Responses of fruit-feeding butterflies to selective logging in Sabah, Borneo

Benedick, Suzan

Responses of Fruit-feeding Forest Butterflies to Selective Logging in Sabah, Borneo.

M.Sc. thesis submitted

to

University of Durham

Department of Biological Sciences

by

Suzan Benedick

2001

Declaration

The candidate confirms that the work submitted is her own and that appropriate credit has been given where reference has been made to the work of others.

Copyright ©

Responses of Fruit-feeding Forest Butterflies to Selective Logging in Sabah, Borneo.

M.Sc. thesis submitted by Suzan Benedick, 2001

ABSTRACT

This study investigated the impacts of selective logging on tropical butterflies in lowland dipterocarp rainforest of Sabah, Malaysia (Borneo). Fruit-baited traps were used to survey butterflies in unlogged forest and forest that had been selectively logged 10 - 12 years previously in 1988 and 1989. The study focused on butterflies in the sub-families Satyrinae, Nymphalinae, Morphinae and Charaxinae (Nymphalidae). Traps were set up along four transects on existing paths and trails in unlogged forest (two transects, total length 4 km) and logged forest (two transects; total length 4 km). Traps were hung 1-2 m from the ground at 100 m intervals along transects (total of 80 traps). Traps were operated for 12 days each month. A total of 3996 adult butterflies was recorded from 63 species over a period of one year (October 1999 - September 2000). Most of the butterfly species that were present in unlogged forest were also present in logged forest. There was little difference between habitats in numbers of individuals or numbers of species recorded in Shannon-Wiener, Simpson's or Margalef's diversity indices. These results show that selective logging had little effect on butterfly species diversity 10 – 12 years after logging. There was, however, a significant difference among transects, and transects in logged forest had both lowest and highest species diversity (Shannon-Wiener). These results may be due to differences between transects in the intensity of logging. There was no evidence that selective logging resulted in the loss of butterfly species with more restricted geographical distributions. Dispersal and longevity were investigated in several of the more abundant species. Dispersal and longevity distributions fitted negative exponential functions showing that the study species were dispersing randomly and had a constant rate of survival over time. Dispersal and longevity did not differ between habitats or sexes but did differ between species in relation to body size and subfamily. The maximum distance moved by an individual in this study was 4670 m and the maximum lifespan was 175 days (*B. dunya* in both cases).

ACKNOWLEDGEMENTS

My greatest gratitude goes to my supervisors Dr Keith C. Hamer, Dr Jane K. Hill and Dr Tom N. Sherratt for their invaluable guidance throughout my MSc studies. Thanks to them for their expertise, knowledge and skills in making this project efficient and successful, as well as making my stay at Durham wonderful and comfortable.

I would also like to thank the British Government's Darwin Initiative (DETR) for their financial support, which has made my project so successful. I also thank the Danum Valley Management Committee for permission to work at Danum (project number DV 158). This research was carried out whilst I was a participant in The Royal Society's South East Asia Rainforest Research Programme.

It is my pleasure to thank to Datin. Assoc. Prof. Dr Maryati Mohamed (Institute for Tropical Biology and Conservation, UMS) for advising and encouraging me to further studies. Thanks also to Dr Chey V. Khen (Section of Entomology, Forest Research Centre, Sepilok) for sharing his expertise in butterfly genitalia dissection and identification. To all my friends, particularly Glen Reynolds (Senior Scientist), Joseph Tangah, Mohd. Fairus Jalil, Mahadimenakbar M. Dawood, Nazirah Mustaffa, Mike Bernadus, Hamzah Tangki, Januarius Gobilik, David Magintan, Aning Amat, Nasir, Johnny, Mael, Saidih, Jamil, Apek, Alex, Karim, Melvin, Asnah, and all who know me. Thanks for your help and friendship.

For my father (Benedick Ahkin) and mother (Loyni Egoy), brothers and sister - thank you for your constant support, love and encouragement. Especially to Harry Benedick, thanks for the wonderful maps and photographs, and Ricky Godwin, thanks for your support, love and understanding.

Suzan Benedick
Universityof Durham
Winter / Spring 2001

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

Pages

CHAPTER ONE

GENERAL INTRODUCTION

1.1 Biodiversity

Biodiversity can be defined as the variety and variability among living organisms and the ecological systems in which they exist (Gaston & Spicer 1998). It can be divided into genetic diversity, organismal diversity and ecological diversity (Gaston & Spicer 1998). Ecological diversity refers to the diversity of natural habitats, organismal diversity is the variety of living organisms on earth and genetic diversity refers to the variety of genes within a species. All these three types of biodiversity are currently threatened by many different kinds of disturbance including habitat destruction, pollution, overharvesting, introduction of alien predators and pathogens, wholesale exchanges of species among regions and climate change (Diamond 1989; Leemans 1996).

Anthropogenic perturbations to natural habitats are altering the earth's ecological systems and structures, disrupting interdependencies between species and isolating populations. As a result biodiversity is an issue of great concern (Janzen 1986; Myers 1989; Vrijenhoek 1989). Biodiversity studies are still lacking because a large proportion of biodiversity still remains undescribed particularly in poorly known habitats such as marine environments, savannas, soils and tropical rainforests, and poorly known taxa such as microorganisms and some invertebrates (Wilson 1989).

The total number of described species on earth has been estimated to be between 1.5 and 1.6 million (Terbough 1992) and estimates of the number of undescribed living species range up to about 5 million, with the majority of undescribed species being from the tropics (Cohen and Porter 1993). Tropical regions lie between the Tropic of Cancer (23.5^0 N) and the Tropic of Capricon (23.5^0S) and in most cases have higher biological diversity than temperate regions (Wilson 1992; Orians *et al.* 1996). Tropical regions are also characterized by small annual temperature fluctuation and high annual precipitation, with rain occurring throughout the entire year (Ewusie 1980). Many theories have been proposed to explain high tropical diversity but none of the theories have been universally accepted as adequate.

One possibility is that tropical ecosystems have developed for a longer period of time and are more stable climatically than other ecosystems. Fossil evidence shows that some primitive tree genera and other organisms from the Cretaceous and early Tertiary periods some seventy million years ago, are found in tropical rainforests (Richards 1996). Tokeshi (1999) also suggested that higher tree species richness in tropical forests is due to the long period of time available for the taxonomic diversification of tropical tree lineages.

One of the most powerful factors controlling tropical species diversity is probably climate (Wilson 1992; Richards 1996). High solar radiation, temperature and rainfall promote high net primary productivity (ca 16 tonnes of carbon ha^{-1} $year^{-1}$; Mahli & Grace 2000) and high humidity additionally promotes a wide variety of plant growth forms, allowing species to grow beneath the canopy by increasing their leaf area, without experiencing difficulties of water loss through stomata (Huston 1994). These both provide abundant niches for herbivorous animals. In addition, constant availability of resources such as fruit and nectar promote specialization and coevolution of plants and animals, which can further increase diversity. However more research is needed to fully understand species diversity in the tropics and there are many other factors that need to be considered such as short generation times and poor dispersal leading to higher rates of speciation (Heard 1991).

Insects are the most diverse animals on earth, with an estimated 750,000 species (Speight *et al.* 1999) and more than 50% of all insects species are phytophagous (Atkin 1988). Coleoptera are the most diverse order of insects (300, 000 species), followed by Lepidoptera (110, 000 species) and Diptera (85, 000 species) (Speight *et al.* 1999). Insects are thought to have higher diversity in tropical rainforests than any other habitat (Stork 1991; Speight *et al.* 1999). For instance Park (1992) estimated that each species of rainforest tree might support more than 400 species of insect.

Insects play an important role in ecosystem functioning by acting as decomposers, pollinators, herbivores, predators, parasites and natural enemies of potential pests (Atkins 1988). Some groups of insects have been suggested as good indicators of impacts of habitat modification on biodiversity and ecological processes (Speight *et al.* 1999). For example, tiger beetles (Coleoptera; Cicindelidae) (Rodriguez *et al.* 1997) and ants (Hymenoptera) (King *et al.* 1998) have been suggested as being suitable for indicating ecological changes in tropical forest due to their rapid response to habitat disturbance, in particular their sensitivity to the clearance of the tree canopy. Suitable insects in this context have stable and well-known taxonomy, well understood biology and natural history, and are sensitive to habitat change (Speight *et al.* 1999). Tropical butterflies have also been suggested as good indicators due to their sensitivity to environmental changes (Corbet & Pendlebury 1992; Kremen 1992).

Butterflies are well known taxonomically and their life histories and larval food plants are generally well understood (Yong 1983). Butterfly species richness is higher in tropical regions than in temperate regions (Hawksworth and Kallin-Arroyo 1995; New 1997). In Borneo, there are about 1000 species of butterflies (Otsuka 1988) whereas in the whole of Europe, there are only about 360 species of butterfly with only 68 species in the United Kingdom (Sterry 1995).

1.2 Tropical rainforest

Tropical forests have existed for more than 70 million years since the early Tertiary period (Richards 1996). They occur in the inter tropical zone around the equator and include rainforest, monsoon forest, thorn forest and savanna forest (Collins *et al.* 1991). Tropical rainforests are defined as evergreen moist forest with trees ranging from 20m to 45m high and often taller, rich in thick-stemmed lianas, and in woody as well as herbaceous epiphytes (Whitmore 1998). They occur in perhumid climates, where rain occurs during the entire year with monthly rainfall more than 60mm. Tropical rainforest occurs in all three tropical land areas: neotropical forest in South America (total area = 4 x 10^6 km^2), Malesian forest in Southeast Asia and tropical Australia (total area = 2.5 x 10^6 km^2) and African tropical forest (total area = 1.8 x 10^6 km^2).

Tropical forests are rich in animal life and plants compared to temperate forests (Richards 1996). For example, although lowland forests in Malaysia only cover about 19 million hectares of land, they contain 20,000 to 80,000 species of invertebrate (Sham 1998), 200 species of mammals, 624 species of birds, 140 species of snakes and 165 species of frogs and toads (Yong 1998).

Tropical forests are important in maintaining climatic conditions, increasing penetration of water into the soil, slowing down water run-off and preventing erosion (Whitmore 1998). They are also important as sources of oxygen and sinks of carbon dioxide and as filters of dust particles and pollutants (Sham 1998). Global climates are becoming warmer, probably because of the increasing amount of certain gases in the atmosphere, particularly carbon dioxide, nitrous oxides, methane and chloro-flurocarbons which absorb thermal radiation emitted by the earth's surface. The recent rapid loss of tropical forests is contributing to this warming through increased emission of carbon into the atmosphere (Myers 1986; Mahli & Grace 2000). Forests also provide shelter and food for animals and plants, and are the sources of timber and other forest products.

1.3 Commercial Logging in Southeast Asia

The most distinctive feature of some Southeast Asian rainforests is the abundance and richness of species in the family Dipterocarpaceae. These species make up more than 50% of the total volume of large trees in the forest (Marsh and Greer 1992; Newbury *et al.* 1992). In Borneo, there are about 287 species and 9 genera belonging to the Dipterocarpaceae (Whitmore 1984). The Dipterocarp timber trade began in the 1950s and occurred first in the Philippines, followed by Peninsular Malaysia and Sabah in the 1960s and Indonesia in the 1970s (Collin *et al.* 1991). In Malaysia, log production peaked at 43.5 million m^3 in 1992, then decreased to a predicted 33 million m^3 per annum in 2000 (May 1998). Commercial logging is responsible for one quarter of the annual loss of primary rainforest around the world and causes serious damage to tropical forests through soil disturbance and compaction, stream sedimentation and damage to residual trees and understorey vegetation.

There are two types of commercial logging techniques that are used in Southeast Asia: clear felling and selective logging. Clear felling is considered the most environmentally damaging of all logging systems because it removes all trees in an area and the forest is converted to a different land use (Park 1992). By contrast, selective logging removes only 12 to 15 stems per hectare of the most valuable timber trees. However extraction levels average 52 m^3 ha^{-1} in Peninsular Malaysia, 90 m^3 ha^{-1} in Sarawak and 120 m^3 ha^{-1} in Sabah (Johns 1988). Selective logging can remove 50% of the total tree cover in the forest and can cause widespread damage to understorey plants either directly or indirectly through changes in forest microclimates (Whitmore 1990). Seedlings, saplings, and poles of commercial species are also lost during logging operations. It is estimated up to 30% of the area is left as bare ground and 30-60% of remaining trees are also damaged (Mabberly 1992). In recently logged forest, loss of canopy cover results in more light reaching the forest floor, higher temperatures at ground level and greater wind turbulence. Skid trails (networks of bulldozer paths) and landing areas (where logs are stored and processed) are usually left with much soil compaction and erosion and are often infertile.

In Sabah (northern Borneo), both clear felling and selective logging are practised. During the 1980s, many areas were selectively logged using conventional practices; all commercial stems of Dipterocarpaceae > 0.6m DBH were extracted using tractors and high lead techniques. Timber trees were removed from up to 25^0 slopes but buffer zones were left around major rivers and in river catchment areas. High lead sites were usually on tops of hills and slopes and enabled logs to be winched out using cables to collecting points. Alternatively, tractors dragged the logs to landing areas. High lead extraction is no longer practised in Sabah because it was considered too damaging to the forest structure (Whitmore 1984).

Reduced Impact Logging methods are being tried out in some part of Malaysia, for example at Hulu Langat Forest Reserve, in the state of Selangor, Peninsular Malaysia and at Danum Valley, Sabah. Guidelines for reducing the impact of logging include cutting of climbers before logging, improving layouts of roads and skid trails, minimal use of bulldozers and post-harvest removal of stream obstructions (Putz *et al.* 1996). Directional felling is also carried out to prevent damaging fruit and non-timber trees and some 'mother' trees are also left to provide future seeds and improve regeneration.

1.4 Effects of disturbance on forest biological communities

Disturbance, both natural and anthropogenic, has long been recognized as an important factor affecting natural forest ecosystems (Foster 1980; Diamond 1989). Logging disturbance effects the forest fauna for a number of reasons including direct effects of the logging operation, the impacts of the loss of the forest canopy and the subsequent slow regeneration rate of the vegetation (Whitmore 1984, 1998). However habitat disturbance may have different implications for different species of animals; some species will usually be found at higher density in more disturbed areas (e.g. *Elephas maximus*) whereas other species achieve higher densities in undisturbed forest (e.g. *Dicerorhinus sumatrensis* and *Pongo pygmaeus*) (Johns 1988). A study at Danum Valley, Sabah found a lower birth rate and greater mortality among infant primates in logged forest due to a drastic reduction in food availability. However the effects on primates were temporary and populations quickly returned to normal, probably because of their ability to change their diet and feeding behaviour (Johns 1992; Laidlaw 1998).

Several authors have suggested that gap and forest edge species might benefit from selective logging (e.g. Lambert 1992; Hill *et al.* 1995) although species dependent on closed-canopy forest might be reduced in density and become locally extinct following logging (Holloway *et al.* 1992; Heydon & Bulloh 1997). Species with broad ecological niches such as some primates, squirrels and threeshrews (Laidlaw 1998) may be less vulnerable to commercial logging because they are able to cope and persist in the fragmented areas, although their density and diversity may be affected. However more work is needed to investigate the effects of logging disturbance on different animal communities in tropical rainforest.

Butterflies are sensitive to changes in temperature, humidity and light levels, which are all affected by habitat disturbance (Smart 1991). Some studies have shown that moderate disturbance through selective logging may increase butterfly diversity (Damborgh & Aaen 1999; Willott *et al.* 2000). However, other studies have found the opposite (see review by Hamer & Hill 2000). Moreover, butterflies that are restricted to closed-canopy dense forest may be more vulnerable than other species to logging disturbance which opens up the canopy (Hill *et al.* 1995; Hamer *et al.* 1997). More work is needed to explain the effects of habitat disturbance on butterfly faunas in tropical rainforests.

In many tropical areas, butterflies are dependent on the seasonal availability of larval food resources and suitable weather conditions (Wolda 1988). For instance Braby (1995) reported that some Satyrinae (Lepidoptera; Nymphalidae) peaked during the wet season in response to an increase of the availability and quality of their larval food plant, whilst Owen *et al.* (1972) recorded that the abundance of *Acraea lycoa* was influenced by the availability of *Pouzolzia guineensis* Benth (Urticaceae), a plant which disappears in the dry seasons, and which is only really abundant towards the end of the wet season. This indicates that tropical butterfly populations may exhibit seasonal variation in abundance, particularly in the seasonal tropics. Long-term studies are thus required to account for possible seasonal variation in species richness and abundance.

1.5 Study site

The Malaysian state of Sabah covers an area of 73, 731 km^2 on the island of Borneo (Figure 1.1). Large trees in Sabah, particularly in the eastern half of the state provide the most important source of the state income. Less than 50% of Sabah (191, 835 ha) is currently forested, whereas in 1953, 86% of the state was covered by forest (Marsh & Greer 1992). Large areas of the forest in Sabah (1.0 million ha) are owned by the state, but timber harvesting is contracted to private companies in the form of concessions administered by the Sabah Department under the Forest Enactment 1986. This study took place at Danum Valley (Figure 1.1) in the Ulu Segama Forest Reserve (USFR), one of the seven forest reserves in the Yayasan Sabah concession.

1.5.1 The Yayasan Sabah Concession

Yayasan Sabah (The Sabah Foundation) was established under the enactment of Sabah state legislature in 1966 (Marsh & Greer 1992). In 1970, Yayasan Sabah was allocated 854, 700 ha of timber land with which to generate revenue from log sales. In 1984, this area was increased to 972, 804 ha, including the two conservation areas that remain unlogged; Danum Valley Conservation Area (43, 800 ha) and Maliau Basin (58, 840 ha). The Yayasan Sabah concession (excluding Danum Valley and Maliau Basin) are divided into annual 'coupes' of between 2000 ha and 5000 ha, and then sub-divided into logging blocks (Nussbaum 1995). In Sabah, logging is carried out on a 25-40 year cycle, and Yayasan Sabah will still own the concession during the second rotation of logging.

This thesis investigates the impacts of selective logging on the diversity and abundance of tropical rainforest butterflies at Danum Valley. The study areas include forest which was selectively logged in 1988 and 1989, approximately 10 years prior to this study, and unlogged forest within the largest Protection Forest Reserve (43, 800 ha) in Sabah. Chapter 2 describes the study site in more detail and the general methodology I used for this study. Chapter 3 describes the impacts of selective logging on diversity and abundance of butterflies. Chapter 4 describes butterfly dispersal and longevity in logged and unlogged forest. Chapter 5 describes the impacts of selective logging on butterfly species in relation to their geographical distribution. Chapter 6 discusses the findings of this study and suggests some recommendations for future studies on tropical rainforest butterflies.

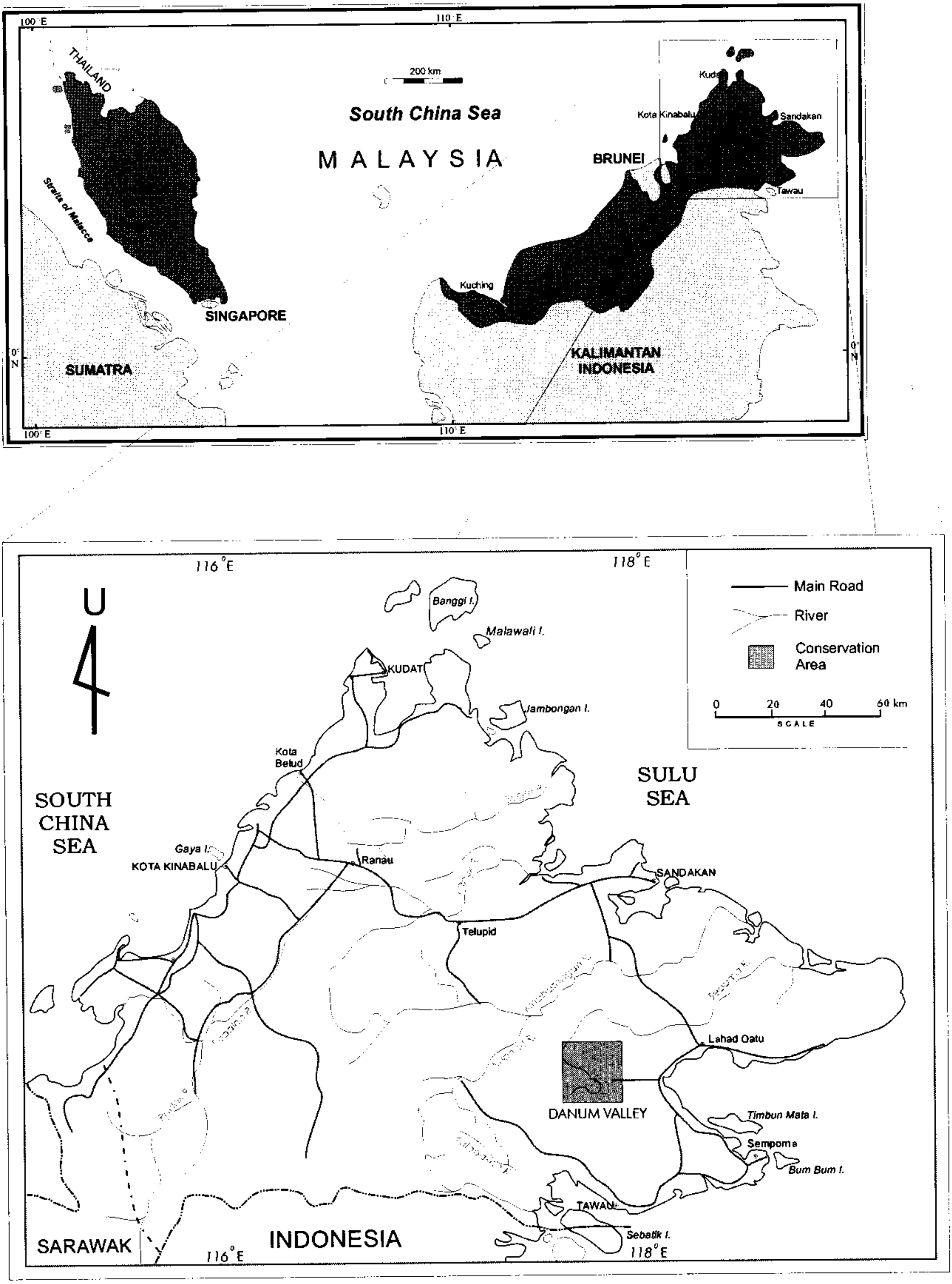


Figure 1.1 : Location of Danum Valley in State of Sabah, Malaysia.

