1, this variable had a strong relation with distance to nearest stream. *R.makuta* did change its habitat requirements due to habitat modification but the changes were relatively small for these two variables. *Selagenella* cover was still the most important factor determining *R.makuta* abundance and this relation was easily understood because *Selagenella* spp. is *R.makuta*'s larval food-plant.

This study shows that selective logging had little impact on *R.makuta* abundance but impacts of repeated selective logging are unknown. Biodiversity may be maintained following the first cut in logged forest. However if *R.makuta* could not substantially change its requirements in disturbed habitat, or the changes on forest structure were more marked, then this species may experience reductions in population size in production forest after the next round of logging. Therefore, there is an urgent need to understand both the immediate impacts of selective logging on forest structural and compositional characteristics and biodiversity. How these features change over periods of forest recovery between logging events have to be identified.

Chapter 4: Seasonal Effects of Rainfall and Sunshine on Ragadia makuta Abundance

4.1 Introduction

People generally refer to temperate regions when considering seasonal effects on organisms. In fact, tropical regions can also experience marked seasonal changes (Bailey 1996). In aseasonal tropical rainforest, rainfall is more than 2,000 mm at all times of the year and there is no dry drought season. On the other hand, in seasonal tropical forests, dry seasons are more pronounced (Bailey 1996). Thus, studies on seasonal changes in tropical regions may be as important as in temperate regions.

In temperate regions, the annual cycle of biological activity is associated with a clearly defined winter and summer and rather less clearly defined spring and autumn (Owen 1971). Thus, much biological activity is reduced in winter when the temperature drops below temperature thresholds for development, and day lengths are shorter. Seasonality greatly influences the abundance of butterflies in temperate regions and their distribution depends on many abiotic factors, particularly temperature and photoperiod which influence the development of eggs, larval and pupae (Pollard & Yates 1995). Significant associations have also been reported between rainfall and the numbers on temperate butterflies (Pollard & Yates 1995). For example, high spring rainfall was reported to have a positive effect on *Aglais urticae* abundance in summer (Pollard *et al.* 1997).

Tropical rainforests are also affected by changes in seasons but there have been very few studies examining seasonal effects on insects, compared with temperate regions. In the absence of pronounced temperature and photoperiod changes over the year in the tropics, rainfall is the primary determinant of season (Readings *et al.* 1995) In some places, rainfall can vary markedly, resulting in clear wet and dry seasons which have strong effects on community structure (Krebs 1978). Rainfall and humidity are two factors that affect butterfly abundance in tropical regions (Braby 1995). For instance, in equatorial Africa, rainfall plays an important role in determining seasonal changes of butterflies (Owen 1971). Rainfall may have positive and negative effects on butterflies. Rainfall is important for plant growth and thus affects host-plant quality. On the other hand, intensive and prolonged rainfall might increase larval and adult mortality and affect adult reproductive activity (Speight *et al.* 1999).

Although tropical regions receive more than 10 hours of daily sunlight, the amount of bright sunlight is generally much less than this due to cloud cover. Typically, average daily sunshine in the tropics is around 5.5 hours (Ewusie 1980). There are three types of sunshine that reaches the forest floor; light passing between leaves (sunflecks), light through gaps and light reflected from leaf and branch surfaces (Mabberley 1992). Sunlight reaching the forest floor is necessary for photosynthesis of ground herbs and larval host plants. For most adult butterflies, including tropical species, sunlight is necessary for flight (Pollard & Yates 1995). Thus, sunlight not only directly affects insects, but also affects their food plants (Krebs 1978).

Tropical lowland rainforest climate is marked by high and even temperature all year with mean temperatures of about 27°C (Mabberly 1992). It is unusual for the temperatures in lowlands to fall below 17°C (Rudloff 1981). The small seasonal variation of temperature of the tropical zone depends partly on the small variation of length of day. For example, mean temperature during the fieldwork months in this study was 26.5°C (March 1999 to February 2000). The highest mean temperature recorded was 27°C which was in April and June 1999, and the lowest temperature was 25.5°C in January 2000 during the study period. Variation in temperature recorded during fieldwork periods in the field centre was therefore small and this is typical for a wet equatorial climate. Monthly temperatures from January 1999 until February 2000 are

shown in figure 4.1. From the graph, it is clear that the temperature was almost constant throughout the study period.