CHAPTER TWO

GENERAL METHODOLOGY

2.1 Introduction

The Ulu Segama Forest Reserve contains the Danum Valley Conservation Area (DVCA) which covers an area of 43, 800 ha of protected unlogged forest (Figure 2.1). DVCA was established in 1984-85 through a Memorandum of Understanding between Sabah Forestry Department, Yayasan Sabah, and the University Kebangsaan Malaysia (Sabah Campus). In 1995, DVCA was redesignated as a First Class Protected Forest Reserve; this area will remain undisturbed and is protected from any form of timber concession. This area has been shown to be highly diverse for plants (Newbury *et al.* 1992; Marsh and Greer 1992) and animals (Collins *et al.* 1991; Johns 1992; Lambert 1992).

Adjacent to the Ulu Segama Forest Reserve, on the eastern edge of DVCA, is the Danum Valley Field Field Centre (DVFC; 5.01^{0}N, 117.47^{0}E). DVFC is ideally located for access to both primary forest and logged forest at different stages of forest recovery. The development of DVFC began in 1984 and was completed in August 1986, to provide facilities for scientific research, education and conservation.

2.1.1 Ecology of the Danum Valley Conservation Area

2.1.1a Geography and Physiography

Most of the DVCA lies in rugged terrain at moderate elevation in a complex and actively eroding landscape (Marsh & Greer 1992). These areas are of undulating to steep terrain and lie approximately 150m above sea level.

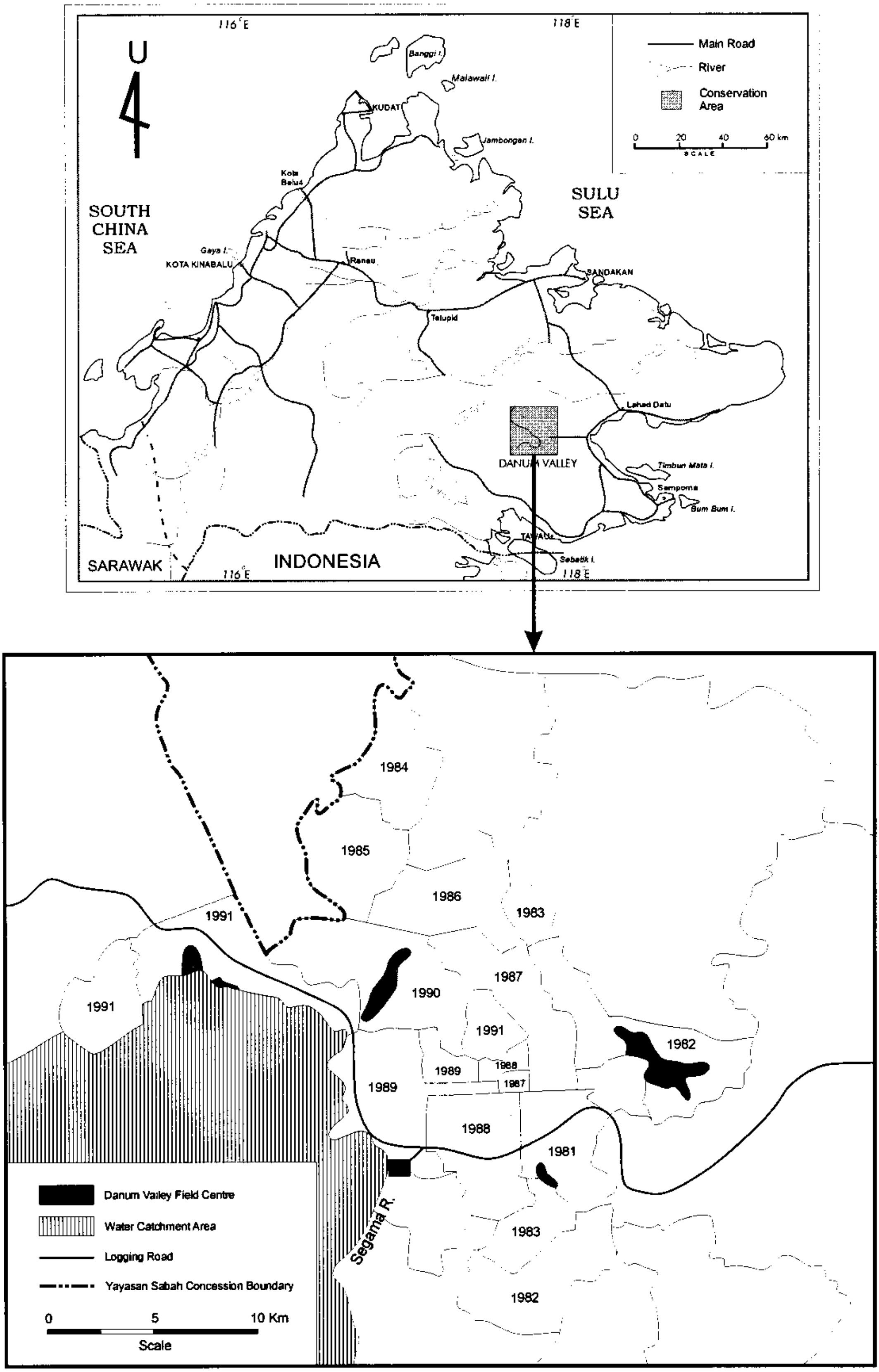


Figure 2.1 : Map of Danum Valley Conservation Area in the Ulu Segama Forest Reserve.

2.1.1b Rainfall

Annual average rainfall at DVCA from 1986 to 1999 was 2555 mm (DVFC unpublished data). The area has relatively constant rainfall but is influenced by two monsoons, the wetter northeastern monsoon from November to March and the drier southwestern monsoon in June and July (Walsh 1996). The month of April is generally lower in rainfall than the rest of the year (DVFC unpublished data). However, this general pattern masks considerable year to year variation. From 1985 until 1999, the longest dry sequence recorded was four months in 1992, with less than 100mm in total, reflecting the Field Centre's location close to the drought prone east of Sabah (Walsh 1996). Highest daily rainfall recorded in DVFC was 169mm on one day in December 1996, which caused flooding in DVFC (DVFC unpublished data).

2.1.1c Temperature and Relative Humidity

As is typical of tropical areas, there is little monthly variation in temperature or relative humidity at DVCA. The highest monthly temperature from 1986 to 1999 was 36.0° C and the lowest was 22.5°C (DVFC unpublished data). Relative humidity showed little seasonal variation, with an annual mean of 94.5% at 0800h and 72% at 1400h, but falling as low as 57% during the afternoon during the drier months of April and August (Walsh 1996).

2.1.1c Vegetation

In total, 88% of the volume of large trees in the DVCA are Dipterocarps (Marsh and Greer 1992). In undisturbed primary forest, there are scattered patches of early successional vegetation in treefall gaps and along waterways. However in logged areas, soil compaction by tractors and larger gaps result in greatly increased light intensity, lower humidity levels and decreased soil water content. These areas are usually colonised by pioneer tree species such as *Macaranga* spp, *Mollutus* spp, *Trema* spp and *Neolamarckia cadamba* and along the skid trails there are bamboos (Graminae), gingers (Zingiberaceae) and wild bananas (Musaceae) (per.obs; Kennedy & Swaine 1992).

The flowering and fruiting of dipterocarps at DVCA is highly synchronous (Whitmore 1984), with mass fruiting occuring at intervals of 5-10 years (Whitmore 1990). It is thought that a period a cool weather during February is the trigger for mass fruiting.

2.2 Butterfly sampling programme

Butterflies were sampled along four transects, two in primary forest (Main West Trail and Rhino Trail) (Figure 2.2) and two in logged-over forest (Coupe 88 and Coupe 89) (Figure 2.3). Each transect was 2 km long with 20 sampling stations placed 100m apart (80 stations in total). Two of the four transects (one in unlogged forest, the other in logged forest) were sampled for 12 days consecutively each month. Sampling was then rotated to the other two transects the following month (Table 2.1). Butterflies were sampled using fruit-baited traps, one placed at each sampling station. Trapping was

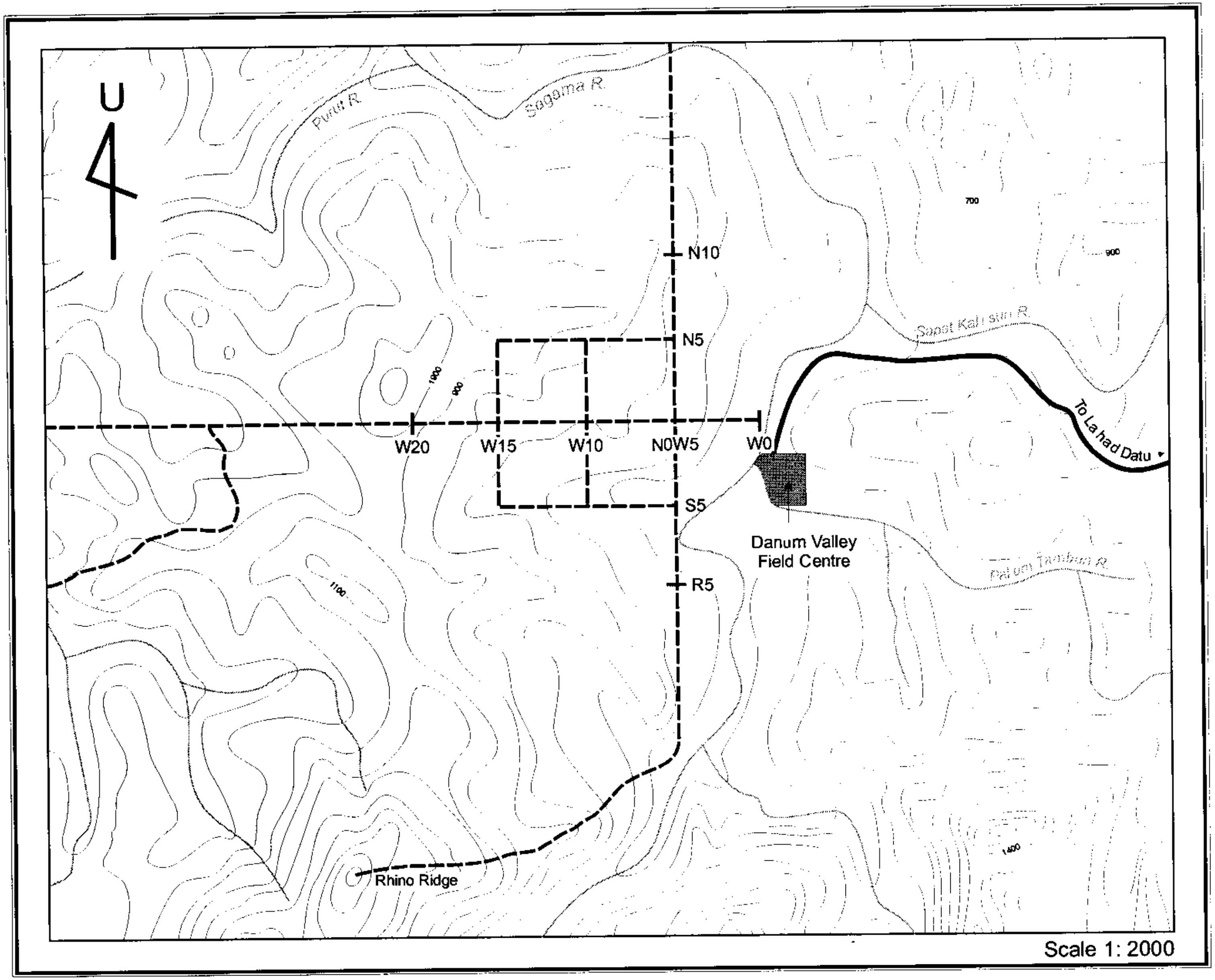


Figure 2.2 : Location of study areas in primary forest, transect 1 (W1-W20) & transect 2(N9-R6).

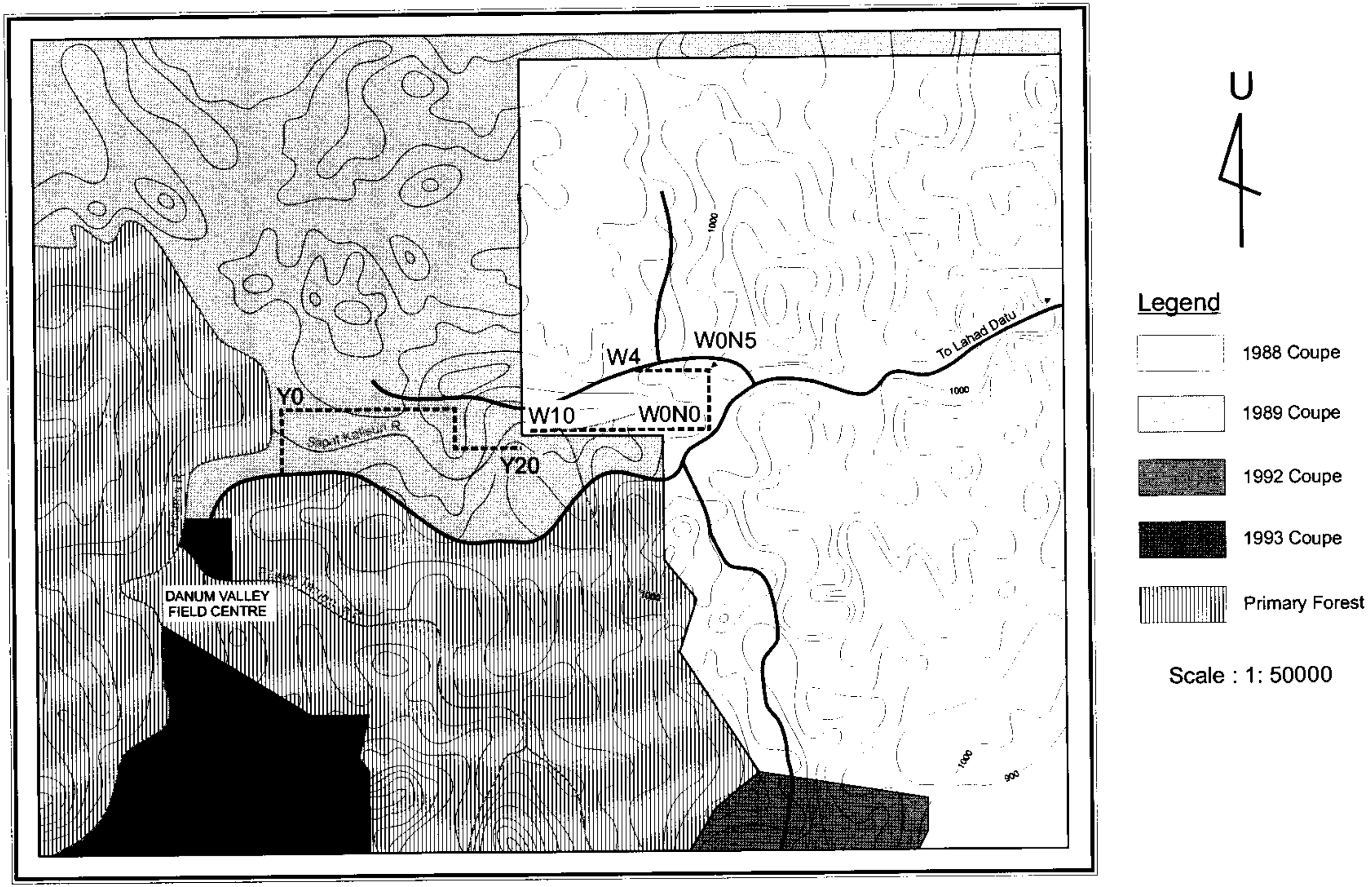


Figure 2.3 : Location of study areas in selectively logged forest, transect 3 - coupe 89 (Y0 - Y19) & transect 4 - coupe 88 (N5W4 - N0W10).

carried out from October 1999 - September 2000, resulting in a total of 5760 trap - days during the study.

Table 2.1 Table of sample locations and months.

MONTH OF TRAPPING	UNLOGGED	LOGGED
October 1999	Rhino Trail	C88
November 1999	**West Trail**	**C89**
December 1999	Rhino Trail	C88
January 2000	**West Trail**	**C89**
February 2000	Rhino Trail	C88
March 2000	**West Trail**	**C89**
April 2000	Rhino Trail	C88
May 2000	**West Trail**	**C89**
June 2000	Rhino Trail	C88
July 2000	**West Trail**	**C89**
August 2000	Rhino Trail	C88
September 2000	**West Trail**	**C89**

All traps were hung from a branch at eye level, at a distance of 2m from the trail. The material of the net was nylon so as not to absorb rainwater (Smart 1991) because wet netting can damage any captured butterflies. When the trap was set up in the correct position, the bait (rotting banana) was placed on an inverted pot in the centre of the tray. One fresh banana was placed in each trap on the first day of trapping each month and a small piece of banana was added each subsequent day to ensure all traps had a mixture of fresh to well-rotten bait (see Figure 2.4 for trap design).

Two different people sampled traps on the different transects at the same time (09.30h - 13.00h) each day. All captured butterflies were identified immediately in the field and marked with either a unique number or colour dot (according to the size of the butterflies) on the left hind-wing using a permanent-ink pen (Figure 2.5). All species

Figure 2.4 Trap used to sample butterflies.

Figure 2.5 *Bassarona dunya* marked on the underside of hindwing.

which were marked and identified were released immediately. Any unidentified species were killed and taken back to the laboratory, where they were identified using keys, colour plates and text in Otsuka (1988) and Corbet & Pendlebury (1992).

2.3 Collection and preparation of specimens

All butterflies collected were kept as specimens after setting in the laboratory. Setting is the process in which butterflies are pinned out so that they dry into a permanent standardised posture, which displays their structure as fully as possible. Setting is necessary not only to obtain a uniform appearance but also to facilitate the arrangement and comparison of specimens in a collection (Smart (1991).

2.3.1 Setting and Wing Spreading

It is important to spread the wings since this facilitates examination and later identification. There are several processes in setting:

a) The groove in the setting board should be slightly wider than the body and legs of the butterfly.

b) Select the pin appropriate to the size of butterfly body.

c) Pin the insect down in the groove of the board so the wings are flush with the surface of the board.

d) A correct display involves the pin being at right angles to the wing dorsum, which in turn is at right angles to the body.

e) Anchor paper setting-strips to the head of the board with pins and arrange the wings.

f) When the wings are in the correct position, anchor the strips with pins to maintain tension.

g) Keep the board in a dry atmosphere for two weeks before unpinning.

h) All specimens should be labelled with the following information: species, place and date of capture, name of the collector.

2.4 Dissection of genitalia

All *Euthalia* spp. and *Tanaecia* spp. (see Figure 2.6) can only be reliably identified from male genitalia (Corbet & Pendlebury 1992). Dissection of genitalia was carried out in the section of Entomology, Forest Research Centre, Sandakan, Sabah. The following procedure was used (Holloway *et al.* 1987):

1. Detach abdomen of the butterfly using fine forceps.
2. Immerse the abdomen in a test tube containing 5ml of 10% KOH. Leave abdomen to soak for 12-24 hours or heat the test tube in a water bath for about 15-20 minutes until soft.
3. Remove the softened abdomen from KOH and transfer to the petri dish of 20% alcohol. Remove tissues, scales etc. from the abdomen.
4. Transfer the abdomen to 80% alcohol. Remove and clean the genitalia.
5. Stain the genitalia and abdomen with a permanent dye.

Figure 2.6 Species of *Euthalia* and *Tanaecia*.

a) Male and female *Euthalia iapis*.

b) Male of *Tanaecia aruna*.

6. Tranfer the abdomen and genitalia to a petri dish of 100 % alcohol for final cleaning.

7. Set the abdomen and genitalia in Euparal on a glass slide with a suitable slide cover.

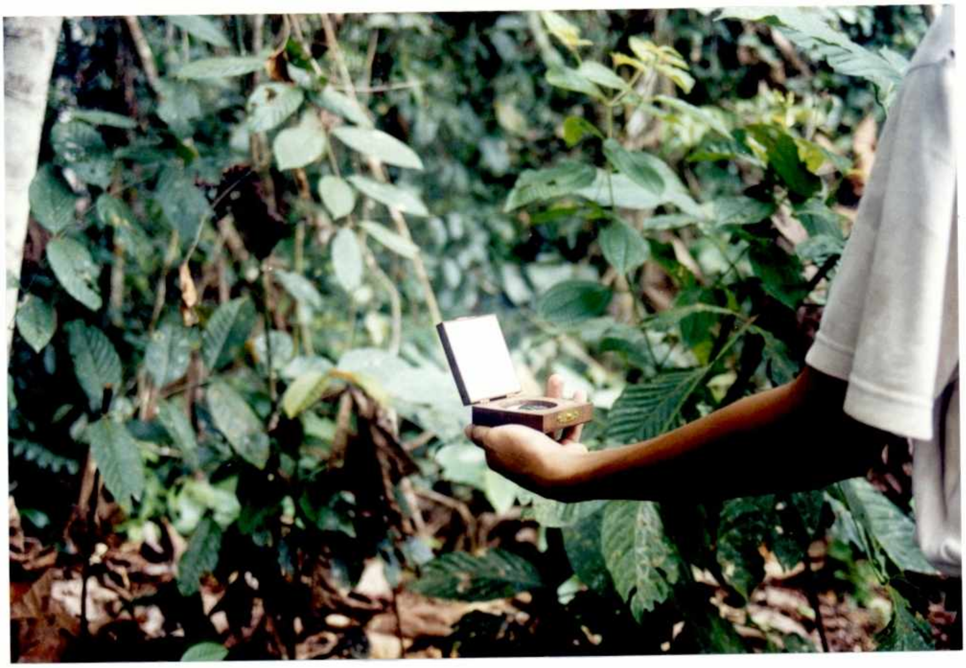
2.5 Canopy openness measurement

Canopy openness was measured using a spherical densiometer (Lemmon 1957) at every trapping station at the end of the study in October 2000 (Figure 2.9). The densiometer was held at elbow height in front of the recorder and canopy openness was measured as the number of squares marked on the convex mirror of the densiometer which did not reflect any canopy. Four readings were taken separately by two observers at each of 80 trapping stations, facing north, south, east and west. The average value of these eight readings was used as an estimate of canopy openness.

2.6 Statistical analysis

Statistical tests and data manipulations were carried out using Microsoft Excel, SPSS version 10.0 and the computer program "Species Richness and Diversity" (Henderson & Seaby 1998). All data were tested for normality using Kolmogorov-Smirnov one sample tests before applying parametric analyses. Non-normal data were either $\log_{10}$ transformed or analysed non-parametrically.

Figure 2.7 Canopy openness was measured using a spherical densiometer.



CHAPTER THREE

IMPACTS OF SELECTIVE LOGGING ON DIVERSITY AND ABUNDANCE OF BUTTERFLIES.

3.1 Introduction

Tropical forests are generally more complex ecosystems than temperate forest, with higher biological diversity (Richards 1996; Whitmore 1998). However, much of this diversity is threatened by forest clearance for agriculture, ranching and timber (Myers 1989; Collins *et al.* 1991). Thus, tropical biodiversity is an issue of great current concern and urgent studies are needed of the impacts of habitat disturbance on biological diversity and ecosystem functioning in tropical forests (Collins *et al.* 1991). Forest clearance and conversion to agriculture has generally resulted in decreases in species diversity (Payne 1982; Heydon & Bulloh 1997). However, impacts of moderate levels of habitat disturbance (e.g. selective logging) are less well understood (Wolda 1983; Hill 1999). Selective logging may affect species composition in many different ways depending on the volume of timber extracted, the harvesting system used, and the extent of damage to the forest structure (e.g. vegetation, microclimate, soils) (Johns 1988) and further studies are needed before a clear picture emerges (Hamer & Hill 2000).

In Sabah, the family Dipterocarpaceae represents about 90% of the total volume of commercial timber trees extracted (Newbury *et al.* 1992) and the average levels of timber extraction in Sabah are about 8-15 trees per hectare. During selective logging, trees with diameter at breast height (dbh) greater than 60cm are removed (Nussbaum *et al.* 1995). Average timber volumes extracted are usually between 2000 m^3 and 3000 m^3 per ha (Costa & Karolus 1995). During selective logging, heavy machinery such as bulldozers, lorries and trucks are used to extract logs from the forest (Pinard & Putz

1996) and it has been estimated that about 30-40% of the area can be damaged during these operations. Continuous disturbance along skid trails (networks of bulldozer paths) and log landings result in soil compaction, removal of topsoil, and damage to the residual vegetation (Pinard & Putz 1996). The loss of topsoils and soil compaction also lead to an increased volume of overland rainwater flow, reducing the amount of water in the soil and increasing soil erosion and the loss of nutrients (Douglas *et al.*1992; Sinun *et al.* 1992).

Previous studies have shown that about 50% of remaining trees are damaged during logging operations resulting in increased canopy openness in selectively logged forest. This may increase the light intensity reaching the forest floor, and thus change the forest microclimate (e.g. temperature and humidity) (Johns 1988). In Sabah, pioneer tree species such as *Macaranga* spp., and *Acacia* spp. often colonise disturbed forest, however in the most disturbed areas, with exposed and compacted soils with very little nutrient content, only vines, gingers, grasses and bamboos are found (Pinard *et al.* 1996). Thus selective logging may affect forest structure, which may in turn affect other species that are dependent on undisturbed forest.

Insects are likely to be highly sensitive to changes in microclimate caused by habitat disturbance because many aspects of their development and survival are a function of temperature, light and humidity (Smart 1991; Speight & Wainhouse 1989; Speight *et al.* 1999). Butterflies are ideal organisms for study because they are comparatively easy to sample (Holloway 1984; Spitzer *et al.* 1997; De Vries *et al.* 1997), sensitive to changes in the physical environment (Kremen 1992; Kremen *et al.* 1993) and in many cases, highly dependent on particular larval and adult host plants (Ehrlich *et al.* 1972; Owen *et al.* 1972; Pollard & Eversham 1995; Brown & Hutching 1997). A number of previous studies have examined the impacts of habitat disturbance on species diversity of tropical forest butterflies, but no consensus has emerged (Hill *et al* 1995; Hamer *et al* 1997; Willot *et al.* 2000) and different studies have reported increased diversity, decreased diversity and no change in diversity following moderate habitat disturbance (see Hamer & Hill 2000 for a review).

On Borneo, there are about 1000 species of butterflies, of which 936 species are recorded in Sabah (Otsuka 1988; Maruyama & Otsuka 1991; Seki *et al.* 1991). Impacts of logging on butterfly diversity in Sabah have been investigated by Tangah (2000), Dawood (2000) and Willott *et al.* (2000) but previous work has been limited to those species that can be observed and identified on transects. There are many species of butterfly that feed on fruit and carrion and are very seldom observed during transects. The responses of these species to habitat modification are very poorly understood. A further problem arises because most previous studies have sampled butterflies for only short periods (often less than one month), which may further reduce the number of species in the study area that are actually recorded and therefore the reliability of the results.

Species abundance distributions of tropical butterflies have been studied by Hill *et al.* (1995), Hamer *et al.* (1997) and Hill (1999). These studies indicated that butterfly species abundance in unlogged forest fitted log-normal distributions better than log-series distributions, whereas butterfly abundance in selectively logged forest fitted log-series distributions better than log-normal distributions. Log-normal distributions tend to be characteristic of communities influenced by a wide variety of ecological factors, whereas log-series distributions tend to be more typical of communities affected by only one or two major factors (May 1981; Magguran 1988; Tokeshi 1993). It has been suggested by Hill & Hamer (1998) that the goodness of fit to either a log series or log normal distribution may be a useful indicator of the impacts of habitat disturbance on community composition, but this has received little study.

3.1.1 Aims

The aims of this chapter are:

1. To investigate impacts of selective logging on butterfly diversity in terms of species richness and evenness.
2. To relate any changes in butterfly diversity to changes in canopy openness following selective logging.
3. To investigate species abundance patterns in unlogged and logged forest.

3.2 Materials and methods

3.2.1 Butterfly data

This study was carried out at Danum Valley Conservation Area (DVCA), Sabah. Butterflies were sampled along transects; two in unlogged forest and two in logged-over forest. Each of the four transects consisted of 20 observation stations at 100m intervals (total 80 stations; 8 km of transects). Two transects (T1 & T3 or T2 & T4) were sampled each month and sampling was switched from one pair of transects to the other pair every month. Butterflies were sampled for 12 consecutive days each month for one year (October 1999 – September 2000) using traps baited with rotting banana. Further details are given in Chapter 2.

All butterflies that were captured in traps were identified, marked using a permanent-ink pen with a unique number or a habitat-specific colour dot (according to their size) on the underside of the left hindwing and immediately released. Any species that could not be identified in the field were brought back to the laboratory for subsequent identification using Otsuka (1988) and Corbet & Pendlebury (1992). Species of *Euthalia* and *Tanaecia* can only be identified from genitalia. These individuals were dissected in the lab and identified following Corbet & Pendlebury (1992).

3.2.2 Canopy openness

Canopy openness was measured at every station at the end of the study in October 2000, using a spherical densiometer (Lemmon 1957). Four readings were taken at each station by a recorder facing north, south, east and west. The number of grid sectors not covered by canopy was counted. Data were collected independently by two observers and combined to obtain a mean percentage canopy openness at every station (see Chapter 2).

3.23 Statistical analysis

The rate of species accumulation in logged and unlogged forest was examined by randomly shuffling samples 20 times to produce smoothed accumulation curves (Hendersen & Seaby 1998), which were then linearised by $\log_{10}$ transformation. Rates of species accumulation were then compared between unlogged and logged forest using analysis of covariance. Following recommendations by Maguran (1988), Shannon Wiener's (H'), Margalef's (D_M) and Simpson's (D_S) indices were used to measure butterfly species diversity, richness and evenness, respectively in unlogged and logged forest, using the following formulae;

a) Shannon-Wiener's Index

$$H' = -\sum pi (\ln pi)$$

where pi = proportion of total sample belonging to the ith species

b) Margalef's Index

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

where S = total number of species
N = total number of individuals in the sample

c) Simpson's Index

$$D_S = \sum \frac{ni(ni-1)}{N(N-1)}$$

where ni = number of individuals in the ith species
N = total number of individuals in the sample

Mean values of species diversity, richness and evenness were calculated for every station in logged and unlogged forest. Data were then analysed using nested ANOVA (nesting transects within habitats). Goodness of fit tests were also carried out to investigate whether butterfly species abundance distributions in unlogged and logged forest best fitted log-normal or log-series distributions. This analysis used chi-square tests to compare the observed results with those predicted from each model. The null hypothesis was that any observed deviation from each model was due to chance, and so $P > 0.05$ indicated that the data fitted the model (i.e. the null hypothesis was accepted). Non-parametric Spearman correlations were used to investigate relationships between canopy openness and diversity. Mann-Whitney *U* tests were used to investigate differences in canopy openness between unlogged and logged forest.

3.3 Results

3.3.1 Species accumulation in unlogged and logged forest

A total of 3996 individuals from 63 species was recorded during the study; 2065 individuals from 54 species in unlogged forest and 1931 individuals from 56 species in logged forest. Of all species recorded during the study, *Ragadia makuta* had the highest number of individuals (536 = 13.4 %), followed by *Neorina lowii* (12.9 %), *Bassarona dunya* (10.3%) and *Mycalesis oroatis* (9.6%); Table 3.1.

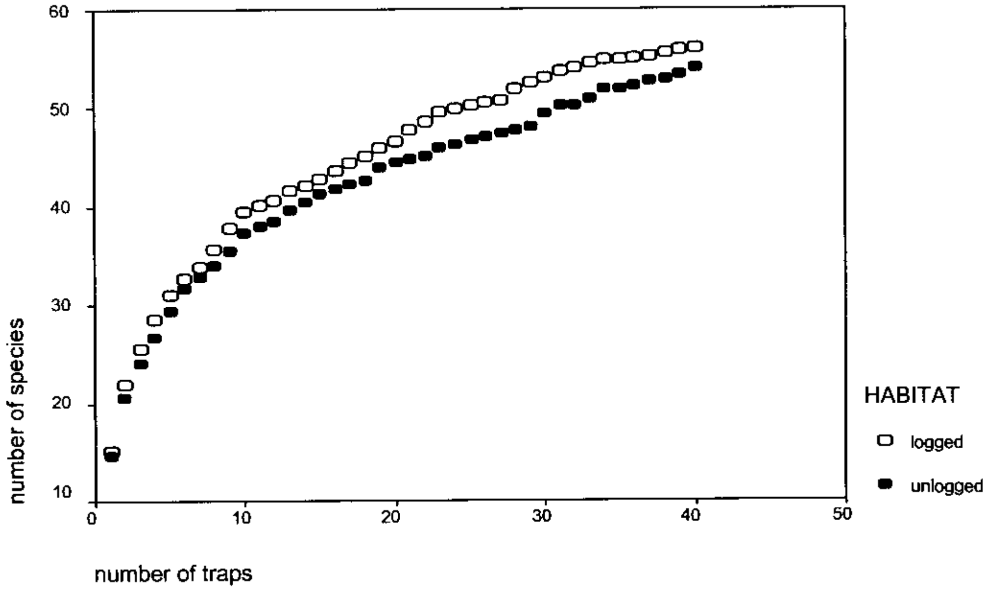
The rate of species accumulation was significantly faster in logged forest (slope = 30.00, SE = 0.4) than in unlogged forest (slope = 25.1, SE = 0.4) (Figure 3.1; ANCOVA; interaction between no. species and $\log_{10}$ sample; $F_{1,76} = 11.91$, $P = 0.001$).

Table 3.1: The tropical fruit-feeding nymphalids butterflies sampled in unlogged (UL) and selectively logged forest (L).

	Unlogged(UL)			Logged(L)			
Family (Subfamily/Species)	**T1**	**T2**	**UL (T1+T2)**	**T3**	**T4**	**L (T2+T3)**	**Total (UL+L)**
Nymphalidae							
Satyrinae							
1. *Neorina lowii*	114	111	225	170	119	289	514
2. *Ragadia makuta*	158	100	258	171	107	278	536
3. *Mycalesis orseis*	31	85	116	112	107	219	335
4. *Mycalesis maianeas*	53	41	94	71	130	201	295
5. *Mycalesis anapita*	1	46	47	17	64	81	128
6. *Mycalesis kina*	41	33	74	15	24	39	113
7. *Mycalesis dohertyi*	36	30	66	13	13	26	92
8. *Mycalesis oroatis*	151	231	382	0	0	0	382
9. *Mycalesis mineus*	0	2	2	0	1	1	3
10. *Mycalesis patiana*	8	6	14	4	7	11	35
11. *Mycalesis janardana*	0	0	0	0	6	6	6
12. *Mycalesis fusca*	1	0	1	3	2	5	6
13. *Mycalesis horsfieldi*	0	1	1	0	6	6	7
14. *Melanitis leda*	11	29	40	9	16	25	65
15. *Melanitis zitenius*	2	1	3	1	8	1	4
16. *Erites elegans*	1	7	8	4	0	12	20
17. *Erites argentina*	2	0	2	2	1	2	4
18. *Xanthotaenia busiris*	1	7	8	2	1	3	11
19. *Elymnias panthera*	0	1	1	0	2	2	3
20. *Elymnias dara*	0	0	0	0	2	2	2
21. *Ypthima pandocus*	0	0	0	0	1	1	1
Nymphalinae							
22. *Bassarona dunya*	107	74	181	131	100	231	412
23. *Bassarona teuta*	18	22	40	12	16	28	68
24. *Rhinopalpa polynice*	0	11	11	1	1	2	13
25. *Amnosia decora*	3	6	9	9	13	22	31
26. *Dophla evelina*	21	24	45	12	4	16	61
27. *Euthalia monina*	0	0	0	1	2	3	3

28. *Euthalia iapis*	0	2	2	0	4	4	6
29. *Dischorragia nesimachus*	2	3	5	2	4	6	11
30. *Lexias pardalis*	15	25	40	27	48	75	115
31. *Lexias dirtea*	9	18	27	6	11	17	44
32. *Lexias canescens*	2	8	10	2	1	3	13
33. *Kalima limborgi*	4	2	6	11	7	18	23
34. *Cirrochroa emalea*	1	15	16	1	2	3	19
35. *Athyma reta*	0	1	1	0	2	2	3
36. *Athyma pravara*	0	1	1	0	2	2	3
37. *Neptis hylas*	0	1	1	0	0	0	1
38. *Neptis harita*	0	1	1	0	0	0	1
39. *Cupha erymanthis*	0	2	2	0	1	1	3
40. *Paduca fasciata*	1	1	2	3	1	4	6
41. *Terinos clarissa*	0	1	1	0	0	0	1
42. *Moduza procis*	0	0	0	0	1	1	1
43. *Parthenos sylvia*	0	0	0	1	0	1	1
44. *Tanaecia aruna*	26	14	40	15	46	61	101
45. *Tanaecia pelea*	2	2	4	1	0	1	5
46. *Tanaecia clathrata*	2	0	2	0	2	2	4
Morphinae							
47. *Discophora necho*	21	25	46	30	27	57	103
48. *Amathuxidia amythaon*	4	3	7	2	2	4	11
49. *Zeuxidia doubledayi*	4	0	4	1	8	9	13
50. *Zeuxidia aurelius*	12	8	20	5	8	13	33
51. *Zeuxidia amethystus*	5	6	11	6	7	13	24
52. *Thaumantis nouredin*	0	1	1	0	3	3	4
53. *Amathusia phidippus*	3	3	6	3	9	12	18
54. *Faunis canens*	0	0	0	2	0	2	2
55. *Faunis stomphax*	0	3	3	1	2	3	6
56. *Faunis gracilis*	0	1	1	0	0	0	1
57. *Faunis kirata*	0	0	0	0	4	4	4
58. *Lethe dora*	1	0	1	0	0	0	1
Charaxinae							
59. *Charaxes bernardus*	7	11	18	1	3	4	22
60. *Charaxes durnfordi*	0	1	1	0	0	0	2
61. *Polyura athamas*	0	0	0	0	1	1	1
62. *Prothoe franckii*	65	89	154	43	41	84	238
63. *Agatasa calydonia*	1	2	3	3	6	9	12
Total	**947**	**1118**	**2065**	**926**	**1005**	**1931**	**3996**

Figure 3.1 Species accumulation in unlogged and logged forest.



3.3.2 Species diversity in unlogged and logged forest

Table 3.2 shows Shannon, Margalef and Simpson diversity indices in the four transects in unlogged and logged forest. There were no significant differences between logged and unlogged habitats for Shannon (ANOVA by habitat with transect nested within habitat, $F_{1,76}$ = 1.31, P = 0.3), Simpson ($F_{1,76}$ = 0.05. P = 0.8) or Margalef ($F_{1,76}$ = 0. 57, P = 0.5). However, there was a significant difference among transects in the Shannon index ($F_{2,76}$ = 4.32, P = 0.02). Post-hoc Tukey tests indicated that Transect 3 in logged forest was significantly less diverse than the other transects.

Table 3.2 Diversity indices for four transects in unlogged and logged forest.

	Unlogged			Logged		
	T 1	**T 2**	**Overall**	**T 3**	**T 4**	**Overall**
No. of sp.	39	49	54	41	51	56
No. of ind.	947	1118	2065	926	1005	1931
Shannon	2.31ab (0.18)	2.36b (0.21)	2.34 (0.20)	2.20a (0.19)	2.37b (0.21)	2.30 (0.20)
Simpson	9.50a (2.90)	9.43a (4.48)	9.47 (3.69)	8.07a (2.43)	10.54a (3.37)	9.31 (2.90)
Margalef	3.60a (0.62)	3.72a (0.71)	3.66 (0.67)	3.33a (0.60)	3.76a (0.71)	3.55 (0.66)

Values show means and standard deviations (SD) based on 20 stations in each transect. Means followed by a different letter are significantly different at the 5% level.

3.3.3 Canopy openness and relationship with butterfly diversity

Logged forest had significantly greater canopy openness than unlogged forest (Table 3.3; Mann-Whitney Z = -5.73, $P < 0.001$). There was no significant relationship between canopy openness and butterfly diversity as measured by Shannon, Simpson or Margalef diversity indices (Spearman correlations, $P > 0.3$ in all cases).