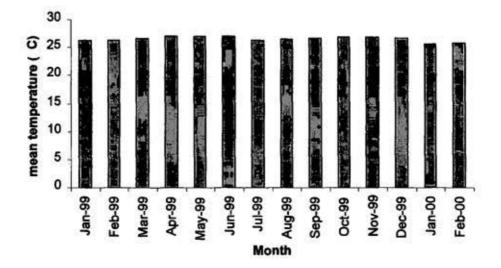


Figure 4.1: Monthly mean temperature recorded at DVFC from January 1999-February 2000

At large scales, climate plays an important role in determining the distribution and abundance of insects, either through its direct effects on population processes or through its effects on the host plants (Sutherst *et al.* 1995). This chapter will investigate the influence of rainfall and sunshine on the distribution and abundance of *R.makuta*. The aims of this chapter were:

- To investigate seasonal changes in *R. makuta* abundance from month to month.
- To examine seasonal changes in *R.makuta* distribution from month to month in terms of the number of observation stations occupied.
- To examine the influence of rainfall and sunshine on *R.makuta* abundance during the study period.

4.2 Methods

4.2.1 Survey technique

R.makuta was surveyed at 80 observation stations along transects T1, T2, T3 and T4 in unlogged and logged forest (see chapter 2) from March 1999 to February 2000. I used methods described by Pollard (1977) and modified by Hill *et al.* (1995), Hamer *et al.* (1997) and Hill (1999). All adult *R.makuta* seen 5m in front and within 5m to the left and right of the transect were recorded while walking at a constant pace from station to station. In addition, *R.makuta* was also recorded within a 10 m radius of each station for 5 minutes. Surveys were conducted during good weather between 10.00 to 14.00 h, corresponding with peak flight activity (Hill 1999). Data were collected by two people (J. Tangah and myself). Each transect was walked twice each month by each recorder. Data from the two recorders were combined for analysis. Sunshine and rainfall data were obtained from the meteorological station at the field centre.

4.2.2 Climate of study area

4.2.2.1 Rainfall

Average rainfall from 1989 to 1999 in DVFC was 2723.4 mm per year (Fig. 4.2). This area is influenced by the effects of two monsoons, with the wetter north-east monsoon from November to March and the south-western monsoon in June and July (Marsh & Greer 1992) and relatively drier seasons between these two periods. 1995 was the highest total rainfall recorded (3,294 mm) and the lowest was in 1997 (1909 mm).

Rainfall in 1997 to 1998 was low due to a severe El Nino-Southern Oscillation (ENSO) event, with was associated with a widespread drought in many parts of SE Asia (Hill 1999). In the past, major El-Nino occurrences were recorded in 1925-26, 1939-41, 1957-58, 1972-73 and 1982-83 (Barry & Chorley 1995, Walsh 1995). ENSO events tend to start in March to May and last for a year and sometimes longer. In Sabah, the

main drought tends to occur from January to May in the second year of the ENSO event and such droughts have occurred regularly over the past 115 years (Walsh 1996). Annual rainfall at DVFC in 1999 was 3,253.50 mm. Monthly rainfall data from December 1998 until February 2000 are shown in figure 4.3. Total monthly rainfall varied from 489.40 mm (January) to 144.80 mm (September).

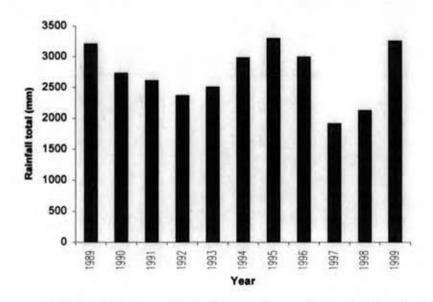


Figure 4.2: Annual rainfall (mm) recorded at DVFC from 1989-1999

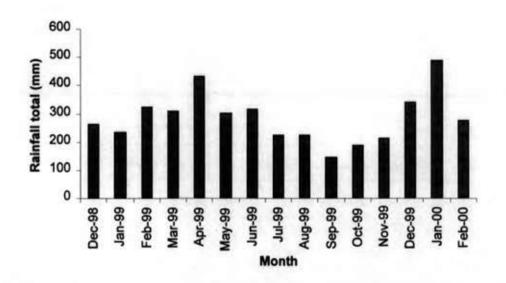


Figure 4.3: Monthly rainfall recorded during the study period

4.2.2.2 Sunshine

At the field centre, sunshine was recorded by using a Cambel-Stokes sunshine meter. This defined periods of bright sunshine from a trace burnt by the sun on a card. Total sunshine recorded during the study period was 1838.8 hours and varies from 89.1 hours in March to 183.8 hours in July. Monthly sunshine hours from December 1998 until February 2000 are shown in figure 4.4.

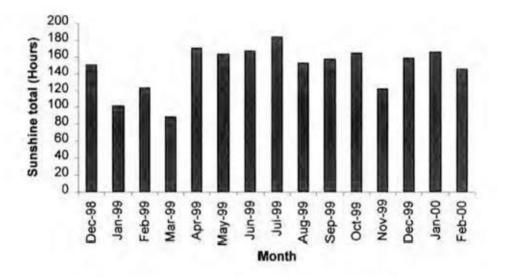


Figure 4.4: Sunshine hours recorded during the study period

4.2.3 Changes in distribution and abundance

The presence or absence of *R.makuta* at each station was recorded each month to investigate monthly changes in the distribution of *R.makuta*. Differences in the relative frequency stations occupied by *R.makuta* each month was investigated by Pearson chi-square. Data were analysed by Kruskal-Wallis one way ANOVA to examine differences in abundance of *R.makuta* when present at every station month by month.