Table 3.3 Canopy openness

	Unlogged			Logged		
Transects	**T1**	**T2**	**Overall**	**T3**	**T4**	**Overall**
Median	7.07	8.13	7.50	11.94	11.19	11.63
IQR	6.01-8.25	8.13-9.32	6.25-9.08	11.94-13.78	11.20-15.54	9.19-14.38

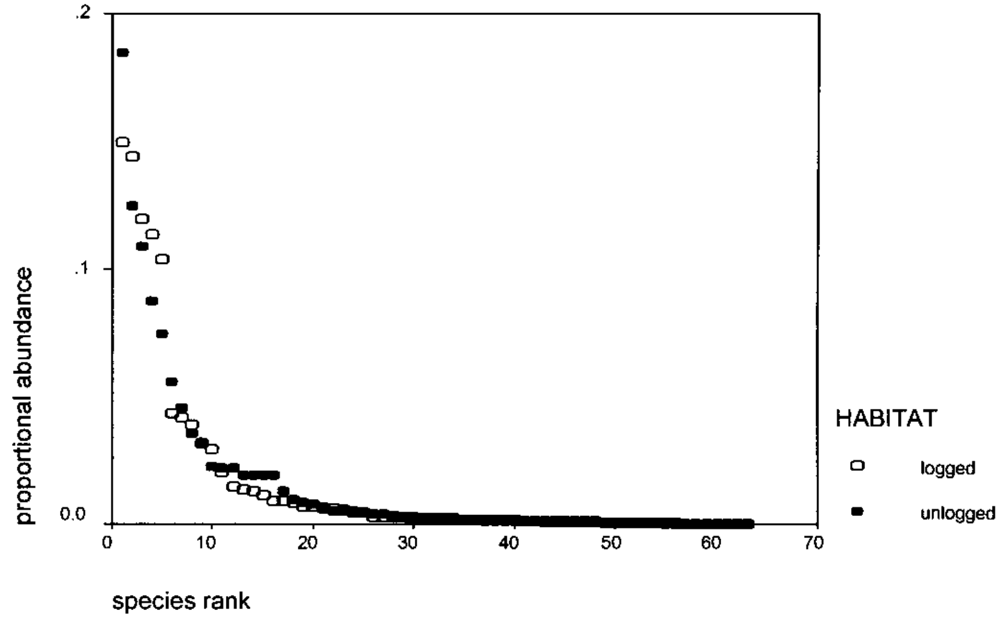
3.3.4 Species abundance distributions

Species abundance in both habitats fitted both log series and log normal distributions (Figure 3.2; P > 0.4 in all cases). There was some indication that the data best fitted a log normal distribution in unlogged forest and a log series distribution in logged forest (Table 3.4)

Table 3.4 Goodness of fit to log-series and log-normal distributions in unlogged and logged forest

			Unlogged	Logged forest
Fit to Log series	chi-square	=	4.63	5.64
	df	=	8	8
	P	=	0.80	0.69
Fit to Log normal	chi-square	=	3.22	5.64
	df	=	8	8
	P	=	0.92	0.45

Figure 3.2 Species abundance distributions in unlogged and selectively logged forest.



3.4 Discussion

3.4.1 Butterfly species accumulation in unlogged and logged forest

A total of 63 species of butterflies in the family Nymphalidae were sampling during this study (Table 3.1), a much larger total than other studies, for example Hill *et al.* (1995), 41 species from four families; Hamer *et al.* (1997), 28 species from four families; Beck & Schulze (2000), 28 species from one family. The higher number of species recorded in this study probably resulted from the much longer sampling period than other studies. This study was also carried out at a relatively large spatial scale (transects 2 km in length).

The rate of butterfly species accumulation was higher in selectively logged forest than unlogged forest (Figure 3.1). This was probably because selective logging resulted in wider variation in vegetation structure and species composition from one station to the next. Thus butterfly species composition differed more between stations in logged forest than in unlogged forest, resulting in a higher rate of species accumulation. However the difference in rates was not large, and total species richness was only slightly higher in logged forest (56 species) than in unlogged forest (54 species) (Table 3.1).

3.4.2 Response of fruit-feeding butterflies to selective logging

There were no significant differences in species diversity between habitats (Table 3.2). These results contrast with some other studies of insects, which reported that selective logging resulted in decreases in species diversity (e.g. Holloway *et al.* 1992; Davis 1993; Chung & Maryati 1996; Hill *et al.* 1995; Hamer *et al.* 1997; Spitzer *et al.* 1997; Watt *et al.* 1997). However previous studies at Danum Valley showed no impacts of selective logging on butterfly diversity (Dawood 2000; Tangah 2000; Willott *et al.* 2000). This might suggest that selectively logged forest in this study was approaching similar conditions to those in unlogged forest (Willott *et al.* 2000). However, this is not supported by the fact that canopy openness was significantly higher in logged forest than in unlogged forest (Table 3.3). There was no relationship between butterfly species diversity and canopy openness and this agrees with other studies which found that moderate loss of canopy cover in selectively logged forest had no effect on butterfly diversity (Wood & Gillman 1998; Willott *et al.* 2000). However other studies have shown that in some cases, higher canopy openness resulted in increases in diversity

(Spitzer *et al.* 1997). This is probably because forest edge species and species more associated with forest gaps can persist in these disturbed areas as forest species (Hill *et al.* in press).

Hill *et al.* (1995) and Hamer *et al.* (1997) found that butterfly assemblages in unlogged forest fitted log-normal distributions much more closely than log-series, whereas butterfly assemblages in selectively logged forest fitted log-series distributions better than log normal. This indicated that species assemblages in unlogged forests may be influenced by a more complex set of ecological factors. Data from this study showed that species abundance distributions fitted both log-series and log-normal distributions in unlogged and logged forest (Table 3.4), which was probably due to the relatively small effects of logging on species diversity. There was an indication from the data that species abundance might have best fitted a log normal distribution in unlogged forest and a log series distribution in logged forest as predicted by Hill & Hamer (1998). However, further data are required to confirm this pattern.

3.4.3 Variation within logged forest

In Danum Valley, timber trees were only removed from slopes less than 25° and buffer zones were left around river catchment areas (Marsh & Greer 1992; Pinard & Putz 1996). The logged forest in this study consists of many areas of steep terrain (e.g. ridges) and river catchments (Marsh & Greer 1992; Douglas *et al.* 1992; Sinun *et al.*1992; Willott *et al.* 2000), resulting in many undisturbed or less damaged areas within the selectively logged forest. This suggests that patches of undisturbed habitat in selectively logged forest might sustain relatively diverse butterfly communities (Hill 1999; Hamer & Hill 2000). This suggestion is supported by the comparison among transects, which showed that Transect 3 in logged forest was the least diverse and Transect 4, which was also in logged forest, was the most diverse (Table 3.2). Transect 4 was more heavily disturbed by logging with many skid trails and log landing areas and with many large pioneer trees such as *Macaranga* spp., while Transect 3 included forest close to river catchments, where logging was much less intensive (Douglas *et al.* 1992, Hill 1999). Thus, different topographical and landscape features resulted in variation in the degree of disturbance within the logged forest, which in turn influenced species diversity. The conflicting results from different transects in logged forest in this study indicate the importance of accounting properly for environmental heterogeneity when designing sampling programs.

CHAPTER FOUR

BUTTERFLY DISPERSAL AND LONGEVITY IN UNLOGGED AND SELECTIVELY LOGGED FOREST.

4.1 Introduction

There are about 20,000 species of butterfly that have been described in the world, of which more than 50% are tropical species (New 1997). In comparison to temperate butterflies, dispersal and longevity of tropical butterflies have received very little attention and are very poorly understood (Corbet & Pendlebury 1992; New 1997). This is probably because few studies in the tropics have used appropriate methods or lasted sufficiently long to address these tropics (Didham *et al.* 1996). In temperate areas, adult butterflies that do not enter diapause generally have life spans less than 20 days (Warren 1992) and the maximum distance moved by non-migrant temperate species is generally less than 2 km (Shreeve 1995; Lewis *et al.* 1997). One study in tropical rainforest by Beck & Schulze (2000) recorded that some fruit-feeding nymphalids may live up to six weeks but there are few data on this topic.

Destruction of natural habitats is increasing at a rapid rate around the world, and this reduces species diversity and population sizes (Sutton & Collins 1991; Terbough 1992; Wilson 1992). Habitat isolation in fragmented landscapes (eg. forest blocks surrounded by agricultural plantations) is likely to affect the distribution of insects species because of their inability to cross non-habitats that separate habitat patches (Diamond 1992). A study in Lago Guri rainforest, Venezuela by Shahabuddin *et al.* (2000) indicated that butterfly species on small islands can disperse to several different islands during their life times but have lower reproduction and higher rates of mortality than species on mainland areas. This and other studies have suggested that higher rates of movement in isolated habitats were probably related to limited availability of resources such as host plants for larvae and adults (Srygley & Chai 1990; Spitzer *et al.* 1997). In temperate areas, metapopulation biology has been widely used to describe and predict insect population dynamics in fragmented landscape (Hanski & Gilpin 1997). For instance, a study on temperate butterflies by Thomas *et al.* (1992) indicated that a network of habitat patches was important for supporting species, and that dispersal between habitat patches was important for population persistence. So far, there are few data on dispersal and longevity of butterflies in the tropics, and very few data to compare survival and longevity in disturbed and undisturbed habitats, or to compare males and females.

There are 240 species of butterflies on Borneo belonging to the family Nymphalidae (Otsuka 1988) and adults of approximately 75% of these species feed on rotting fruits (Hill *et al.* in press). In this study, nymphalid butterflies were sampled using fruit-baited traps, which are commonly used for this purpose in the tropics. However, very little is known about how efficient traps are at sampling butterflies, or how butterflies respond to traps. Several studies have investigated butterfly trap addiction and trap aversion in rainforests (Hughes *et al.* 1998; Beck & Schulze 2000). These studies indicated that individuals might recognise traps as a source of food and become 'trap happy'. Thus, Beck & Schulze (2000) and Hill *et al.* (in press) highlighted that it is important to exclude recaptured individuals from some analyses to avoid problems of non-independence of data. However, more data are needed to examine the responses of different species and in different habitats.

In previous studies of dispersal, inverse-power functions and negative-exponential functions have both commonly been used to describe the distribution of distances moved by individuals (Southwood 1978; Begon *et al.* 1996). A study on temperate butterflies by Hill *et al.* (1996) showed that the distribution of distances moved by dispersing butterflies fitted an inverse-power function better than a negative-exponential. Both of these models may be useful to describe dispersal and longevity of different butterfly species, but this has not previously been examined in the tropics.

4.1.1 Aims

The aims of this chapter are;

1. To examine trap addiction and aversion in fruit-feeding nymphalid butterflies.
2. To investigate differences in butterfly dispersal and longevity between species, sexes and habitats.

4.2 Materials and methods

4.2.1 Butterfly data

Butterflies were sampled using fruit-baited traps for 12 days each month from October 1999 until September 2000 (see Chapter 2 for details). All butterflies were individually marked on the underside of the left hindwing using a permanent-ink pen, identified and released. All identification was based on Otsuka (1988) and Corbet & Pendlebury (1992). Large butterflies (> 30 mm wingspan) were marked with a unique number (24 species in total) and only these larger species are included in this chapter. Dispersal was calculated as the total distance moved by each individual between all successive recaptures. Minimum longevity was calculated as the time in days from first capture to the last recapture. For those species that exhibit sexual dimorphism, sexes were identified from a combination of colour patterns, body size and abdomen shape (Cobet & Pendlebury 1992).

4.2.2 Statistical analysis

Butterfly trap addiction and aversion, dispersal and longevity were only investigated for the most abundant species with sufficient numbers of recaptures. Trap addiction and aversion were examined for each species by comparing the observed frequency distribution with the frequencies expected from a zero-truncated Poisson distribution based on the total number of captures (see Greenwood 1996 for details of method). In addition, data on distances moved and longevity were linearly transformed using both a semi-ln plot (negative exponential function) and a double-ln plot (inverse power function). Linear regression was then used to test whether the distribution of species dispersal and longevity best fitted a negative exponential or inverse power function. Three-way ANOVA was used to investigate differences in butterfly dispersal and longevity between sexes, species and habitats.

4.3 Results

Twenty four species of butterfly were individually marked during the study (Table 4.1). Of these, individuals of five species (*Neorina lowii, Discophora necho, Prothoe franck, Melanitis leda* and *Amathuxidia amythaon*) moved 1000 - 4000 metres and individuals of two species (*Bassarona dunya* and *Lexias pardalis*) moved > 4000 metres. Six species (*L. pardalis, L. dirtea, N. lowii, P. franck, B. dunya* and *B. teuta*) had minimum lifespans of 50 – 175 days Among all species recorded, *B. dunya* moved the greatest distance (4670 metres) and had the greatest minimum lifespan (175 days) and there was a significant correlation between minimum lifespan and distance moved (Table 4.1; Spearman correlation; $r_s = 0.56$, $n = 23$, $P < 0.01$, excluding one species, *Dischorragia nesimachus*, which was never recaptured). Four species (*N. lowii, B. dunya, P. franck* and *L. pardalis*) were captured in large numbers (115 – 514 individuals; Table 4.1) and all further analysis in this chapter is restricted to these four species. Figure 4.1 shows adults of *N. lowii* (Figure 4.1a) and *B. dunya* (Figure 4.1b).

4.3.1 Trap addiction and aversion.

The distribution of recaptures differed significantly from a zero-truncated Poisson distribution for *N. lowii* (chi-square = 127.7 df = 4 $P < 0.001$) and *B. dunya* (chi-square = 15.8 df = 4 $P < 0.001$), but there was no significant difference for *P. franck* (chi-square = 4.8 df = 2 $P > 0.05$) or *L. pardalis* (chi-square = 2.75 df = 2 $P > 0.10$). Table 4.2 shows observed and expected numbers of butterflies caught different numbers of times. For *N. lowii* and *B. dunya* there were more individuals than expected caught only once, indicating some trap aversion. However there were also more individuals than expected caught more than four times, suggesting that once an individual was caught twice, it had an increased probability of being recaptured repeatedly. The greatest number of recaptures was an individual *N. lowii* that was caught ten times.

Figure 4.1: Monographs of adult *N. Lowii* (a) and *B. dunya* (b).

a) *N. lowii*

b) *B. dunya*

Table 4.1 **Butterfly recapture data**

Species	**Number of individuals**	**Number of recaptures**	**Rate of recapture**	**Maximum distance moved (m)**	**Minimum life span (days)**
1. *N. lowii*	514	176	0.34	1580	66
2. *B. dunya*	412	168	0.40	4670	175
3. *Z. doubledayi*	13	1	0.08	0	1
4. *K. limborgi*	23	7	0.30	300	127
5. *D. necho*	103	14	0.14	1300	24
6. *P. franck*	238	53	0.22	1190	69
7. *Z. amethystus*	24	1	0.04	540	11
8. *A. decora*	31	9	0.29	600	11
9. *Z. aurelius*	33	3	0.09	0	10
10. *M. leda*	65	11	0.17	1090	11
11. *D. evelina*	61	8	0.13	1200	6
12. *A. amythaon*	11	2	0.18	1000	2
13. *D. nesimachus*	11	0	0.00	0	0
14. *B. teuta*	68	15	0.22	854	101
15. *L. pardalis*	115	29	0.25	4080	56
16. *A. calydonia*	12	1	0.08	0	6
17. *L. dirtea*	44	6	0.14	900	55
18. *A. phidippus*	18	2	0.11	1000	2
19. *L. canescens*	13	1	0.08	100	3
20. *C. bernadus*	22	3	0.14	0	3
21. *C. emalea*	19	2	0.11	0	3
22. *X. busiris*	11	4	0.36	0	4
23. *T. nouredin*	4	1	0.25	200	3
24. *R. polynice*	13	1	0.08	0	4

Table 4.2 Goodness of fit of recaptures to zero-truncated Poisson distributions. Multiple recaptures are combined to reduce the proportion of cells with expected frequencies < 5.

a) *Neorina lowii*

Number of captures	Observed	Expected	$\frac{(O-E)^2}{E}$
1	338	279.34	12.32
2	97	156.01	22.32
3	39	58.09	6.27
4	16	16.22	0.003
5+	24	4.42	86.74
	514	514	127.65

b) *Bassarona dunya*

Number of captures	Observed	Expected	$\frac{(O-E)^2}{E}$
1	244	223.91	1.80
2	105	125.05	3.22
3	38	46.56	1.57
4	16	13	0.69
5+	9	3.53	8.48
	412	412	15.76

c) *Prothoe franck*

Number of captures	Observed	Expected	$\frac{(O-E)^2}{E}$
1	185	176.85	0.38
2	38	50.14	2.94
3+	15	10.98	1.47
	238	238	4.79

d) *Lexias pardalis*

Number of captures	Observed	Expected	$\frac{(O-E)^2}{E}$
1	86	80.16	0.43
2	20	27.38	1.99
3+	9	7.44	0.33
	115	115	15.09

4.3.2 Distribution of species dispersal distances

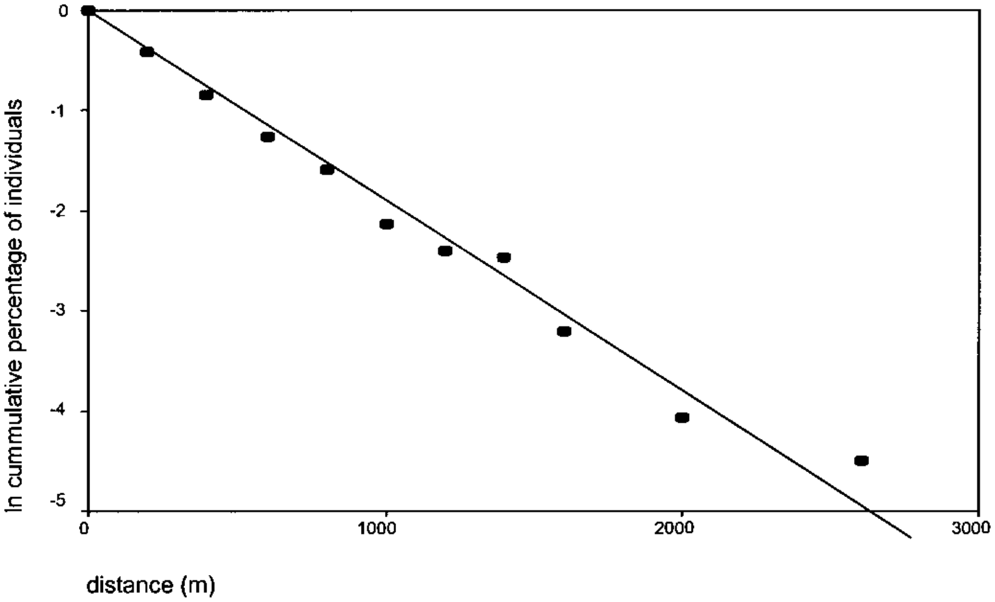
The distribution of dispersal distances of *N. lowii, B. dunya* and *P. franck* all fitted negative exponential functions better than inverse power functions (Table 4.3). However, there was no difference for *L. pardalis* in the goodness-of-fit between an inverse power function and an exponential function. Figure 4.2 shows semi-ln plots of cumulative proportions of individuals moving different distances for the four species.

Table 4.3 Goodness of fit of species dispersal distributions to negative exponential and inverse power functions.

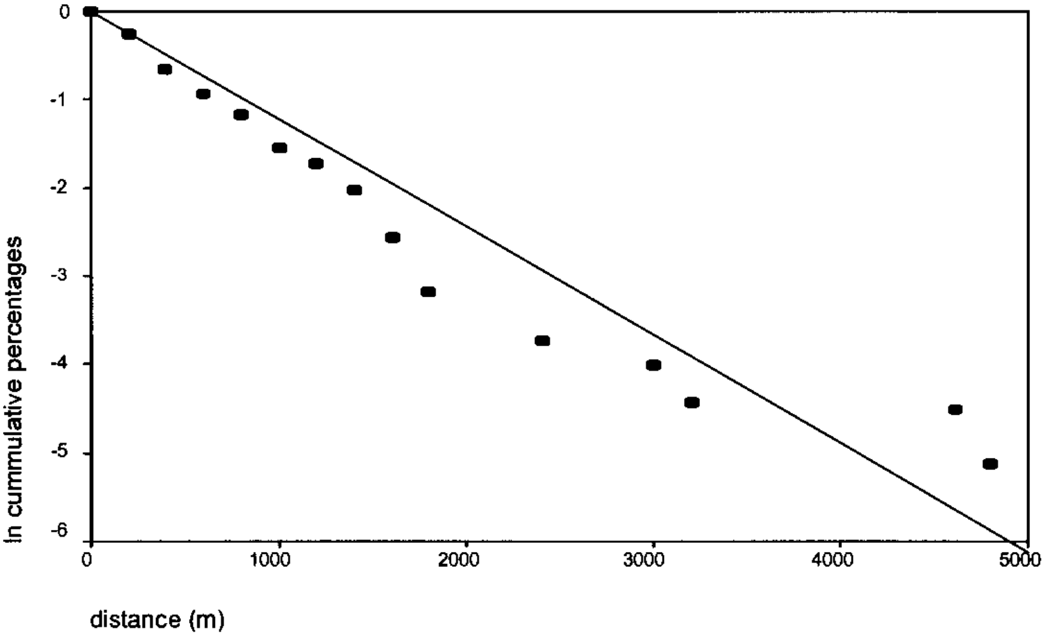
Negative exponential function		**Inverse power function**	
a) ***N. lowii***			
Slope	= - 0.002 (SE < 0.01)	Slope	= - 0.48 (SE ± 0.15)
Intercept	= - 0.13 (SE ± 0.10)	Intercept	= 0.92 (SE ± 0.99)
R^2	= 0.98	R^2	= 0.53
$F_{1,9}$	= 520.7, P < 0.001	$F_{1,9}$	= 10.2, P = 0.01
b) ***B. dunya***			
Slope	= - 0.001 (SE < 0.001)	Slope	= - 0.60 (SE ± 0.15)
Intercept	= - 0.48 (SE ± 0.20)	Intercept	= 1.63 (SE ± 1.07)
R^2	= 0.92	R^2	= 0.54
$F_{1,13}$	= 149.1, P < 0.001	$F_{1,13}$	= 15.30, P < 0.002
c) ***P. franck***			
Slope	= - 0.003 (SE < 0.001)	Slope	= -0.43 (SE ± 0.17)
Intercept	= 0.114 (SE ± 0.120)	Intercept	= 0.48 (SE ± 0.17)
R^2	= 0.99	R^2	= 0.55
$F_{1,5}$	= 390.1, P < 0.001	$F_{1,5}$	= 6.23, P = 0.06
d) ***L.pardalis***			
Slope	= - 0.0007 (SE < 0.001)	Slope	= - 0.37 (SE ± 0.12)
Intercept	= - 0.89 (SE ± 0.39)	Intercept	= 0.52 (SE ± 0.74)
R^2	= 0.031	R^2	= 0.66
$F_{1,5}$	= 8.77 , P = 0.031	$F_{1,5}$	= 9.58, P = 0.03

Figure 4.2 Semi-ln plots of cumulative proportions of individuals moving different distance for a) *N. lowii*, b) *B. dunya* c) *P.franck* and d) *L. pardalis*.

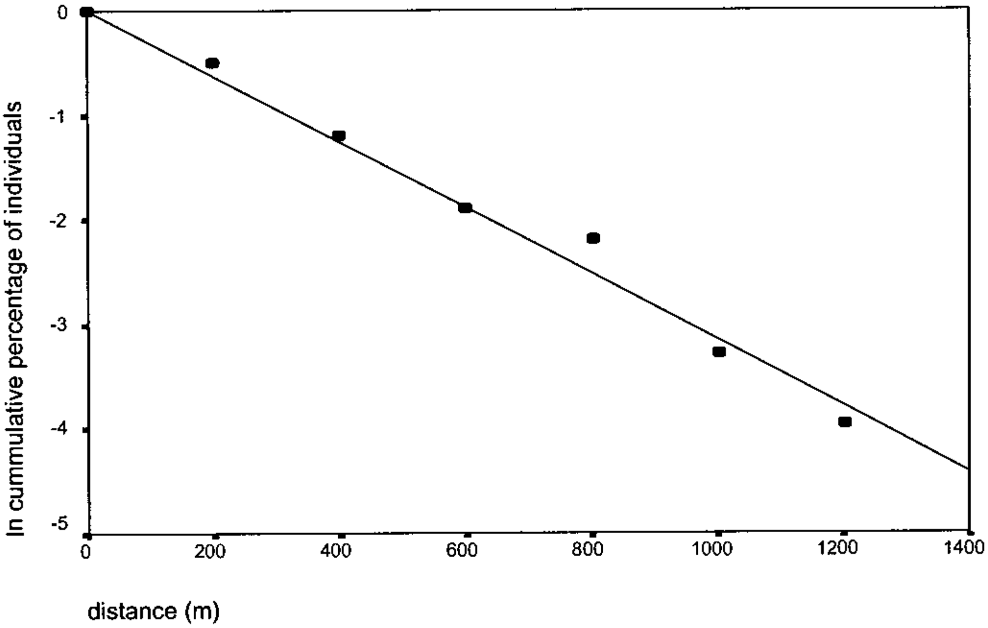
a) *N. lowii*



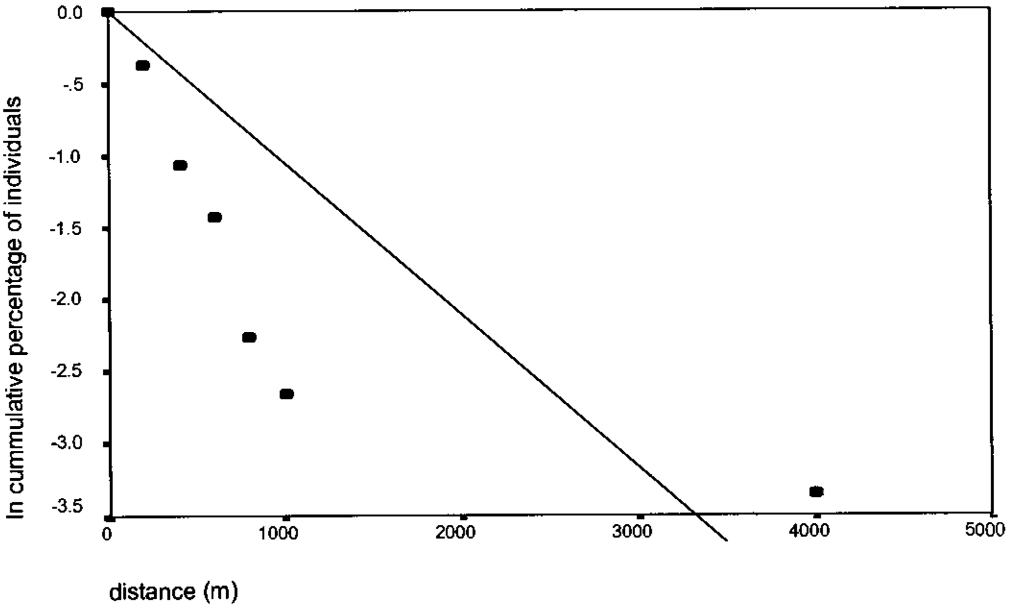
b) *B. dunya*



c) *P. franck*



d) *L. pardalis*



4.3.3 Distribution of species longevity

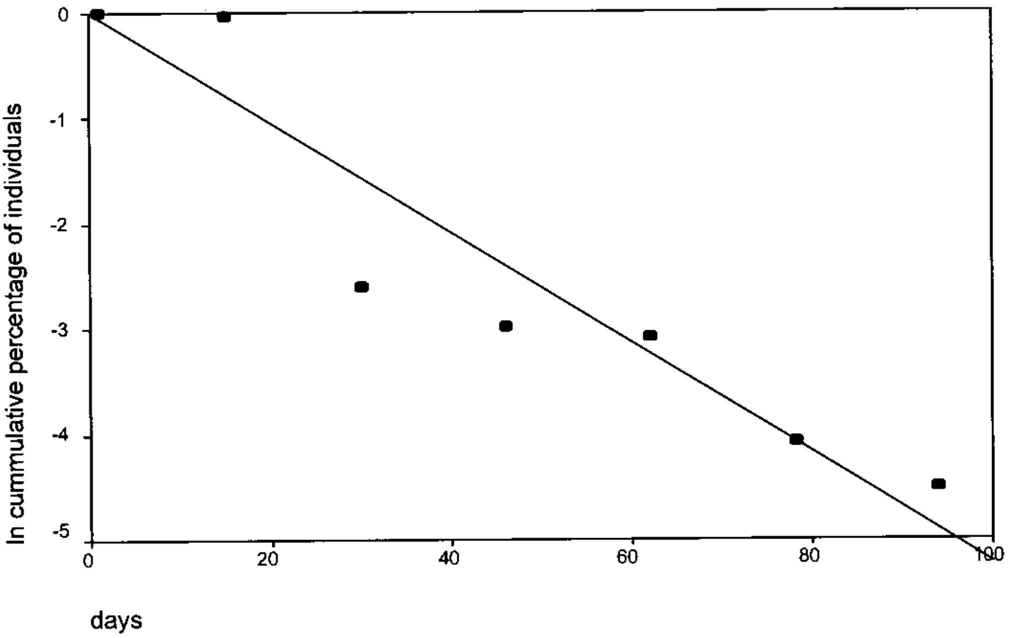
Longevity of *N. lowii*, *B. dunya*, *P. franck*, and *L. pardalis* all fitted negative exponential functions better than inverse power functions (Table 4.4). Figure 4.3 shows semi-ln plots of the cumulative proportion of individuals surviving different time periods.

Table 4.4 Goodness of fit of species longevity distributions to negative exponential and inverse power functions.

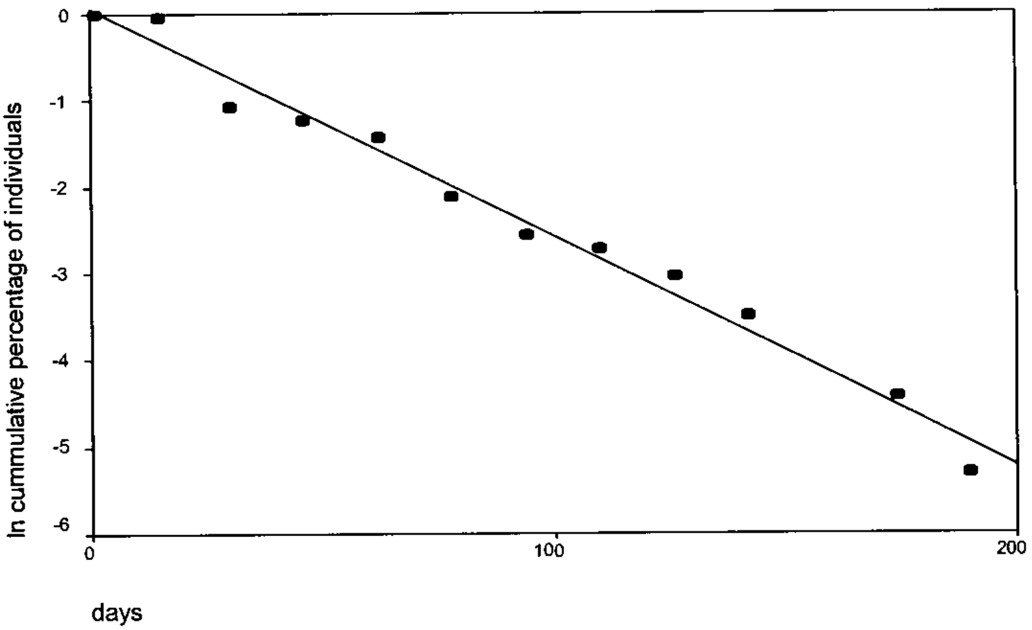
Negative exponential function		**Inverse power function**	
a) ***N.lowii***			
Slope	= -0.05 (SE ± 0.01)	Slope	= - 0.98 (SE ± 0.26)
Intercept	= -0.12 (SE ± 0.44)	Intercept	= 0.75 (SE ± 0.94)
R^2	= 0.89	R^2	= 0.74
$F_{1,5}$	= 40.8, $P = 0.001$	$F_{1,5}$	= 14.2, $P = 0.01$
b) ***B.dunya***			
Slope	= -0.027 (SE ± 0.001)	Slope	= -0.91 (SE ± 0.21)
Intercept	= -0.069 (SE ± 0. 12)	Intercept	= 1.32 (SE ± 0.89)
R^2	= 0.98	R^2	= 0.65
$F_{1,10}$	= 591.9, $P < 0.001$	$F_{1,10}$	= 18.7, $P = 0.002$
c) ***P.franck***			
Slope	= -0.04 (SE ± 0.01)	Slope	= -0.62 (SE ± 0. 20)
Intercept	= -0.02 (SE ± 0.32)	Intercept	= 0.43 (SE ± 0.67)
R^2	= 0.89	R^2	= 0.71
$F_{1,4}$	= 31.99, $P = 0.005$	$F_{1,4}$	= 9.98, $P = 0.03$
d) ***L.pardalis***			
Slope	= -0.05 (SE ± 0.01)	Slope	= -0.63 (SE ± 0.25)
Intercept	= 0.2 (SE ± 0.40)	Intercept	= 0.38(SE ± 0.79)
R^2	= 0.88	R^2	= 0.69
$F_{1,3}$	= 21.9, $P = 0.02$	$F_{1,3}$	= 6.53, $P = 0.08$

Figure 4.3 Semi-ln plot of cumulative proportion of individuals surviving different time spans for a) *N. lowii*, b) *B. dunya* c) *P. franck* and d) *L. pardalis*.

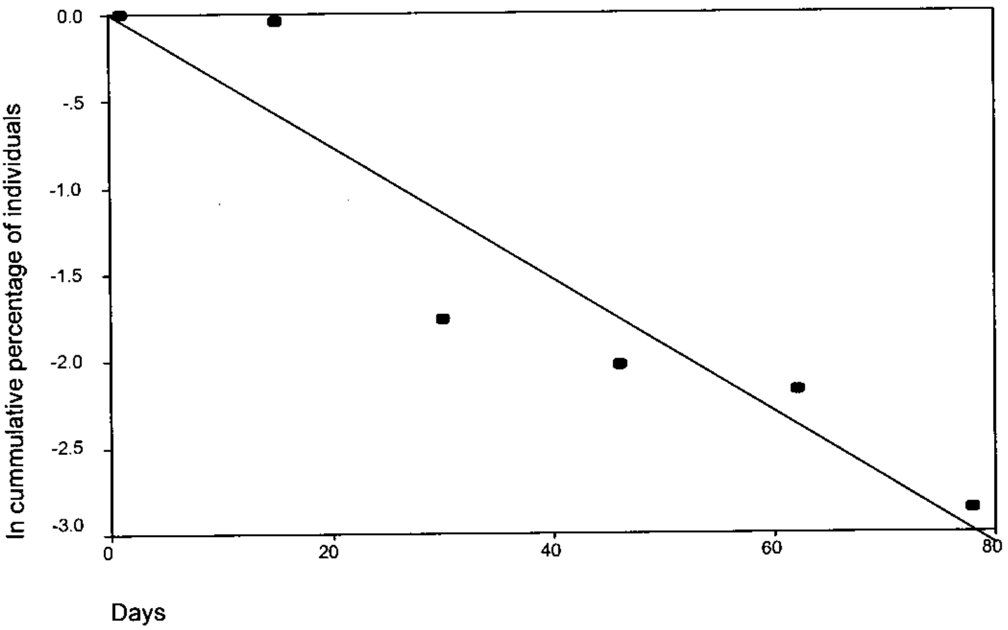
a) *N. lowii*



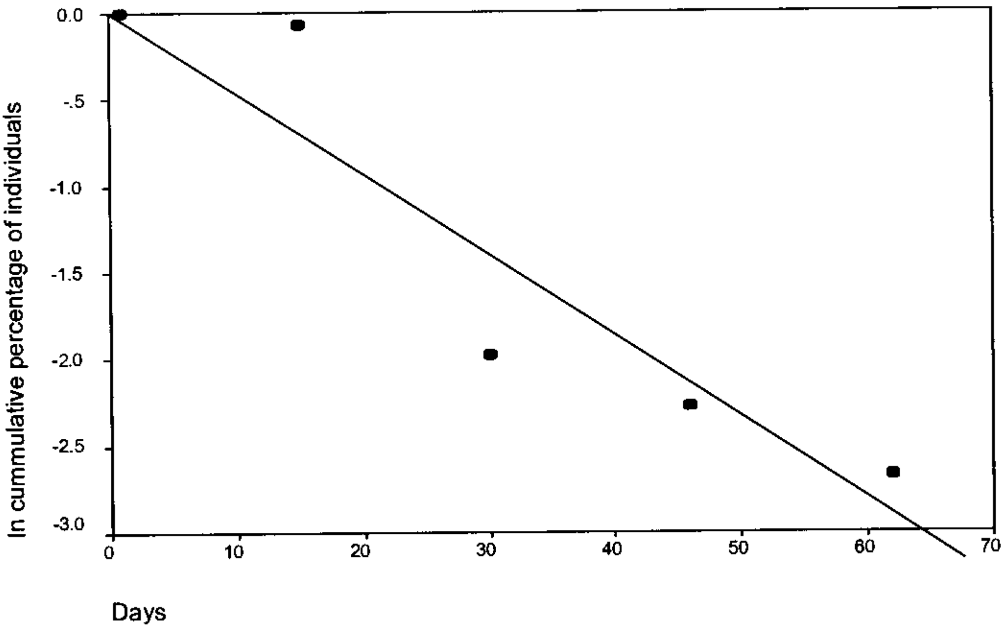
b) *B. dunya*



c) *P. franck*



d) *L. pardalis*



4.3.4 Butterfly dispersal

In this study, three way ANOVA by ranks (Zar 1996) was used to investigate differences in dispersal and longevity between sexes, species (*N. lowii, B. dunya, P. franck*) and habitat (Table 4.5). *L. pardalis* was excluded from this analysis because there were too few cases in some cells. There was a significant difference in dispersal between species (Figure 4.4; Kruskal – Wallis H' = 13.56, df = 2, P < 0.001), and *B. dunya* moved further than either of the other two species (Table 4.5). However, there was no significant difference in dispersal between sexes (H' = 0.45, df = 1, P = 0.50) or habitats (H' = 0.46, df = 1, P = 0.50). There were no significant interactions between any of these variables (P > 0.20).

Figure 4.4 Dispersal of butterfly species based on marked individuals moving between traps over one year.

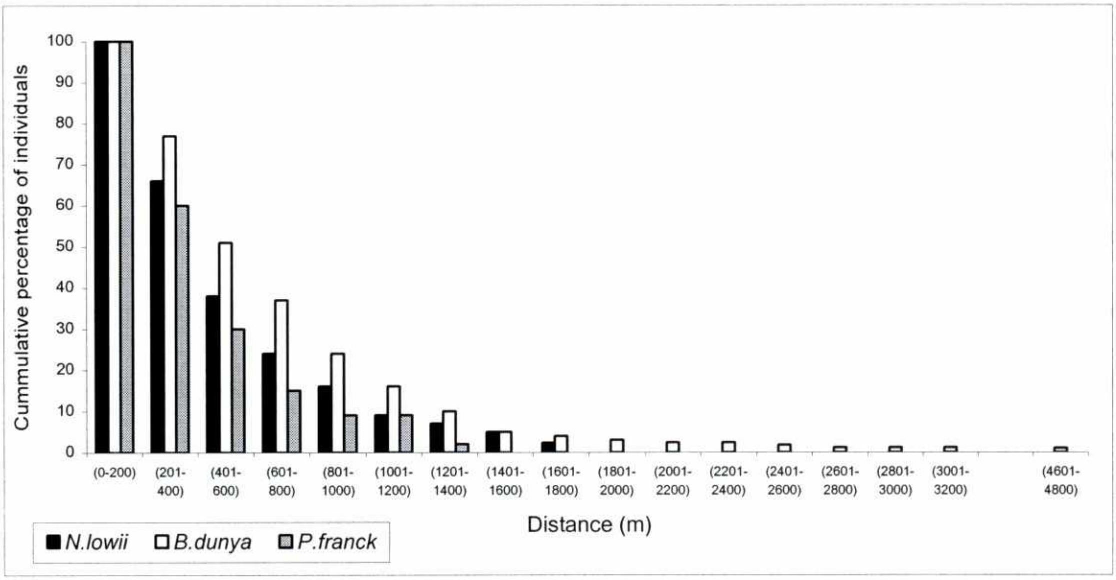


Table 4.5 Dispersal distances (m) of males and females of three species of butterfly in unlogged and selectively logged forest.

	Unlogged		**Logged**	
	Male	**Female**	**Male**	**Female**
1. *N.lowii*				
Median	200	300	150	100
IQR	0-625	0-700	0-487	0-500
N	38	23	80	35
2. *B.dunya*				
Median	200	400	200	290
IQR	0-741	0-721	100-715	100-638
N	50	31	53	34
3. *P.franck*				
Median	200	150	0	150
IQR	0-400	0-300	0-390	150-285
N	19	11	13	9

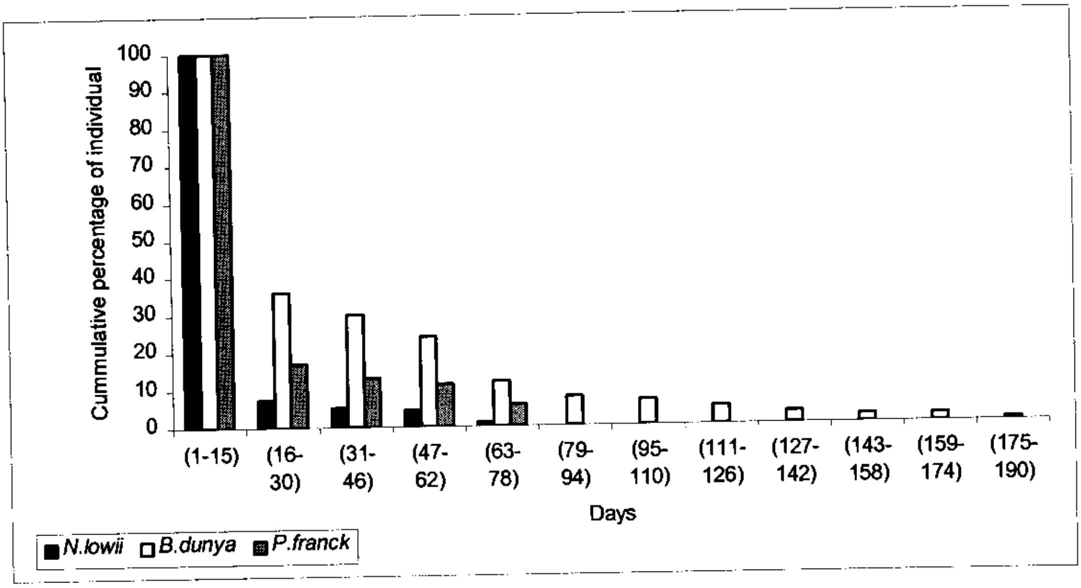
4.3.5 Butterfly longevity

There was a significant difference in longevity between species (Figure 4.5; three-way ANOVA by ranks; Kruskal-Wallis H' = 27.96, df = 2, $P < 0.001$) and *B. dunya* lived longer than other two species (Table 4.6). However there was no significant difference in longevity between sexes (H' = 1.02, df = 1, $P > 0.25$) or habitats (H' = 1.86, df = 1, $P > 0.10$). There was a significant sex*species interaction (H' = 7.31, df = 2, $P < 0.05$) and sex*habitat interaction (H' = 7.65 df = 1 $P <0.01$) but not species*habitat interaction (H' = 1.59, df = 2, $P > 0.3$).