4.2.4 Influence of rainfall and sunshine on R.makuta abundance

To investigate the influence of rainfall and sunshine on *R.makuta* abundance at each station, an analysis was carried out relating the total number of *R.makuta* seen each month with four sets of monthly rainfall and sunshine data.

Butterfly abundance was related to rainfall and sunshine on a month by month basis, relating butterfly abundance to rainfall and sunshine in the months of the survey, the previous month's rainfall and sunshine, sunshine and rainfall two months previously and rainfall and sunshine three months previously. These data were analysed by using multiple stepwise regression incorporating the eight climate variables where the dependent variable was the total number of *R.makuta* seen each month combining all 80 stations. Climate data were calculated over a three month period to cover the development period of eggs and larvae giving rise to adults seen in surveys.

4.3 Results

4.3.1 R.makuta abundance

Table 4.1 shows the number of stations in which *R.makuta* was recorded each month in unlogged and logged forest. Abundance of *R.makuta* when present was also calculated by dividing the total number of adults seen by the number of stations where *R.makuta* was present and is also shown in table 4.1.

Total number of *R.makuta* seen every month in unlogged and logged forest is shown in figure 4.5. From the figure we can see that abundance *R.makuta* was highest in both habitats between August to November 1999. The highest number recorded was in November 1999 with 124 individuals, followed by October 1999 (120 individuals). The lowest number recorded was in May 1999 in both habitats. Over the entire study, the total number of *R.makuta* seen in logged forest was 431 and in unlogged forest was 354.

Month	Number of pres		Abundance when present	
	Unlogged	Logged	Unlogged	Logged
Mar 99	12	12	2.1	1.7
Apr99	17	11	1.3	1.7
May99	8	11	1.4	1.3
Jun99	14	15	1.4	1.5
Jul99	14	13	1.4	1.9
Aug99	16	19	1.9	2.1
Sep99	19	17	2.7	2.2
Oct99	23	24	2.4	2.7
Nov99	22	28	2.1	2.8
Dec99	18	25	1.7	2.2
Jan00	17	18	2.1	1.7
Feb00	13	18	1.4	1.8

 Table 4.1: Total numbers of R.makuta seen each month in logged and unlogged forest

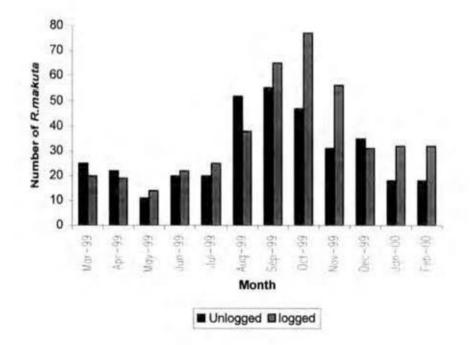


Figure 4.5: Monthly R.makuta abundance in unlogged and logged forest.

4.3.2 Correlations between rainfall and sunshine

To examine the relations of weather data, Pearson correlation analysis was used to investigate the inter-relationships among all three sets of rainfall and sunshine data. Results showed that only sunshine 3 months and 2 months previously were related (Pearson correlation; r = -0.71, P = 0.01). No other variables were related.

4.3.3 Monthly effect

The abundance of *R.makuta* was significantly different between months in both unlogged and logged forest (Kruskal-Wallis chi-square = 27.02, d.f. = 11, P = 0.005) and the number of stations where *R. makuta* occurred was also significantly different from month to month (chi-square = 48.96, d.f. = 11, P < 0.001).

4.3.4 Influence of rainfall and sunshine on R.makuta abundance

Results from multiple stepwise regression showed that rainfall from one month previously had a significant negative effect on *R.makuta* abundance (rainfall previous month; $F_{1,10} = 17.51$, P = 0.002, Slope = -0.26, S.E. = 0.06). There was no effect of rainfall or sunshine at any other interval. Figure 4.6 shows the relation between abundance of *R.makuta* with rainfall one month previously.

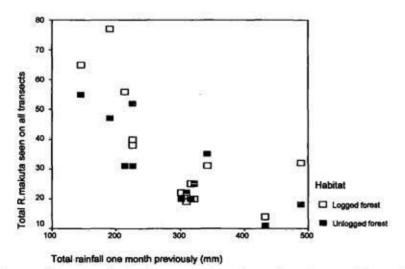


Figure 4.6: Correlation between *R. makuta* abundance with total rainfall one month previously.

4.4 Discussion

There were significant differences in *R.makuta* distribution and abundance from month to month. There was a peak in abundance of *R.makuta* in October and November 1999 and May 1999 recorded the lowest number of *R.makuta* for the year.

Results showed that rainfall from one month previously was significantly negatively correlated with *R. makuta* abundance. Total rainfall in April was the highest for 1999 and this may account for the drop in numbers of adult *R.makuta* seen in May 1999. By contrast, September rainfall was the lowest for the year and the abundance of *R.makuta* increased in October 1999. Rainfall in the previous month might have affected developmental stages of *R.makuta* larvae, and thus affected the abundance of adult *R.makuta* in the following month. Intensive rain might also kill feeding larvae which fall on the ground and die (Speight *et al.* 1999).

Rainfall may disturb the reproductive cycle of insects (Krebs 1978). The poorlyflying *R.makuta* may be affected by rain which may prevent reproductive activities such as mating and oviposition. The effects of rainfall on insects are complex and do not always act directly (Speight *et al.* 1999). Other studies have shown that some butterflies increased in abundance during dry months (Owen 1971, Jones & Reienks 1987 in Braby 1995) although other studies have shown that butterfly abundance increased in wet season (Braby 1995). Sunshine had no apparent affect on *R.makuta* abundance, and there are no other studies showing that sunshine influences tropical insect abundance. Sunshine data sets were not significantly related to rainfall data sets. Only sunshine 3 months previously was negatively correlated with rainfall 2 months previously. This suggested that there was no strong relationship between sunshine and rainfall.

There is no apparent seasonal temperature fluctuation in Borneo and the temperatures are constant all year round. In this study the difference between the highest and lowest temperature recorded was only 1.5 deg C throughout the year. Therefore,

temperature is not likely to be an important environmental variable affecting the tropical butterflies (Owen 1971).

This study showed that rainfall had the greatest influence on *R.makuta*. Braby (1995) suggested that rainfall is an important factor influencing the abundance of *Mycalesis* species through its effects on the quality of larval host plants. Interestingly, Braby's (1995) study was based in the seasonal tropics where there is a marked drought. Other studies have shown that high humidity shortens the development time of insects and prolongs the life of adults (Szujecki 1987). Hill (1999) reported that a severe ENSO drought had a negative effect on *R.makuta*. Butterflies in temperate regions were also affected negatively by drought. For example, drought in 1976 caused local extinction of *Aphantopus hyperatus* in the UK (Sutcliffe *et al.* 1997). During the present study, there was no drought period and rainfall was more than 150 m every month.

In summary, *R.makuta* was negatively affected by rainfall one month previously. This is the first study to show seasonal changes in butterflies in areas that are greatly considered to be aseasonal.

5.1 Introduction

5.1.1 The use of bioindicators

There are three main types of bioindicators; environmental indicators, ecological indicators and biodiversity indicators (McGeoch 1998). The aim of studies using environmental indicators is to select and monitor an indicator taxon that is sensitive to changes in environmental conditions such as soil fertility and pollutant level (e.g. pesticides, heavy metal and acidic pollutant levels). These are the most well-known and widely used indicator taxa in scientific studies (Mitchell *et al.* 1987, Blasco & Puppo 1999). Indicator taxa can also be used to demonstrate the effects of environmental changes (ecological indicator) such as habitat alteration and fragmentation and climate change on ecosystems, or to predict the richness of one or more other taxa (biodiversity indicator; Jeffries 1997, McGeoch 1998). Biodiversity indicators can also be used to select or evaluate protected areas that represent most of the biodiversity of a particular area (Balmford 1988, Faith & Walker 1996, Reyers *et al.* 2000). However, selecting the best indicator taxon for bioindication purposes is always difficult and sometimes controversial (Debinski & Brussard 1992, Pearson 1996, Noss 1999).

A definition of a biological indicator that encompasses all three of these main applications has been developed by McGeoch (1998) "An indicator is a species or a group of species that readily reflects the abiotic and biotic state of an environment, represents the impact of environmental change on a habitat, community or ecosystem, or is indicative of the diversity of a subset of taxa, or wholesale diversity, within an area". Indicator species may be important in conservation research if the chosen species can

act as a 'gauge', such that by studying the indicator species, we can detect the condition of a particular habitat, community or ecosystem.

Given the high diversity of tropical regions, it is impossible to study all taxa. However, if an indicator species could be used to represent the whole community, labour and time could be minimised (Pearson 1996). Data on species richness are important in the conservation of biodiversity and biogeography studies, but the enormous number of species in tropical regions make it extremely time-consuming to evaluate total species richness (Schulze & Fiedler 1999). In order to investigate the usefulness of a potential ecological indicator, it is necessary to find out if it is sensitive to environmental changes.