Table 4.6 Longevity (days) of males and females in unlogged and selectively logged forest.

	Unlogged		Logged	
	Male	**Female**	**Male**	**Female**
1. *N.lowii*				
Median	7	4	5	3
IQR	4-10	2-7	3-7	2-6
N	38	23	80	35
2. *B.dunya*				
Median	9	9	6	7
IQR	4-48	3-37	3-49	5-23
N	50	31	53	34
3. *P.franck*				
Median	6	3	2	3
IQR	4-7	2-6	2-5	2-52
N	19	11	13	9

Figure 4.5: Longevity of butterfly species based on recaptures of marked individuals.



4.4 Discussion

The results of this study showed that *B. dunya* moved the greatest distance (4670 metres), followed by *L. pardalis* (4080 metres) and *N. lowii* (1580 metres). *B. dunya* also had the longest minimum lifespan (175 days), followed by *K. limborgi* (127 days) and *B. teuta* (101 days). It should be stressed that individuals were not necessarily newly emerged when they were first caught, and so these data indicate minimum lifespan. It is also possible that by providing food, I increased the lifespans of some individuals. My data are therefore only an approximate indication of minimum lifespan under natural conditions. A previous study on fruit-feeding nymphalids recorded lifespans up to 45 days (Beck & Schulze 2000) but that study sampled butterflies for less than three months. Thus the longer lifespans recorded in my study probably resulted form a longer sampling period.

4.4.1 Trap addiction and aversion

This study found that different species had different recapture rates (Table 4.1). This may reflect differences in relative abundance and / or dispersal, but may also indicate that different species responded differently to traps. The frequency of captures differed significantly to that expected if individuals were captured at random for *N. lowii* and *B. dunya*, with evidence of both trap addiction and trap aversion (see Results). Trap addiction can occur when individuals recognize traps as a source of food (Hughes *et al.* 1998; Hill *et al.* in press) and in this study, individuals of both *N. lowii* and *B. dunya* returned repeatedly to the same traps every day for more than 7 days. Trap aversion may be an effect of marking and handling individuals, which can affect the subsequent behaviour of marked specimens (Morton 1981).

4.4.2 Frequency distribution of dispersal and longevity

Dispersal of *N. lowii, B. dunya* and *P.franck* all fitted negative exponential functions better than inverse power functions, whilst dispersal of *L. pardalis* fitted both functions equally well (Table 4.3), indicating that all four species were dispersing randomly within the forest. Non-random dispersal can result from individuals having territories or home ranges, from competition for resources and from resources having a patchy distribution (Andrewartha 1961; Southwood 1978; Hill *et al.* 1996). My results indicate that these were not important factors influencing the dispersal of the four species in this study.

Data for longevity fitted a negative exponential function better than an inverse power function for all four study species (Table 4.3), indicating a constant rate of survival in each case (Southwood 1978). Longevity may be influenced by many factors including predation, pathogens, parasites, food resources and weather conditions in the forest (Yong 1983; Speight *et al.* 1999). Extreme weather such as high temperatures or very dry or wet conditions may also affect butterfly mortality (Smart 1991). Further data are needed for adults of known time since emergence, to study changes in survival over an adult's lifespan.

4.4.3 Butterfly dispersal and longevity

B. dunya moved longer distances than *P. franck*, with *N. lowii* having intermediate values. Differences in dispersal among butterfly species are related to adult body size (Chai & Srygley 1990; Srygley & Chai 1990) and *B. dunya* and *N. lowii* (wing length 43 – 50mm and 45 – 52mm respectively) are larger than *P. franck* (wing length 37 – 43 mm: Otsuka 1988). The thorax contains many flight muscles and, in addition to body size, larger thoraxes are related to increased flight speed in butterflies (Hill *et al.* in press). Nymphalinae and Charaxinae are generally reported to have relatively larger thoraxes and body sizes than Satyrinae (Hill *et al.* in press), which are likely to affect capability to disperse in the forest. *B. dunya* is in the Nymphalinae and this probably explains why it had greater dispersal than *N. lowii*, which is in the Satyrinae.

There was no significant difference in dispersal between sexes (Table 4.5). There was also no significant difference between unlogged and logged forest. This study took place in forest that was selectively logged 10 years before the study and habitat regeneration over that time may have resulted in selectively logged forest providing suitable breeding and feeding sites for butterflies (Willott *et al.* 2000). This may explain why there was no impact on butterfly dispersal. It should be pointed out, however, that the three species compared in this study are all relatively mobile and many other species are likely to be more sedentary. Habitat disturbance may affect dispersal in species that are less mobile (New 1997; Shahabuddin *et al.* 2000) and thus deserves more study.

This study found that species that lived longer moved greater distances. Beck (1999) indicated that minerals, proteins and carbohydrates are all essential for adults of some species of butterfly to increase longevity and flight capacity. Those species which are more dispersive may have more opportunity to select and utilize more widespread resources (Andrewartha 1961), thus increasing their longevity. Alternatively, greater distances moved by long-lived species may result from both lifespan and dispersal being related to body size, or simply from more time available to disperse in longer-lived species. Compared with temperate species, adults of tropical species appear to have much longer lifespans. This may explain why a high proportion of species are dependent as adults on nutrients available in rotting fruit and other resources (Karlsson 1998; Beck *et al.* 1999; Hall & Willmott 2000).

CHAPTER FIVE

Impacts of selective logging on butterflies in relation to their geographical distribution.

5.1 Introduction

The area of Southeast Asia which constitutes the Malay Archipelago covers about 3 million km^2 with more than 20, 000 islands, of which 13, 000 make up Indonesia in a chain 5, 000 kilometers long between Asia and Australia (Whitmore 1984). The Malay Archipelago comprises west Malesia (Sumatra, Malaya (West Malaysia and Singapore), Borneo (Sabah, Brunei, Sarawak and Kalimantan) and the Philipines), south Malesia (Java and the Lesser Sunda Islands) and east Malesia (New Guinea, Moluccas and Sulawesi) (Balgooy 1987). The Malaysian state of Sabah is situated at the northern tip of Borneo, in the centre of the Malay Archipelago and is surrounded by the Sulu Sea, South China Sea and Java Sea.

During the Pleistocene period about 2.5 million years ago when sea levels were much lower than at present, all the islands in Sundaland were joined together and connected to mainland Asia (Cox & Moore 2000). At the end of the glacial after the present islands were formed as sea levels rose, the various species on the different islands began to evolve and speciate in isolation (Whitmore 1987; Audley Charles 1987; Holloway & Hall 1998). As a result, many species evolved on the separate islands of Sumatra, Borneo, Java and others, but these species share close floristic and faunistic relationships due to their similar origins. For example, a study by Holloway (1976) recorded that 548 species of moths found on Borneo shared closest relatives with other places in the Southeast Asian region, such as the Malay Peninsular (61%), Sumatra (12%), Java (16%) and India (31%).

The flora and fauna within the Oriental and Australasian regions are separated by Wallace's line (Holloway 1987), which extends from the Indian Ocean through the Selat Lombok (between the islands of Bali and Lombok), northward through the Makassar Strait (between Borneo and Sulawesi), and eastward, south of Mindanao, into the Philippine seas (Figure 5.1). Wallace's line follows approximately the boundary between the Australasian and Oriental continental plates. Large changes in the flora and fauna occur over relatively short distances across this line. Currently, Borneo has approximately 936 species of butterfly of which 94 (10%) are endemic (Otsuka 1996). The species on Borneo have close affinities with other species of butterflies in Peninsular Malaysia, Singapore, Sumatra and Java (Otsuka 1988; Corbet & Pendlebury 1992).

Forest disturbance that opens up the canopy may particularly affect those butterfly species with narrow geographical distributions. For example the endemic species, Schomburgk's deer (*Cervus schomburgki*) in Thailand, (Jintanugool *et al.*1982) and proboscis monkey (*Nasalis larvatus*) in Borneo (Payne 1982) were greatly affected by forest disturbance. Similarly, a growing number of studies (Thomas & Mallorie 1985; Hill *et al.* 1995; Hamer *et al.* 1997; Spitzer *et al.* 1997; Lewis *et al.* 1998) have shown that impacts of forest disturbance on tropical butterflies have particularly affected those species with narrow geographical ranges.

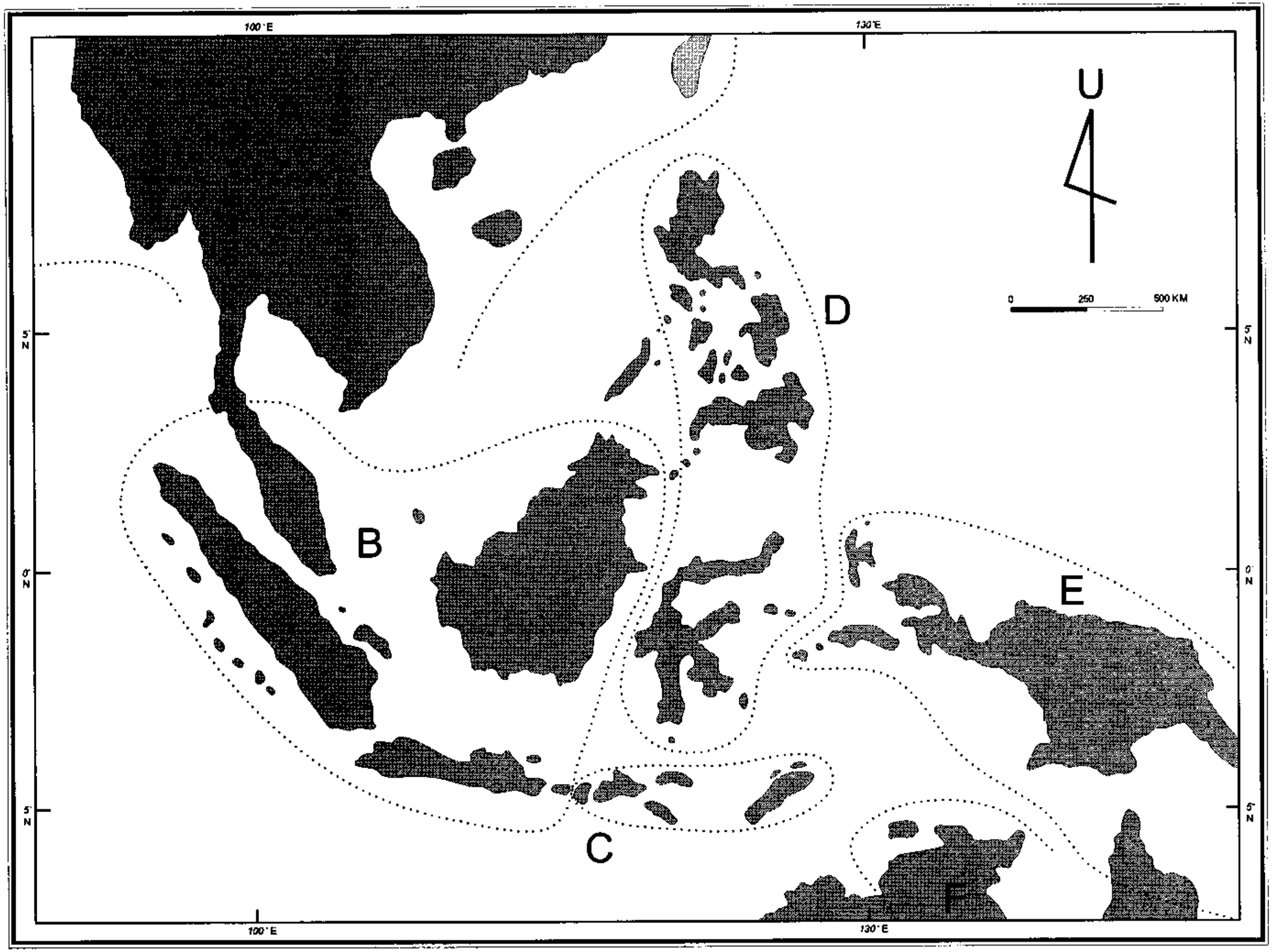


Figure 5.1 : Map of discontinuities in lepidoptera faunas (after Holloway 1987). Dotted lines enclose areas with high species affinities. A : Mainland Asian; B: Sundaland; C: Lesser Sunda; D: Wallacean; E: Melanesian; F: Tropical Australian.

The focus of this study was butterfly species of the family Nymphalidae (subfamilies Satyrinae, Morphinae, Nymphalinae and Charaxinae). The majority of species of Satyrinae and Morphinae prefer forest understorey layers of dense forest but Nymphalinae and Charaxinae generally prefer more open areas, forest gaps and forest canopy layers (De Vries 1988; Corbet & Pendlebury 1992; Schulze *et al.* in press). Hill *et al.* (in press) suggested that nymphalid butterflies in forest gaps in Borneo were capable of faster flight allowing them to be more mobile and to exploit more ephemeral resources in the forest than butterflies that are confined to the shade. Those species that were more abundant in forest gaps also had more widespread geographical distributions (Hill *et al.* in press). This suggests that species with more widespread distributions may be less affected by forest disturbance that opens up the canopy. However this has not previously been tested on Borneo.

5.2 Aims

The aims of this chapter are:

1. To examine the geographical distributions of butterflies sampled in logged and unlogged forest.
2. To test the hypothesis that endemic species and species with restricted geographical distributions are more sensitive to habitat disturbance.

5.3 Materials and methods.

Butterflies were sampled using fruit-baited traps on four transects in unlogged and selectively logged forest. Butterflies were sampled on transects for 12 days each month from October 1999 until September 2000; two transects were sampled each month, one in unlogged and one in logged forest and the pair of transects sampled was alternated each month (see chapter 2 for details). All butterflies that were trapped were identified using Otsuka (1988), marked using a permanent ink pen and immediately released.

All species recorded during the year's study were ranked according to their geographical distribution following Otsuka (1988). A species that is endemic to Borneo such as *Mycalesis kina,* was given the highest rank (rank 1) and the most widespread species, *Melantis leda*, was given the lowest rank (rank 63). Some species have very similar distributions, egg. those species confined to Sundaland, and these species were given the same rank.

5.4 Statistical analysis

For all 63 species, I recorded whether the species was more abundant in either unlogged or logged forest. I also recorded the transect on which each species was most abundant. Non-parametric Mann-Whitney tests and Kruskal-Wallis one way analysis of variance were used to investigate geographical distributions of butterflies. For some species, only a few individuals were trapped, making it difficult to decide objectively whether the species was more abundant in one habitat than another. I therefore repeated the analysis only including those 33 species with ≥ 10 individuals. For these species, I also calculated their habitat preference, as number in logged forest / number in unlogged + number in logged forest. This index ranged from 0 (only in unlogged forest) to 1 (only in logged forest). Spearman correlations were used to test whether there was any significant relationship between species geographical distribution and habitat preference.

5.5 Results

5.5.1 Butterfly geographical distributions in unlogged and selectively logged forest.

A total of 63 species was recorded during the study, of which one species (*Mycalesis kina*) is endemic to Borneo and 22 species are restricted to Sundaland (Table 5.1). Twenty eight species were more abundant in unlogged forest and thirty five species were more abundant in selectively logged forest. Six species occurred only in unlogged forest; *Mycalesis oroatis* (n = 382 individuals), *Neptis harita* (1), *Neptis hylas* (1), *Terinos clarissa* (1), *Faunis gracilis* (1) and *Charaxes durnfordi* (1). Nine species occurred only in logged forest; *Mycalesis janardana* (n = 6 individuals), *Elymnias dara* (2), *Ypthima pandocus* (1), *Euthalia monina* (3), *Moduza procis* (1), *Parthenos Sylvia* (1), *Faunis canens* (2), *Faunis kirata* (4) and *Polyura athamas* (1).

There was no significant difference in species geographical distributions among subfamilies (Kruskal Wallis anova; H' = 0.04, N = 63, P = 0.84). There was also no significant difference in species geographical distributions between unlogged and logged forests (Mann Whitney test; $Z = -0.51$, $N = 63$, $P = 0.61$). However transect 2 in unlogged forest had more widespread species than the other transects (Table 5.2; $H' = 50.3$, $N = 63$, $P < 0.001$). There was no significant relationship between species geographical range and habitat preference (Figure 5.2; $r_s = -0.12$, $N = 33$, $P = 0.52$).

Figure 5.2 Relationship between species habitat preferences and their geographical distribution. See text for method of calculating habitat preference.

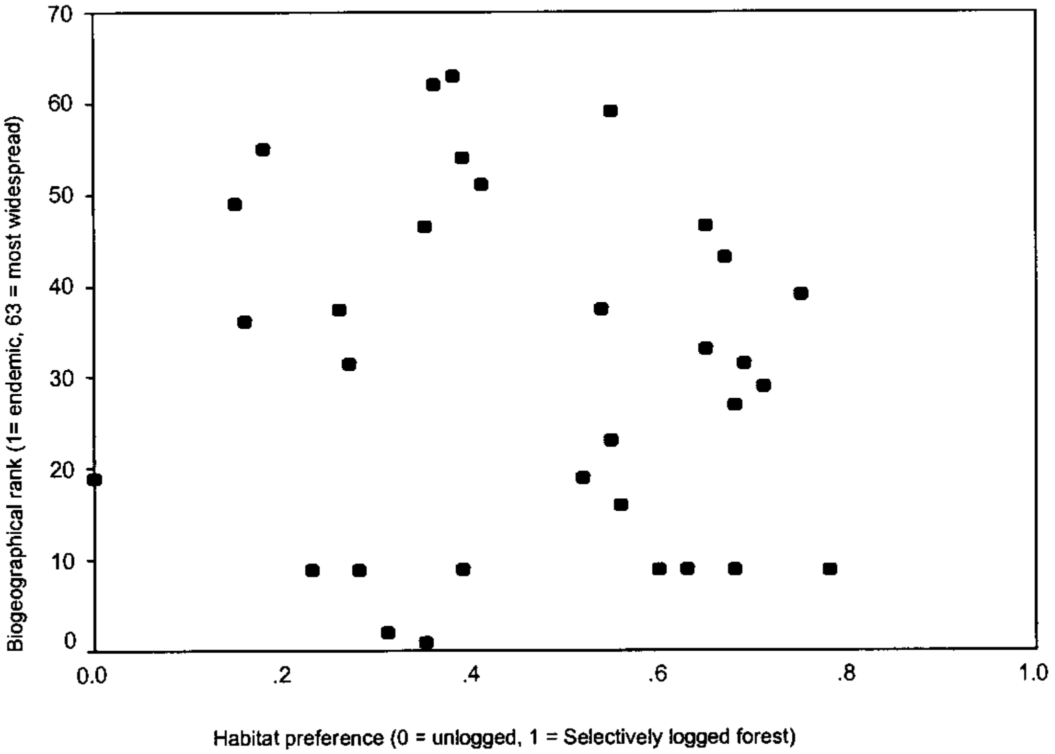


Table 5.1 Fruit feeding nymphalid butterfly species recorded on transects, with geographical distribution and the habitat (**L**-Selectively Logged, **U**-Unlogged), where they were most abundant.