Marine and aquatic organisms are popular among scientists as indicators of water quality (Lucey 1987, Caffrey 1987). The detection of changes in behavioural patterns and/or a physiological response of aquatic organisms such as fish and crustacea have been used as biological early warning systems for acute toxicity in aquatic environments (Kramer & Botterweg 1993). In terrestrial systems, the use of invertebrate indicators is more recent but the basic concepts and methods originate from the aquatic literature (McGeoch 1998). There have also been some studies using vertebrates such as small mammals and birds as bioindicators. Lunnon and Reynolds (1993) suggested that monitoring the distribution of otter in Ireland can be a useful way of indicating changes in overall habitat and water quality, and the study of bird community structure can be used as a bioindication of landscape deterioration (Bohac & Fuchs 1993).

5.1.2 Insects as bioindicators

Insects comprise one of the largest groups of terrestrial organisms both in terms of species richness and biomass (Speight *et al.* 1999). Insects play a significant role as pollinators, herbivores, predators, prey and parasites, and are thus important in ecosystem functioning (Price 1997). For example, plants which rely on insects for their pollination, may have reduced pollination successes if the distribution and abundance of pollinating insects were reduced, thus disturbing the ecosystem equilibrium. Besides having a strong influence over many ecosystem processes and being highly diverse, insects also consume a wide range of food resources. There are also many species that depend on specific resources and that are sensitive to changes in temperature, humidity, light levels and environmental gradients (McGeoch 1998). Furthermore, their high rates of reproduction also make insects sensitive to environmental changes (Engelmann 1984). In addition, they are generally easy to sample and their taxonomy is often well known (Wettstein & Schmid 1999, Jones & Eggleton 2000).

Most insects rely on plants to survive at least during one of their developmental stages (Hagen *et al.* 1984, Price 1997). Butterflies, for instance, are phytophagous and their larvae are often host-specific (Corbet & Pendlebury 1992, Fiedler 1998). In addition, most adult butterflies feed on nectar or fruits (Owen 1971). This close association with plants has led to the suggestion that insects could potentially be used as bioindicators. Butterflies, termites and dung beetles have been used as bioindicators of habitat quality and species richness and there have been many studies discussing the selection of suitable indicator taxa for the quantitative assessment of biodiversity (Kremen 1992, Pearson 1996, McGeoch 1998). For example, Kremen (1992) found that butterfly assemblages could be used as indicators of habitat heterogeneity due to their sensitivity to topographic and moisture gradients. Beccaloni & Gaston (1995)

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successfully used Ithomiinae butterflies as indicators to predict species richness of other forest butterflies in neotropical regions. Schulze & Fiedler (1999) also suggested that papilionid butterfly diversity could be used to estimate total butterfly diversity in the tropics. Recent studies have shown that moth assemblages can be used as indicators of forest disturbance in Australian rainforest remnants (Kitching *et al.* 2000). Jones & Eggleton (2000) suggested that termites have potential as ecological indicators because termite assemblage composition shows a strong response to habitat disturbance. In this chapter I examine the usefulness of *R.makuta* as an indicator of diversity of other butterflies, particularly species from the sub families Satyrinae and Morphinae and family Riodinidae.

There are several reasons why *R.makuta* might be suitable as an indicator species; it is relatively common in closed-canopy forests and is easy to identify in flight. This species also occurs at high abundance compared to other forest species, but it is not a 'weedy' species and its distribution is restricted to Sundaland and thus it has considerable conservation value. The adults have conspicuous wing colouring making them easily seen even under dense canopy. Although the wing size is relatively small (forewing length 25-30mm) compared with many other tropical butterflies, it is a low-flying species with slow flapping flight which makes it easy to see and therefore is easily recorded from ground-based surveys without having to gain access to the canopy. Being a poor flier, it has been suggested that it might be vulnerable to forest disturbance since this species is confined to closed-canopy forest (Hill 1999). In addition, the larval food-plants for this butterfly (*Selagenella* spp.) can be readily recorded from the ground (Hill 1999).

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The aim of this chapter is:

 To examine the potential use of *R.makuta* as a bioindicator of diversity of other butterflies, particularly species from the sub families Satyrinae and Morphinae and family Riodinidae.

5.2 Materials and Methods

5.2.1 Butterfly data

Butterfly data were collected at 80 observation stations along four transects in unlogged and logged forest using methods described in chapter 2. Data were collected monthly from March 1999 to February 2000. Recording took place only during good weather between 10:00 and 14:00h, which is the time of peak flight activity for butterflies. All individuals of species from the sub-families Satyrinae and Morphinae (Nymphalidae) and family Riodinidae and also one species from family Danaidae (*Idea stolli*) were recorded. These butterflies were selected because these are low flying species that can be recorded from the ground. In addition, most of these species are easy to identify on the wing. All adults seen within 5m in front and 5m to the left and right of the observer were recorded. Each transect (T1, T2, T3 and T4) was surveyed four times per month by two recorders (J. Tangah and myself) and data for the four surveys each month were combined for analysis. Before these surveys were carried out, both recorders were trained to identify all butterflies mentioned above. An identification book was also carried during the surveys to help identify difficult species.

5.3 Statistical Analysis

5.3.1 R.makuta as an indicator for diversity of other forest butterflies

To examine whether *R.makuta* could be used as a biodiversity indicator for other butterflies, a correlation analysis was carried out between the total number of *R.makuta* recorded at each station (total of 80 stations in unlogged and logged forest) and Shannon, Margalef and Simpson's diversity indices of all other butterfly species recorded (Satyrinae, Morphinae, Riodinidae and *Idea stolli*). Two species (*Mycalesis anapita* and *M.patiana*) cannot be distinguished in flight so data were combined for these species for the calculations of diversity indices. Diversity indices were calculated excluding *R.makuta* data. These species diversity indices were selected because these indices are widely used in biodiversity studies and included indices which measure species richness (Margalef's index), species evenness (Simpson's index) and a combination of richness and evenness (Shannon-Weiner index; Magurran 1988).

The equation use to calculate the Shannon index is;

 $H' = -\sum p_i \ln p_i$

Where P_i is the proportional abundance of the *i*th species.

Margalef's index is an estimate of species richness. The equation is as follows;

 $D = (S - 1) / \ln N$

Where S = species number, and N = total number of individuals in the sample Simpson's index is a measure of species evenness. The equation is as follows;

$$D = \sum [n_i (n_i - 1)] / [N(N - 1)]$$

Where n_i = the number of individuals in the *i*th species, and N= the total number of individuals.

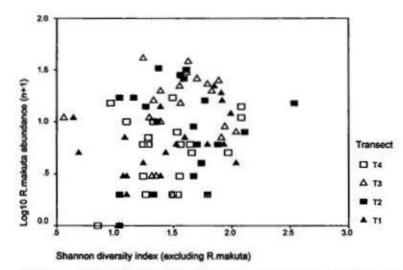
5.4 Results

5.4.1 R.makuta and other butterflies

A total of 34 species of butterflies were recorded from the sub-families Satyrinae and Morphinae and Riodinidae, including *Idea stolli* (Danaidae; Table 5.1). Only 10 individuals (0.5%) could not be identified and these were not included in subsequent analyses. Approximately equal numbers of unidentified individuals were recorded in unlogged and logged habitat and thus are unlikely to affect subsequent analysis.

Pearson correlation analysis showed a significant positive relationship between *R.makuta* abundance and Shannon diversity index of other butterflies at each station (r=0.27, P= 0.02). A positive and significant r value in the data showed that increasing abundance of *R.makuta* occurred at stations with increasing diversity of other butterflies (figure 5.1). This suggests that *R.makuta* abundance is a good indicator of diversity of other satyrid and riodinid butterflies. Figure 5.1 shows the relationship between *R.makuta* abundance and diversity of other butterflies at stations. There were no significant correlations between *R.makuta* abundance and either Margalef's (r = 0.17, P = 0.13) or Simpson's (r = 0.19, P = 0.10) diversity indices.

Qualitatively different results were obtained if the analyses were carried out separately for unlogged and logged habitats. There were no significant correlations between *R.makuta* abundance in unlogged forest (40 stations) and logged forest (40 stations) with any of the diversity indices of other butterflies (in unlogged forest; Shannon index r = 0.31, P = 0.06; Margalef index r = 0.19, P = 0.23; Simpson's index r = 0.17, P = 0.29, and in logged forest; Shannon index r = 0.13; Simpson's index r = 0.19, P = 0.23; Margalef index r = 0.16, P = 0.33; Simpson's index r = 0.19, P = 0.25).



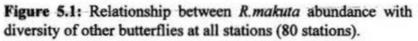


Table 5.1: Abundance of butterfly species recorded in logged and unlogged forests at the study site.