Family Nymphalidae

	Subfamily/Species)	Habitat	Geographical distribution	Rank distribution
No.	Satyrinae			
1.	*Neorina lowii*	**L**	WM,Sum,Pal	16
2.	*Ragadia makuta*	**L**	WM,Sum,Java	19
3.	*Mycalesis orseis*	**L**	Thai,WM,Sum,Pal.	33
4.	*Mycalesis maianeas*	**L**	WM,Sum	9
5.	*Mycalesis anapita*	**L**	WM,Sum	9
6.	*Mycalesis kina*	**U**	Borneo **(End)**	1
7.	*Mycalesis dohertyi*	**U**	WM,Sum	9
8.	*Mycalesis oroatis*	**U**	WM,Sum,Java	19
9.	*Mycalesis mineus*	**U**	Sundaland	23
10.	*Mycalesis patiana*	**U**	WM	2
11.	*Mycalesis janardana*	**L**	WM,Sum,Java,Pal,Min	30
12.	*Mycalesis fusca*	**L**	WM,Sum,Java	19
13.	*Mycalesis horsfieldi*	**L**	Sum,Java,Pal,Sul	42
14.	*Melanitis leda*	**U**	Or,Aust	63
15.	*Melanitis zitenius*	**L**	Or(except IndoC & Phil)	61
16.	*Erites elegans*	**U**	WM,Sum	9
17.	*Erites argentina*	**L**	Sundaland	23
18.	*Xanthotaenia busiris*	**U**	Thai, WM,Sum	31.5
19.	*Elymnias panthera*	**L**	WM,Sum,Java	19
20.	*Elymnias dara*	**L**	Thai,WM,Sum,Java	34
21.	*Ypthima pandocus*	**L**	Sundaland	23
	Nymphalinae			
22.	*Bassarona dunya*	**L**	WM,Sum,Java,Pal	27
23.	*Bassarona teuta*	**U**	Assam,Bur,Thai,WM, Sum,Java,LS,	51
24.	*Rhinopalpa polynice*	**U**	N.Ind,Bur,Thai,WM, Sum,Java,Phil,Sul	49
25.	*Amnosia decora*	**L**	WM,Sum,Nias,Java	29
26.	*Dophla evelina*	**L**	S.Lanka,Ind,Bur,Thai, WM,,Sum,Java,Sul	37
27.	*Euthalia monina*	**L**	N.Ind,Bur,Thai,WM,Java, LS	50
28.	*Euthalia iapis*	**L**	WM,Sum,Java,Pal	27
29.	*Dischorragia nesimachus*	**L**	N.Ind,S.Chn,N.Ind,Chn,Thai, WM,Sum,Java,Jpn,F,Phil,Sul	59
30.	*Lexias pardalis*	**L**	N.Ind,Bur,Thai,WM, Sum,Java,Phil	46.5

31.	*Lexias dirtea*	U	Phil,N.Ind,Bur,S.Chn,IndoChn, Thai,WM,Sum,Java,Pal	54
32.	*Lexias canescens*	U	WM,Sum	9
33.	*Kalima limborgi*	L	WM,Sum	9
34.	*Cirrochroa emalea*	U	Thai,WM,Sum,Jawa,Flores	36
35.	*Athyma reta*	L	N.E,Ind,Bur,Thai,Sum,Java	44
36.	*Athyma pravara*	L	N.Ind,Bur,Thai,Ichn,WM,Sum Java,Bali	52
37.	*Neptis hylas*	U	Ind,Bur,Chn,Jpn,Hai,For,LS, I.Chn,WM,Sum,Java	60
38.	*Neptis harita*	U	NE,Ind,Bur,Thai,I.Chn,WM,Sum	45
39.	*Cupha erymanthis*	U	I.Chn,WM,Sum,Java,LS	53
40.	*Paduca fasciata*	L	WM,Sum,Java,Phil,Pal	40.5
41.	*Terinos clarissa*	U	WM,Sum,Java,Pal,Phil	40.5
42.	*Moduza procis*	U	Ind,Bur,Thai,S.Chn,I.Chn, WM,Sum,Java,LS	56
43.	*Parthenos sylvia*	L	S.Ind,SEA to NG,Sol	58
44.	*Tanaecia aruna*	U	WM,Sum	9
45.	*Tanaecia pelea*	U	WM,Sum,Java	19
46.	*Tanaecia clathrata*	U	Wm,Sum	9
	Morphinae			
47.	*Discophora necho*	L	WM,Sum,Java,Pal	27
48.	*Amathuxidia amythaon*	U	Or	62
49.	*Zeuxidia doubledayi*	L	Thai,WM,Sum	31.5
50.	*Zeuxidia aurelius*	U	WM,Sum	9
51.	*Zeuxidia amethystus*	L	Bur,WM,Sum.Pal,Mind	37.5
52.	*Thaumantis nouredin*	L	WM,Sum	9
53.	*Amathusia phidippus*	L	Sundaland,Phil,Sul	43
54.	*Faunis canens*	L	Thai,Sundaland	35
55.	*Faunis stomphax*	U	Sum,Pal	25
56.	*Faunis gracilis*	U	WM,Sum	9
57.	*Faunis kirata*	L	WM,Sum	9
58.	*Lethe dora*	U	Sum	9
	Charaxinae			
59.	*Charaxes bernadus*	U	Ind,Bur,S.Chn,I.Chn,Thai, WM,Sum,Java	55
60.	*Charaxes durnfordi*	U	Assam,Bur,Thai,WM,Sum,Java	48
61.	*Polyura athamas*	L	Phil,Sul,Nep,Ind,Bur,Thai, S.Chn,I.Chn,WM,Sum,Java,LS	57
62.	*Prothoe franck*	U	N.Ind,Bur,Thai,WM, Sum,Java,Phil	46.5
63.	*Agatasa calydonia*	L	Bur,Thai,WM,Sum,Java,Phil	39

Butterfly rank and distributions follow Otsuka (1988). WM = West Malaysia, Sum = Sumatra, Pal = Palawan, N.Ind = North India, Bur = Burma, Thai = Thailand, Phil = Philippines, Pal = Palawan, Or = Oriental Region, Aust = Australian Region, Sul = Sulawesi, S.Lanka = Sri Lanka, Ind = India, S.Chn = South China, L.S = Lesser Sundas, For = Formosa, Sundaland = WM,Sum,Borneo,Java, Mind = Mindanao, Hai = Hainan, NE Ind = North East India, IndoChn = Indo China, Jpn = Japan, Nep = Nepal, SEA = South East Asia, NG = New Guinea, Sol = Solomon.

Table 5.2 Rank geographical distributions of nymphalid butterflies according to subfamily, habitat and transect. See Table 5.1 for ranks of each species.

a) **Subfamilies**

	Satyrinae	Nymphalinae	Morphinae	Charaxinae
Median	17	42	25.5	48
IQR	3.0 - 32.50	25.0 - 52.25	3.0 - 36.50	42.50 - 56.00
N	20	26	12	5

b) **Habitat**

	Unlogged	**Logged**
Median	36.0	30.50
IQR	3.0 - 52.50	16.75 - 43.25
N	29	34

c) **Transect**

	Transect 1	**Transect 2**	**Transect 3**	**Transect 4**
Median	3.50	42.50	26	31.0
IQR	2.75 - 51.25	24.25 - 53.25	17.0 - 40.0	3.0 - 44.0
N	10	18	11	23

5.6 Discussion

The results of this study showed there was no significant difference in species geographical distributions in unlogged and selectively logged forests. However the study took place about 10 years after logging and impacts may be more severe immediately after logging. It is possible that the species with narrow geographical distributions e.g. *Mycalesis kina* (endemic to Borneo) may be more affected immediately after logging than more widespread species. Previous studies have shown that species with more narrow geographical distributions are more sensitive to environmental disturbance (Thomas & Mallorie 1985; Spitzer *et al.* 1993; Hill *et al.* 1995; Hamer *et al.* 1997; De Vries *et al.* 1997; Lewis *et al.* 1998; Hill *et al.* in press). However some of these studies may have taken place in areas with more severe disturbance than in this study, which might explain the different results. The result from the Spearman correlation for those species with more than 10 individuals showed there was no significant relationship between species geographical rank and habitat preference. This result confirmed that there was no significant impact of selective logging on butterfly assemblages in this study and supported the results of other analyses in Chapter 3.

There was a significant difference in geographical distributions among transects, with Transect 2 having more widespread species (Table 5.2b). This was because only a relative small number of species (19%) sampled in Transect 2 are confined to Sundaland, and the remaining species have more widespread distributions within the Oriental region. This may be attributed to several large forest gaps resulting from natural tree falls and the location of this transect along river catchments (see Figure 2.2). Thus, increasing canopy openness resulting from natural forest disturbance and open areas along river banks in the undisturbed forest interior may have influenced the occurrence of species with different distributions.

There was no significant difference in butterfly geographical distribution among subfamilies (Table 5.2a). Species of Satyrinae and Morphinae are often reported to be weak in flight, prefering shady conditions and confined to dense forest habitats (Ackery 1988; Schulze & Fiedler 1998). By contrast the Nymphalinae and Charaxinae are often strong in flight and prefer open areas, and are often trapped in the canopy or in forest gaps (Corbet & Pendlebury 1992; Hill *et al.* in press). This suggests that species in the subfamilies Satyrinae and Morphinae might have narrower geographical distributions but this was not observed in this study. Although sampling at DVFC took place over an entire year, only small number of species were sampled in some subfamilies. Thus further data may be required to detect differences in geographical range among subfamilies.

CHAPTER SIX

GENERAL DISCUSSION

6.1 Methodology

In tropical areas, fruit-baited traps are commonly used for sampling butterflies (e.g. De Vries 1988; Kremen 1992; Daily & Ehrlich 1995; Sourakov & Emmel 1995; Hughes *et al.* 1998; Beck & Schulze 2000). In this study, I used fruit-baited traps to sample nymphalid butterflies over one year, and recorded 3996 individuals from 63 species. Four transects of 8 km length in total were sampled, comprising 80 observation stations in total. This resulted in a wide variety of habitats being sampled (e.g. different vegetation structure, topographical and landscape features). This is important when monitoring butterfly assemblages in highly heterogeneous tropical forest environments (Whitmore 1998).

More than 75% of the adult Nymphalidae species occurring on Borneo feed as adult on rotting fruit and in comparison to walk and point-count transects by Dawood (2000) and Tangah (2000), which were carried out over the same length of time (one year) and in the same sample areas, this study sampled a much larger number of species and individuals. Walk and point-count methods may also have difficulties in species identification (Walpole & Sheldon 1999) which is less of problem with traps; any individuals that cannot be identified can be taken as specimens. However, walk and point-count transects and trapping techniques have different advantages and disadvantages when monitoring butterflies in tropical forests. Traps are limited to only sampling those species that are attracted to bait. Some other groups of butterflies (e.g. Lycaenidae and Rhiodinidae) which do not feed on rotting fruit will not enter traps (Corbet & Pendlebury 1992). There is also little information on how butterflies are attracted to traps and whether traps sample all species equally efficiently. Most studies indicate that traps operate similarly in different habitats (Hughes *et al.* 1998; Hill *et al.* in press) and so comparisons between logged and unlogged habitats are likely to be reliable. Traps may sample more individuals than walk and point-count transects because traps are left open all day and night and in rainy weather. Thus they can sample crepuscular species (e.g. *Melanitis leda*) that would be unlikely to be detected on walk and point-count transect as these are usually only carried out in sunny weather in the middle of the day. It is not known if results obtained from traps for Nymphalidae are representative of other butterfly families and further studies are needed to compare results from the two methods. It is likely that a combination of traps and walk and count-point methods will be required for surveying a wide range of butterflies in tropical forests.

6.2 Impacts of selective logging on butterflies

Globally, more than 50 % of biodiversity occurs in tropical regions (Tokeshi 1999) and insects are the most diverse groups in tropical rainforests (Speight *et al.* 1999). However, destruction of natural rainforest is increasing at a rapid rate and many of the species that depend on forests are threatened (Collins *et al.* 1991). Tropical biodiversity and impacts of habitat disturbance on species diversity were discussed in Chapter 1. Among groups of insects, butterflies are relatively well known in terms of taxonomy (Kremen 1992) and thus, this group was chosen for studying impacts of habitat disturbance in tropical forest in this study.

The main objective of this study was to investigate the impacts of selective logging on diversity and abundance of tropical butterflies in Sabah, Borneo (Chapter 3). This study found no impact of selective logging on butterfly species diversity (Shannon-Wiener, Simpson D_S or Margalef D_M). These results agree with previous studies indicating that diversity of butterflies was not affected by moderate levels of forest disturbance (e.g. Kremen 1992; Spitzer *et al.* 1997; Lewis *et al.* 1998; Wood & Gillman 1998; Hill 1999). They also agree with results from other studies in the same area which showed little impact of selective logging (Dawood 2000; Tangah 2000; Willott *et al.* 2000). However other studies found that moderate disturbance may increase or decrease species diversity (review in Hamer & Hill 2000). Thus there is no clear consensus on how forest disturbance affects tropical communities. This may be because different studies have been carried out in different parts of the world or because studies differed in the type or severity of disturbance. Another possibility is that the spatial scale over which studies were carried out has had an impact on the results (Hamer & Hill 2000) and this needs further investigation.

In this study, there were significant differences in diversity between transects in disturbed forest (Chapter 3). This shows that species assemblages may be strongly influenced by topographical and landscape features. Thus, it is very important to sample over a large area including a wide range of microhabitats when monitoring butterflies in heterogeneous forest environments.

The geographical distribution of species was investigated in order to examine the conservation value of species assemblages in different habitats (Chapter 5). Many studies have shown that endemic species and species with restricted geographical distributions are more vulnerable to habitat disturbance (e.g. Spitzer *et al.* 1997; Hill *et al.* 1995). The results from this study indicated no strong evidence that species with narrow geographical ranges were more strongly affected by logging. One possibility for the different results is that other studies sampled more butterfly families which consist of more species with restricted distributions, while this study only focused on one family. However, 60 % of the species recorded in this study had distributions confined to Sundaland and this result supports other results in Chapter 3 which indicated that there was little impact of selective logging on species diversity.

Few studies in tropical regions have been carried out over sufficient time periods to study species longevity and dispersal. This study was carried out over one year which meant that data on adult survival and longevity could be investigated in the most abundant species (Chapter 4). There was evidence of significant differences among species in dispersal and longevity, with the larger species (*B. dunya* and *N. lowii*) moving further than the smaller species (*P. franck*). This supports other studies showing that body size is an important determinant of dispersal (Chai & Srygley 1990; Srygley & Chai 1990). There was also evidence that nymphaline species (*B. dunya*) which have relatively larger thoraxes containing flight muscles, moved further than satyrine species (*N. lowii*) which generally have relatively smaller thoraxes (Hill *et al.* in press). The distance between primary and selectively logged forest in this study was not great (≈ 500m between the nearest points). Thus the results from Chapter 4 indicate that butterflies may be able to move between unlogged and logged forest, which may explain why there was little no impact of selective logging on species diversity. However species that are less mobile might be more vulnerable to selective logging (New 1997; Shahabuddin *et al.* 2000) and more dispersal data are needed.

6.3 Butterfly conservation in Sabah.

Borneo is the largest island on the Sunda shelf and its flora and fauna are one of the most highly diverse, containing many endemic species (Holloway 1980). Currently, a total of 936 species of butterflies occur on Borneo, of which 10% are endemic (Otsuka 1996). In Sabah, large areas of forest have been converted to plantation, clear-felled or selectively logged (Collin *et al.* 1991) and understanding the impacts of this disturbance on different species is very important.

In this study, there was little impact of selective logging on butterfly diversity showing that moderately disturbed areas may provide important resources for forest species. In Sabah, the timber industry is the major sources of income for state development (Sabah State Government 1998) and it is likely that most remaining forest will be selectively logged in the near future. The areas of fully protected forest are relatively small, and so large areas of production forest may become increasingly important to species conservation in the future. However, these production areas are due to be logged on a 35-60 year cycle (Whitmore 1990). Few areas have been repeatedly logged and it is not known what impact this may have on biodiversity. A second rotation of logging in Sabah could decrease the diversity of butterfly species as well as other species of animals that are highly dependent on forest resources.

Although this study found that some species of butterfly can move considerable distances within the forest, they may not able to cross unsuitable habitats. This suggests that isolated forest surrounded by non-forest habitat (e.g. oil palm or cocoa plantation) in Sabah may have lower butterfly species diversity due to an inability of species to cross these barriers. Although the butterfly species assemblages in this study were generally not affected by logging, these species are highly dependent on forest resources (e.g. larval and adult food plants) for survival (Corbet & Pendlebury 1992). Thus extreme forest disturbance such as clear-felling or conversion to plantation is likely to result in the loss of many species of butterfly.

There is no strong legislation to protect insect faunas in Sabah (Andau 1998) and the conservation of large numbers of insect species remains uncertain. Thus, there is an urgent need to conserve and protect insect faunas in Sabah, particularly rare species. It is recommended that conversion to plantation, clear felling or ranching should be discouraged because these factors are the major disturbances contributing the loss of global biodiversity in tropical regions (Didham *et al.* 1996).

A. Recommendation for future research.

This study showed that fruit-baited traps are excellent for studying butterflies in tropical forest. However, only adults that feed on fruit were sampled and different types of baits such as carrion or urine could be used to sample different butterfly groups in future studies. There is no information on how species are attracted to traps in the forest (Hill *et al.* in press) and future investigations on butterflies studying how far adults are attracted to traps and whether some species are more likely to be caught would be useful.

This study found that some butterfly species are highly dispersive and able to move large distances. Thus logged areas may have been supplemented by species dispersing from the nearby undisturbed forest area. Further studies on impacts of logging in areas that are remote from conservation areas thus would be valuable.

REFERENCES

Ackery, P.R. (1988) Hostplants and classification: a review of nymphalids butterflies. *Biological Journal of Linnean Society*. 33, 95 - 203.

Andau, M. (1998) Biodiversity in the context of Sabah's wildlife. Paper presented at the State Level Seminar on National Policy on Biological Diversity in Kota Kinabalu, Sabah, Malaysia, 1998.

Andrewartha, H.G. (1961) *Introduction to the Study of Animal Populations*. Methuen & Co. Ltd., London.

Atkin, M. (1988) *Tinjauan terhadap serangga*. Translated by Syed Shah Tajuddin. Dewan Bahasa & Pustaka, Kuala Lumpur.

Audley-Charles, M.G. (1987) A Plants Geographical Analysis of Sulawesi. Pp 94-102. In T.C. Whitmore (ed.). Biogeographical Evolution of the Malay Archipelago. *Oxford Monographs in Biogeography 4*. Clarendon Press, Oxford.

Balgooy, M.M.J.van. (1987) A plants Geographical Analysis of Sulawesi. pp. 94-102. In T.C. Whitmore (ed.). Biogeographical Evolution of the Malay Archipelago. *Oxford Monographs in Biogeography 4*. Clarendon Press, Oxford.

Beck, J. & Schulze, C.H. (2000) Diversity of fruit-feeding butterflies (Nymphalidae) along a gradient of tropical rainforest successions in Borneo with some remarks on the problem of 'pseudoreplicates'. *Transactions of the Lepidopterological Society of Japan*. **51**(2), 89-98.

Beck, J., Muhlenberg, E. & Fiedler, K. (1999) Mud-puddling behavior in tropical butterflies: in search of proteins or minerals? *Oecologia*. **119**, 140-148.

Begon, M., Harper, J.L., Townsend, C.R. (1996) *Ecology : individuals, populations and communities*. 3rd. edition, reprinted in 1997. Blackwell, Oxford. 1068 pp.

Braby, M.F. (1995) Seasonal changes in relative abundance and spatial distribution of Australian lowland tropical satyrinae butterflies. *Australian Journal of Zoology*, **43**, 209-229.

Brooks, T.M., Pim, S.L. & Collar, N.J. (1997) Deforestation predicts the number of threatened birds in insular Southeast Asia. *Conservation Biology*. **11**(2), 382-394.

Brown, K.S., & Hutchings, R.W. (1997) Fragmentation, and the dynamics of diversity in Amazonian forest butterflies. pp 91-110. In W. F. Lawrence & R. O. Bierregaard. (eds.). *Tropical forest Remnants: Ecology, Management and Conservation of fragmental Communities*. Chicago University Press.

Chai, P. & Srygley, R.B. (1990) Predation and the flight, morphology, and temperature of neotropical rain-forest butterflies. *Am. Nat.* 135, 748-765.

Chung, A.Y.C. & Maryati, M. (1996) A comparative study of the ant fauna in primary and secondary forest in Sabah, Malaysia. pp. 357-366. In D.S. Edwards., W.E. Booth & S.C. Choy (eds.), *Tropical rainforest research-current issues*. Kluwer Academic Publishers, London.

Cohen, J.I. & Potter, C.S. (1993) Introduction: Conservation of Biodiversity in Natural Habitats and the Concept of Genetic Potential. Pp. xix-xxiii. In S.P. Christopher S.P., J.I. Cohen., D. Janczewski. (eds.). *Perspective on Biodiversity: case studies of genetic conservation and development*. Kluwer Academic Publishers, London.

Collins, N.M., Sayer, J.A. & Whitmore, T.C. (1991) *The Conservation Atlas of Tropical Forests-Asia and the Pacific*. (IUCN) Macmillan Press, London.

Corbet, A.S. & Pendlebury, H.M. (1992) *The Butterflies of the Malay Peninsula.* 4th edition. Malayan Nature Society, Kuala Lumpur.

Costa, P.M. & Karolus, A. (1995) Timber Extraction Volumes (1970-1991), Ulu Segama Forest Reserve. *Innoprise Corporation Internal Reports.*

Cox, C.B. & Moore, P.D. (2000) *Biogeography an ecological and evolutionary approach.* 6th edition. Alden Press Oxford.

Damborgh, J. and Aaen, K. (1999) The impact of human disturbance on diversity and species composition in a South East Asian Rainforest. Biological project work, University of Aaarhus, Denmark.

Davis, A.J. (1993) The Ecology and Behaviour of Rainforest Dung Beetles in Northern Borneo. Unpublished Phd Thesis, University of Leeds, United Kingdom.

Dawood, M.M. (2000) Ecology of Ragadia makuta (Lepidoptera: Satyrinae) in tropical rainforests of Sabah, Malaysia. Unpublished MSc Thesis, University of Durham, United Kingdom.