	Unlogged	logged	total
NYMPHALIDAE			
Satyrinae			
Erites argentina Butler	29	28	57
Erites elegans Butler	15	21	36
Ypthima baldus Fabricus	18	19	27
Ypthima fasciata Hewitson	67	85	152
Ypthima pandocus Moore	1	2	3
Lethe chandica Moore	0	1	1
Melanitis leda Linnaeus	1	1	2
Mycalesis anapita/patiana	93	42	135
Mycalesis dohertyii Elwes	9	4	13
Mycalesis fusca (Fruhstorfer)	0	1	1
Mycalesis horsfieldi Moore	0 5 5 5	0	5 5
Mycalesis kina Staudinger	5	0	5
Mycalesis maianeas Hewitson	5	25	30
Mycalesis oroatis Hewitson	26	7	33
Mycalesis orseis Hewitson	7	7	14
Neorina lowii Doubleday	15	9	24
Ragadia makuta Horsfield	367	439	806
Morphinae			
Amathusia phidippus Linnaeus	0	1	1
Thaumantis noureddin Westwood	1	0	1
Thaumantis odona Godart	6	14	20
Faunis canens Hubner	20	22	42
Faunis kirata de Niceville	1	1	
Faunis stomphax Westwood	4	3	2 7
Zeuxidia amethystus Butler	1	0	1
Xanthotaenia busiris Westwood	33	56	89
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Total	903	929	1832
Unidentified	4	6	10
Idea stolli Moore	85	82	167
DANAIDAE			
Taxila haquinus Fabricius	1	1	2
Zemeros flegyas Cramer	1	1	2
Zemeros emesoides Felder	6	6	12
Paralaxita telesia Hewitson	13	11	24
Paralaxita orphna Boisduval	52	30	82
Paralaxita damajanti Felder	11	5	16
Abisara kausambi Felder	0	1	1
Abisara geza Fruhstorfer	0	2	2
RIODINIDAE	1 No. 1		12 180

5.5 Discussion

Transect techniques were used in this study to survey Satyrinae, Morphinae and Riodinidae and also one species from the family Danaidae (*Idea stolli*). Besides being able to cover a wide range of habitats (total of 8 km of transect surveyed), this method has been shown to be more effective in terms of the rate of individuals seen and species accumulation compared with other commonly used methods such as fruit baited-traps (Walpole & Sheldon 1999). Satyrinae, Morphinae and Riodinidae and *Idea stolli* were selected in this study because these butterflies are easy to identify on the wing and fly close to the ground (Corbet & Pendlebury 1992), and thus can be surveyed reliably from the ground. Less than 0.5% of individuals could not be identified to species.

R.makuta was selected for study because it is relatively abundant and is conspicuous and easy to record. Results from this study show that the abundance of *R.makuta* can be used to indicate species richness of other butterflies. This suggests that *R.makuta* could be used as a surrogate species in order to study broader butterfly assemblages in an area. All species recorded in this study have broadly similar habitat requirements in that they are generally confined to dense, closed-canopy forest where they fly close to the ground. Thus the close agreement between *R.makuta* and diversity

of other species may be due to their similar habitat requirements in terms of forest structure. From chapter 3, we know that *R.makuta* generally prefers areas with high host-plant cover which are close to streams. Although other butterflies have different larval host plants, areas close to streams may also be suitable habitats for larval hostplants of other butterfly species. Satyrids feed on a wide variety of grasses and bamboos (Corbet & Pendlebury 1992) and areas close to streams may be favourable for the growth of these host plants as well.

Only the Shannon diversity index gave a significant correlation with *R.makuta* abundance if data from unlogged and logged forests were combined. This may be due to the differences in the calculations of the indices. Simpson's index expresses the degree of species evenness in the data while Margalef index reflects the species richness elements of diversity (Magurran 1988). Shannon index, on the other hand, incorporates species richness and evenness together into a single measure, and thus is more sensitive to species abundance and richness. When calculations were made separately for the unlogged and logged forest habitats the sample size may have been too small to obtain significant results. However, the variance between *R.makuta* abundance and Shannon diversity index in both habitats was high as seen in figure 5.1. Thus *R.makuta* abundance will give a high range of prediction values for diversity of other butterflies.

These results contrast with other studies suggesting that a single species is not suitable as a biodiversity indicator (McGeoch 1998). Beccaloni & Gaston (1995) used ithimiinae butterfly and Schulze & Fiedler (1999) used a papilionid butterfly in order to predict total butterfly diversity and species richness of other forest butterflies. In this study, I only recorded understorey species which fly close to the ground and I have no data to show if *R.makuta* can also be used as an indicator of all forest butterfly species. This deserves further study. This study suggests that *R.makuta* could be used as an

indicator of other understorey butterfly species but there are no data to test if it could be an indicator of other groups of organisms (such as birds or small mammals etc.). Other taxa might respond differently to habitat modifications and disturbances (Lawton *et al.* 1998). Indicator species are likely to be most effective when they are used to indicate changes in other closely-related species with similar ecologies. Given that *R. makuta* can be recorded relatively easily, this species may be an important tool for conservation studies.

Chapter 6: General Discussion

This thesis focuses mainly on *R.makuta*, but is also concerned with more general aspects related to conservation of forest butterflies. Conservationist have realised that many organisms have or are heading towards extinction (Whitmore 1997). In many cases, extinction of organisms can happen very rapidly due to destruction of breeding habitats (Bawa & Seidler 1998). The rapid increase of human populations worsens the situation. Many areas that are rich in biodiversity have been modified for human use (Sharma *et al.* 1992). Fortunately, people are starting to realise that deleterious effects on biodiversity will also affect their lives because humans are dependent on the natural environment for many raw materials such as food, medicines and water (Primack 1998).

The destruction of rainforests is of prime importance to conservationists. More than half of the world's species occupy these areas and the rapid disappearance of rainforests is worrying because this will affect biodiversity in these forests (Lovejoy 1997). Several methods of commercial logging were introduced, such as selective logging and reduced impact logging, that were claimed to be less destructive, but this is often not the case and the loss of biodiversity continues (Lambert 1992). Severe disturbance such as clear felling generally has detrimental impacts for all forest species. Yet not all forest species are adversely affected by less severe forms of disturbance (Wolda 1987).

Chapter 3 investigated of the effects of selective logging on forest butterflies. *Ragadia makuta* was chosen as the target species because this species is among one of the most abundant species in closed-canopy forests and is easy to identify and thus to study. Importantly, the larval host-plant of *R.makuta* is known making it possible to relate butterfly abundance to that of its larval host plant. This has rarely been done in tropical regions. Transects technique were employed in this study because this was the most suitable method for several reasons:- transects cover a large area and sample a wide variety of habitats (Walpole & Sheldon 1999). They also allow the abundance of butterflies to be related to various aspects of vegetation within the same area. A total of 806 individuals of *R.makuta* were observed throughout the year's fieldwork period. Habitat assessment in tropical areas can be difficult due to the high diversity of plant species and heterogeneity of rainforest structure. In this study, vegetation variables were chosen to measure those parts of vegetation structure that were more likely to be most important to butterflies. Selective logging changed forest structure by reducing the number of large trees and thus reducing canopy and understorey cover. There was no significant difference of *R. makuta* abundance in logged and unlogged forest. There was some evidence that R.makuta changed its habitat requirements due to these changes. However, the changes were relatively small and availability of larval food-plants was the most important factor that determined *R.makuta* abundance and distribution in both unlogged and logged forest. Availability of larval food-plant did not differ between habitats and my results indicate that as long as there are suitable resources, R. makuta can survive in selectively logged forest. However, we do not know whether repeated selective logging will affect the availability of habitat for butterflies.

The importance of abiotic factors (sunshine and rainfall) in affecting *R.makuta* abundance was studied in chapter 4. In tropical regions, temperature is generally not an important factor influencing the abundance of butterflies as there is little variation in temperature throughout the year. For example, the difference between the highest $(27^{\circ}C)$ and the lowest $(25.5^{\circ}C)$ mean temperature at the study site during the study period was only 1.5 deg C. Sunshine also did not affect *R.makuta* abundance. However, *R.makuta* abundance was affected by rainfall and increasing rainfall in the month before surveys had a negative effect on *R.makuta* abundance in the subsequent month. This suggests that high and prolonged rainfall may adversely affect the development of larvae. The distribution and relative abundance of *R.makuta* varied from month to

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month. This suggested that communities show seasonal changes even in tropical forests that are generally considered to be aseasonal. This was also true for other forest butterflies in seasonal rainforest (Owen 1971, Spitzer *et al.* 1993, Braby 1995) but to my knowledge has not previously been shown in aseasonal areas.

The potential use of *R.makuta* as an indicator of abundance of other satyrid and riodinid was examined in chapter 5. Abundance of *R.makuta* was positively related to abundance of other satyrinae, morphinae and riodinidae species. One possibility for this result is that broad habitat requirements of other satyrinae, morphinae and riodinidae are similar to those of *R.makuta*. Although *R.makuta* has a different larval host-plant to other species, there might be other biotic or abiotic factors that limit distributions of all these species. Many of these species are dependent on closed canopy forest and the distribution of *R.makuta* may be a good indicator of this habitat. This result suggests that *R.makuta* abundance could be used to indicate relative abundance of these other families. Conservation measure for these two families (or possibly other butterfly families) could then be developed from information gained from *R.makuta*. However, further studies have to be conducted to see if *R.makuta* can be used as an indicator of all forest species.

As areas of natural vegetation decline especially in tropical regions, there is concern that this will be associated with a decline in biodiversity. If the destruction of tropical rainforests continue, it is possible that approximately 50% of tropical species will have gone extinct by 2040 (Price 1997). The best way to conserve insects is to conserve their natural habitats. Speight *et al.* (1999) stated that four major ecological considerations that should be taken into account for insect conservation: 1) all habitat important to insects should be conserved and managed appropriately, 2) habitat areas should be sufficiently large, 3) each habitat type should be represented and 4) appropriate habitat management strategies should be adopted. However, until now, insect conservation has not been considered important compared with the large economic rewards to governments from logging. Commercial logging is likely to continue but for forest insects, selectively logged forests which have been logged using less destructive methods (e.g. Reduced Impact Logging; Pinard & Putz 1996) may still provide suitable breeding habitats. This study has shown that selectively logged forests provide suitable habitats for *R.makuta*. This may be also be the case for other forest insects as well as long as the disturbance is not severe.

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