DeVries, P.J. (1988) Stratification of fruit-feeding nymphalid butterflies in Costa Rican rainforest. *Journal of Research on the Lepidoptera*, **26**, 98-108.

DeVries, P.J., Murray, D. & Lande, R. (1997) Species diversity in vertical, horizontal, and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest. *Biological Journal of the Linnean Society*, **62**, 343-364.

Diamond, J. (1996) Overview of recent extinctions. pp. 37-43. In D. Western., M. Pearl (eds.). *Conservation for the twenty first Century.* OUP, New York.

Didham, R.K., Ghazoul, J., Stork, N.E. and Davis, A.J. (1996) Insects in fragmented forest: a functional approach. *Tree*, **11** (6), 255-260

Douglas, I., Spencer, T., Greer, T., Bidin, K., Sinun, W. and Wong, W.M. (1992). The impact of selective commercial logging on stream hydrology, chemistry and sediment loads in the Ulu Segama rainforest, Sabah. *Phil. Trans. R. Soc. Lond.* **B 335**, 397-406.

Ehrlich, P.R., Breedlove, D.E., Brusard, P.F. & Sharp, M.A. (1972) Weather and the regulation of subalphine populations. *Ecology.* 53, 243-247.

Ewusie, J.Y. (1980) *Elements of Tropical Ecology: With Reference to Africa, Asian, Pacific and New World.* Heinemann, London.

Foster, R.B. (1980) Heterogeneity and disturbance in tropical vegetation. In M.E. Soule & Bruce A. Wilcox (eds.). *Conservation Biology: an evolutionary – ecological prespective.* Sinauer Associates Inc., Massachussetts.

Gaston, K.J. and Spicer, J.I (1998) *Biodiversity an introduction.* Blackwell Science, Oxford.

Greenwood, J.D. (1996) Basic techniques. In W.J. Sutherland (ed.). *Ecological Census Techniques: a Handbook.* Cambridge University Press, Cambridge.

Hall, J.P.W. & Willmott, K.R. (2000) Patterns of feeding behaviour in adult male riodinid butterflies and their relationship to morphology and ecology. *The Linnean Society of London.* **69**, 1-23.

Hamer, K.C. & Hill, J.K. (2000) Scale-dependent effects of habitat modification for species diversity in tropical forests. *Conservation Biology.* **14**(5), 1435-1440.

Hamer, K.C., Hill, J.K., Lace, L.A. and Langan, A.M. (1997) Ecological and biogeographical effects of forest disturbance on tropical butterflies of Sumba, Indonesia. *Journal of Biogeography*, **24**, 64-75.

Hanski, I. & Gilpin, M.E. (1997) *Metapopulation Biology: Ecology, Genetic and Evolution*. Academic Press, London.

Hawksworth, D.L. & Kallin-Arroyo, M.T. (1995) Magnitude and distribution of biodiversity. In V.H. Heywood. (ed.). *Global Biodiversity Assessment*. pp. 107-192. United Nation Environment Programme, Cambride University.

Heards, S. (1991) Bulletin of the Ecological Society of America. **72**(1), 13.

Hendersen, P.A. & Seaby, R.M.H. (1998) *Species and richness diversity program*, version 2. Oxford University, London.

Heydon, M.J. and Bulloh, P. (1997). Mousedeer densities in a tropical rainforest: The impact of selective logging. *Journal of Applied Ecology*, **34**, 484-496.

Hill, J.K., Hamer, K.C., Tangah, T. & Dawood, M. (in press) Ecology of tropical butterflies in rainforest gaps. *Oecologica*.

Hill, J.K. (1999) Butterfly spatial distribution and habitat requirements in a tropical forest: impacts of selective logging. *Journal of Applied Ecology*, **36**, 564-572.

Hill, J.K. & Hamer, K.C. (1998) Using species abundance models as indicators of habitat disturbance in tropical forests. *Journal of Applied Ecology*, **36**, 564-572.

Hill, J.K., Thomas, C.D. & Lewis, O.T. (1996) Effects of habitat patch size and isolation and dispersal by *Hesperia comma* butterflies; implications for metapopulation structure. *British Ecological Society*. **65**, 725-735.

Hill, J.K., Hamer, K.C., Lace, L.A. and Banham, W.M.T. (1995) Effects of selective logging on tropical forest butterflies on Buru, Indonesia. *Journal of Applied Ecology*, **34**, 484-496.

Holloway, J.D. & Hall, R. (1998) SE Asian geology and biogeography: an introduction. pp. 1-23. In R. Hall & J.D. Holloway (eds.). *Biogeographical and Geological Evolution of SE Asia*. Bachuys Pub., Leiden.

Holloway, J.D., Kirk-Spriggs, A.H. and Chey V. K. (1992) The response of some rainforest insect group to logging and conservation to plantation. *Phil. Trans. R. Soc. Lond.* **B 335**, 425-436.

Holloway, J.D., Bradley, J.D. & Carter, D.J. (1987). Lepidoptera. pp.1-16. In C.R. Betts (ed.). *IIE guides to insects of importance to man; 1.* International Institute of Entomology, London.

Holloway, J.D. (1987) Lepidoptera patterns involving Sulawesi: what do they indicate of past geography? pp. 103-118. In T.C. Whitmore (ed.). Biogeographical Evolution of the Malay Archipelago. *Oxford Monographs in Biogeography 4.* Clarendon Press, Oxford.

Holloway, J.D. (1984) Notes on the butterflies of the Gunung Mulu National Park. *Sarawak Museum Journal.* **30**(51), 89-121.

Holloway, J.D. (1976) *The moths of Borneo with special reference to Mount Kinabalu.* Sun U, Kuala Lumpur.

Hughes, J.B., Daily, G.C. & Ehrlich, P.R. (1998) Use of fruit bait traps for monitoring of butterflies (Lepidoptera: Nymphalidae). *Rev. Biol. Top.* **46**, 697-904.

Huston, M.A. (1994). *Biological diversity. The Coexistence of species on changing landscapes.* Cambridge University Press.

Janzen, D.H. (1986) The future of tropical ecology. *Ann. Rev. Ecol. Syst.* **17**, 305-324.

Jintanugool, J., Eudey, A.A., Brockelman, W.Y. (1982) Species Conservation Priorities in Thailand. pp. 41-51. In R.A. Mittermeier & W.R. Konstant. Species Conservation priorities in the tropical forest of Ssouth East Asia. *Proceeding of a Symposium held at the 58th meeting of the IUCN Species Survival Commision (SSC). No.1.* IUCN, Kuala Lumpur.

Johns, A.D. (1988) Effects of 'selective' timber extraction on rain forest structure and composition and some consequences for frugivores and folivores. *Biotropica,* **20**(1) 31-37.

Johns, A.D. (1992) Vertebrate response to selective logging; implication for the design of logging system. *Phil. Trans. R. Soc. London.* **B 335**, 437-442.

Kennedy, D.N. & Swaine, M.D. (1992) Germination and growth of colonizing species in artificial gaps of different sizes in dipterocarps rainforest. *Phil. Trans. R. Soc. London.* **B 335**, 357-366.

King, J.R., Andersen, A.N. & Cutter, A.D. (1998). Ants as bioindicators of habitat disturbance: validation of the functional group model for Australia's humid tropics. *Biodiversity and Conservation.* **7**(12), 1627-1636.

Kremen, C. (1992) Assessing the indicator properties of species assemblages for natural areas monitoring. *Ecological Applications,* **2** (2), 203-217.

Kremen, C., Colwell, R.K., Erwin, T.L., Murphy, D.D., Noss, R.F. and Sanjayan, M.A. (1993) Terrestrial arthropod assemblages: their use in conservation planning. *Conservation Biology*, **7**, 796-808.

Laidlaw, R.K. (1998) A comparison between population of primates, squirrels, tree shrews and other mammals inhabiting Virgin, Logged, Fragmented and Plantation forests in Malaysia. pp. 141–159. *Proceedings of the Malaysia-United Kingdom. 21-24 Oct. 1996. Conservation, Management and Development of Forest Resources.* Forest Research Institute Malaysia, Kuala Lumpur.

Lambert, F.R. (1992) The consequences of selective logging for Bornean lowland forest birds. *Phil. Trans. R. Soc. London.* **B 335**, 443-457.

Leemans, R. (1996) Biodiversity and global change. In J. Gaston (ed.). *Biodiversity a biology numbers on difference.* pp. 77-113. Blackwell Science, Oxford.

Lewis, O.T., Wilson, R.J. & Harper, M.C. (1998) Endemic butterflies on Grande Comore: habitat preferences and Conservation priorities. *Biological Conservation*, **85**, 113-121.

Lewis, O.T., Thomas, C.D., Hill, J.K., Brooks, M.I., Crane, T.P.R. (1997) Three ways of assessing metapopulation structure in butterfly *Plebejus argus*. *Ecological Entomology*. **22**, 283-293.

Magguran, A.E. (1988) *Ecological diversity and its measurement*. Princeton University Press, London.

Mabberly, D.J. (1983) *Tropical rain forest ecology*. Glasgow & London: Blackie & Sons. Ltd.

Mahli, Y. & Grace, J. (2000) Tropical forests and atmospheric, carbon dioxide. *Tree.* **15**(8), 332-337.

Marsh, C.W. & Greer, A.G. (1992) Forest land-use in Sabah, Malaysia: an introduction to Danum Valley. *Phil. Trans. R. Soc. London.* **B 335,** 327-339.

Maruyama, K. & Otsuka, K. (1991) *Butterflies of Borneo.* Vol. 2, No. 2. Tobishima Corporation, Tokyo.

May, R.M. (1981) Patterns in multi-species communities. pp. 197-227. In R.M. May (ed.). *Theoritical Ecology. Principles and Applications.* 2nd edition. Blackwell Scientific Publication, Oxford.

May, D.Y. (1998) Contribution of the Forestry Sector to the Malaysian Economy. In S.S. Lee., V.M. Dan., I.D. Gauld and J. Bishop. *Proceeding of the Malaysia – United Kingdom. 21-24 Oct 1996. Conservation Management & Development of forest Resources.* Forest Reseach Intitute Malaysia, Kuala Lumpur.

Morton, A.C. (1981) The Effects of Marking and Handling on Recapture Frequencies of Butterflies. pp. 55-58. In R.I. Vane-Wright & P.R. Ackery (eds.). The Biology of Butterflies. *Symposium of the Royal Entomological Society.* Academic Press, London.

Myers, S.N. (1989) A major extinction spasm predictable and inevitable? In D.Western & M. Pearl. *Conservation for the twenty first century.* pp. 1-7. OUP, New York.

Myers, S.N. (1986) Tropical forests: patterns of depletion. pp. 9-18. In G.T. Prance (ed.). Tropical rainforets and the world atmosphere. *AAA Selected Symposium 101.* Westview Press, Colorado.

New, T.R. (1997) *Butterfly conservation.* 2^{nd} edition. Oxford University Press, Melbourne.

Newbury, D.M., Campbell, E.J.F., and Lee, Y.F. Ridsdale, C.E. and Still, M.J. (1992) Primary lowland dipterocarp forest at Danum Valley, Sabah, Malaysia; structure, relative abundance and family composition. *Phil. Trans. R. Soc. London.* **B 335,** 341-356.

Nussbaum, R.E. (1995) The effects of Selective Logging of Tropical Rainforest On Soil Properties And Implications For Forest Recovery I Sabah, Malaysia. Unpublished Ph.D. Thesis, University of Exeter.

Nussbaum, R.E., Anderson, J., & Spencer, T. (1995) Factors limiting growth of indigenous tree seedlings planted on degraded rainforest soils in Sabah, Malaysia. *Forest Ecology and Management*, **74**, 149-159.

Orians, G.H., Dirzo, R. & Cushman, J.H. (1996). Introduction. In G.H. Orians, R. Dirzo and J.H. Cushman (eds.). *Biodiversity and ecosystem process in tropical forests.* Springer Verlag. Berlin.

Ohtsuka, K. (1996) *Bornean Butterflies Examined Through Distribution.* Tobishima, Tokyo.

Otsuka, K. (1988) *Butterflies of Borneo.* Vol. 1. Tobishima Corporation, Tokyo.

Owen, D.F. (1971) Species diversity in butterflies in a tropical garden. *Biological Conservation*, **3**(3), 191-198.

Owen, D.F. & Chanter, D.O. (1972) Seasonal changes in relative abundance and estimates of species diversity in a family of tropical butterflies. *Oikos*, **23**, 200-205.

Park, C.C. (1992) *Tropical rainforests*. Routledge, London.

Payne, J. (1982) Special Conservation Priorities in the Tropical Forest of Sabah, East Malaysia. pp. 23-26. In R.A. Mittermeier & W.R. Konstant. Species Conservation priorities in the tropical forest of South East Asia. *Proceeding of a Symposium held at the 58th meeting of the IUCN Species Survival Commission (SSC). No.1.* International Union for Conservation of Nature and Natural Resources, Kuala Lumpur.

Pinard, M.A. & Putz, F.E. (1996) Retaining forest biomass by reducing logging damage. *Biotropica*, **28**, 278-295.

Pollard, E. & Eversham, B.C. (1995) Butterfly monitoring 2 - interpreting the changes. pp. 23-26. In A.S. Pullin (ed.). *Ecology and Conservation of Butterflies*. Chapman & Hall, London.

Putz, F.E. (1996) Soil compaction and water infiltration: overview of group projects. In F. E. Putz., E.P. Sist., D.P. Dykstra & R.C. Henreich (eds.). Research method for Reduced Impact Logging: Workshop Results. *A report on the International Training Seminar on Reduced Impact Timber Harvesting and Natural Forest Management. 14-27 July 1996. Bogor and East Kalimantan, Indonesia.* Center for International Forestry Research (CIFOR) Jakarta.

Rodriguez, J.P., Pearson, D.L. & Barrera, R.R. (1997) A test for the adequacy of bioindicator taxa: are tiger beetles (Coleoptera: Cicindelidae) appropriate indicators for monitoring the degration of tropical forests in Venezuela? *Biological Conservation*, **83**(1) 69-76.

Richards, P.W. (1996) *The tropical rain forest: an ecological study.* 2nd edition. Cambridge University Press, Cambridge.

Sabah State Government. (1992) (Untitled) Map of Sabah, Showing Natural & plantation Forest.

Sayer, J.A. & Whitmore, T.C. (1991) Tropical moist forests: Destruction and Species extinction. *Biological Conservation*, **55**, 199-213.

Schulse, C.H., Linsemair, K.E. & Fiedler, K.C. (in press) Understorey versus canopy-patterns of vertical stratification and diversity among Lepidoptera in a Bornean rainforest. *Plant Ecology*.

Schulze, C.H. & Fiedler, K. (1998) Habitat preference and flight activity of Morphinae butterflies in a Bornean rain forest with a note on Sound Production by Adult Zeuxidia (Lepidoptera: Nymphalidae). *The Malayan Nature Journal*. 52, 163-176.

Seki, Y., Takanami, Y., & Otsuka, K. (1991) *Butterflies of Borneo*. Vol. 2, No.1 Tobishima Corporation, Tokyo.

Shahabuddin, G., Herzner, G.A., Aponte, R.C. & Gomez, M.D.C. (2000) Persistence of a frugivorous butterfly species in Venezueland forest fragments: the role of movement and habitat quality. *Biodiversity Conservation*, **9**, 1623-1641.

Sham, S. (1998) *The environment. The Encyclopedia of Malaysia*. Vol 1. Archipelago Press, Kuala Lumpur.

Shreeve, T.G. (1992) Monitoring butterfly movements. pp. 120-138. In L.H. Dennis (ed.). *The ecology of butterflies in Britain*. Oxford Science Pub, Oxford.

Shuey, J.A. (1997) An optimized portable bait trap for quantitative sampling of butterflies. *Tropical Lepidoptera*, **8**(1), 1-4.

Smart, P. (1991) *The illustrated encyclopedia of the butterfly world.* Reprinted, 1975. Salamander, New York.

Southwood, T.R.E. (1978) *Ecological Methods: with particular reference to the study of insect populations.* Chapman & Hall, London.

Sourakov, A. & Emmel, T.C. (1995) Bait Trapping for butterflies in Kenya. *Tropical Lepidoptera*, **6**(1), 1-2.

Speight, M.R., Hunter, M.D. & Watt, A.D. (1999) *Ecology of insects; concept and applications.* Blackwell Science Ltd., London.

Spitzer, K., Jaroz, J., Havelka, J. & Leps, J. (1997) Effect of small-scale disturbance on butterfly communities of an Indochinese montane rainforest. *Biological Conservation*, **80**, 9-15.

Srygley, R.B. & Chai, P. (1990) Flight morphology of Neotropical butterflies: palability and distribution of mass to the thorax and abdomen. *Oecologia*, 491-499.

Sterry, P.C. (1995) *A photographic guide to butterflies of Britain and Europe.* New Holland Ltd., London.

Stork, N.E. (1991) The composition of the arthropod fauna of Bornean lowland rainforest trees. *Journal of Tropical Ecology*, **7**, 161-180.

Sutton, S.L. & Collins, N.M. (1991) Insects and Tropical Conservation. pp. 405-424. In N.M. Collins & J.A. Thomas (eds.). The Conservation of insects and their habitats. *15th Symposium of the Royal Entomological Society of London. 14-15th Sept. 1989.* Academic Press, London.

Tangah, J. (2000) Impacts of Selective Logging on Tropical Butterflies in Sabah, Malaysia. Unpublished MSc Thesis, University of Durham, United Kingdom.

Terbough, J. (1992) *Diversity and the tropical rainforest.* Scientific American Library, New York.

Thomas, C.D., Thomas, J.A. & Warren, M.S. (1992) Distribution of occupied and vacant butterfly habitats in fragmented landscapes. *Oecologia,* **92**, 563-567.

Thomas, C.D. & Mallorie, H.C. (1985) Rarity, species richness and conservation: butterflies of the Atlas mountains in Moroco. *Biological Conservation*, **33**, 95-117.

Tokeshi, M. (1999) *Species Coexistence: ecological and evolutionary perspective.* Blackwell Science, Oxford.

Tokeshi, M. (1993) Species Abundance Patterns and Community Structure. *Advances in Ecological Research*, **24**, 111-186.

Vrijenhoek, R.C. (1989). Population genetics and conservation. pp. 39-98. In D. Western & M. Pearl. *Conservation for the twenty first Century.* OUP, New York.

Walpole, M.J. & Sheldon, I.R. (1999) Sampling butterflies in tropical rainforest: an evaluation of transect walk method. *Journal of Tropical Ecology*, 2, 302-325.

Warren, M.S. (1992) Butterfly populations. pp. 73-88. In R.H.L. Dennis (ed.). *The Ecology of Butterflies in Britain*. Oxford University Press.

Watt, A.D., Stork, N.E., Eggleton, P., Srivastava, D., Bolton, B., Larsen, T.B., Brendell, J.D. & Bignell, D.E. (1997) Impacts of forests loss and regeneration on insects abundance and diversity. In A.D. Watt., N.E. Stork & M.D. Hunter (eds.). *Forest and Insects*. Chapman & Hall, London.

Whitmore, T.C. (1998) *An introduction to tropical rain forests*. 2nd edition. Oxford University Press.

Whitmore, T.C. (1990) *An introduction to tropical rainforests*. Clarendon Press, Oxford.

Whitmore, T.C. (1987) Biogeographical Evolution of the Malay Archipelago. pp. 1-5. In T.C. Whitmore. Biogeographical Evolution of the Malay Archipelago. *Oxford Monographs in Biogeography 4*. Clarendon Press, Oxford.

Whitmore, T.C. (1984) *Tropical Rain Forests of the Far East*. 2nd Edition, reprinted 1985. Oxford University Press.

Willott, S.J., Lim, D.C., Compton, S.G. & Sutton, L.S. (2000) Effects of selective logging on butterflies of a Borneon rainforest. *Conservation Biology*, **14**, 1-12.

Walsh, R.P.D. (1996) Drought frequency changes in Sabah and adjacent parts of northern Borneo since the late nineteenth century and possible implication for tropical rain forests dynamics. *Journal of Tropical Ecology*, **12**, 385-405.

Wilson, E.O., (1988) The current state of biodiversity. pp 3-18. In E.O. Wilson (ed.). *Biodiversity*. National Academy Press.

Wilson, E.O. (1989) Conservation: The next hundred years. In D. Western & M. Pearl. *Conservation for the twenty first Century*. pp. 39-98. OUP, New York.

Wilson, E.O. (1992) *The Diversity of Life*. Belknap Press, Cambridge.

Wolda, H. (1983) Diversity, diversity indices and tropical cockroaches. *Oecologia*, **58**, 290-298.

Wood, B. & Gillman, M.P. (1998) The effects of disturbance on forest butterflies using two methods of sampling in Trinidad. *Biodiversity and Conservation*, **7**(5), 597-616.

Yong, H.S. (1983) *Malaysian butterflies an introduction*. Tropical Press, Kuala Lumpur.

Yong, H.S. (1998) *Animals. The Encyclopedia of Malaysia*. Vol 3. Archipelago Press, Kuala Lumpur.

Zar, J.H. (1996) *Biostatistical analysis*. 3rd edition. Prentice Hall, London.