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Faculty of Science

**Population structure and dispersal of butterflies in  
tropical rain forests of Papua New Guinea**

Ph.D. Thesis

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## ■ Annotation

The thesis describes the community composition, population structure and dispersal in a lowland rainforest community, extended to changes in butterfly composition along an altitudinal gradient. It tests the feasibility of mark-release-recapture studies in the understories of lowland primary forests, describes dispersal in relation to host plants and compares dispersal and demographic parameters with temperate species. Focusing on primary as well as secondary sites the thesis analyzes species richness and similarity between sites along an altitudinal gradient. It also tests ecological correlates for endemism in New Guinea butterflies, particularly their geographic and altitudinal range, as well as their optimum altitude.

## ■ Declaration [in Czech]

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## ■ List of papers and author's contribution

The thesis is based on the following papers (listed chronologically):

- I. Vlasanek, P., Sam, L., Novotny, V., 2013.** Dispersal of butterflies in a New Guinea rainforest: using mark–recapture methods in a large, homogeneous habitat. *Ecological Entomology* DOI: 10.1111/een.12051 (IF = 1.954).  
*Petr Vlasanek - project design, data collection and analysis, paper writing. Legi Sam - data collection. Vojtech Novotny – project design, paper writing.*
  
- II. Vlasanek, P., Novotny, V.** Demography and mobility of three common understory butterfly species from tropical rain forest of Papua New Guinea. Submitted manuscript.  
*Petr Vlasanek - project design, data collection and analysis, paper writing. Vojtech Novotny – project design, paper writing.*
  
- III. Vlasanek, P., Kimbeng, F., Novotny, V.** Butterfly communities along an altitudinal gradient in the tropical rainforest of Huon Peninsula, Papua New Guinea. Manuscript.  
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**Co-author agreement:**

Vojtěch Novotný, the supervisor of the Ph.D. thesis and co-author of all presented papers, fully acknowledges the major contribution of Petr Vlašánek in all presented papers.

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# **Introduction**



# Population structure and dispersal of butterflies in tropical rain forests of Papua New Guinea

This study is about butterflies, a group that is exceptional by being taxonomically well known not only in temperate but also in tropical regions. Butterflies are active during the day, they are conspicuous and recognizable insomuch that researchers do not have to capture them for identification and, if needed, they are easy to capture. In almost every region there is appropriate literature for identifying butterfly species (in Papua New Guinea it is Parsons 1999), and usually also large numbers of museum specimens documenting their distribution. Butterflies can be used as indicator taxa as they rapidly respond to changes in local vegetation or climate (Kremen 1992). Such focus on one of a few taxa can save time and money compared to the study of all insect species, virtually impossible in tropical regions (Gardner et al. 2008). It is therefore not surprising that butterflies have become a popular model group for studying ecological trends such as dispersal (Hanski et al. 1994), demography (Konvicka et al. 2008, Vlasanek et al. 2009) or habitat conservation (Hill et al. 1995). Studies focused on butterfly demography and life history are mostly limited to temperate areas. Ecological research of butterflies in the tropics is rare compared to temperate regions (Bonebrake et al. 2010), mostly due to constraints such as inaccessibility or cost.

## **Why and how to study butterflies**

There are two main methods used for studying butterfly ecology. Firstly one can conduct transect walks (Pollard 1977), during which the observer walks slowly along a transect of several hundred meters and records butterflies within an area of defined width around the transect. Biologists have been always been interested in how diverse local communities are in the tropics compared to temperate ones (alpha diversity), how many species there are in larger regions (gamma diversity), and how communities composing these regional faunas differ from each other (beta diversity). The transect method can be used to answer all of these questions. It is used to assess community composition and species richness (Despland et al. 2012, Molina-Martinez et al. in press), which can be then analyzed for the effect of disturbance, management, habitat type, seasonality or long-term variability on community composition (Spitzer et al. 1993, Hill et al. 1995, Bhardwaj et al. 2012). The advantage of this method is the ease of butterfly counting, permitting rapid surveys of relatively large areas by replicated

transects. However, it only measures the density of butterflies present within the transects, ignoring wider butterfly movements among transects. Therefore it cannot compute the dispersal characteristics or size of butterfly populations. For these tasks there is the second method - mark-release-recapture (MRR). First used in vertebrates (Petersen 1894, Dahl 1918, Lincoln 1930), it quickly became popular among entomologists (Ehrlich 1965, Cook et al. 1976). Animals are captured, released, and then possibly recapture again (often more than once). In the beginning such data was analysed using simple methods, based on two capture occasions (e.g. the Lincoln index). Later the analyses became more complex and sophisticated as mathematicians got involved. Nowadays MRR analyses can be based on multiple capture occasions. At first these calculations assumed closed populations (Schnabel 1938), but later also open populations could be analyzed (Darroch 1959, Cormack 1964, Jolly 1965, Seber 1965). During the eighties the most sophisticated method to date was developed - constrained linear models (Clobert & Lebreton 1985), which are probably the most reliable method for handling MRR data (Schtickzelle et al. 2003). Among several resulting models it is possible to choose the best one according to lowest Akaike information criterion. MRR studies are uncovering the dispersal of butterflies (Baguette 2003, Zimmermann et al. 2011a), studying metapopulation dynamics (Hanski 1998) and estimating population characteristics such as survival, mortality or population size (Nowicki et al. 2005, Vlasanek et al. 2009, Zimmermann et al. 2011b).

There are two ways to collect MRR data. Either fruit baited traps (Corbet 1942) or insect nets can be used. Traps are a passive way of collecting butterflies attracted to rotting fruits. However this method only works properly with fruit feeding guilds of the butterfly family Nymphalidae and even then it attracts different species with unequal efficiency (Hughes et al. 1998). The alternative method of hand collecting butterflies using a net is suitable for all species, but requires accessible, i.e. non-forest, habitats and its precision depends on the flight activity of the butterflies. In temperate regions MRR studies are done mostly using the insect net method since temperate butterflies mostly inhabit non-forested sites (e.g. meadows, steppes and marshes). In tropical areas traps are more popular because using a butterfly net in dense primary or secondary forest understory is impractical and the forest canopy remains inaccessible. Tropical studies using butterfly nets are mostly focused on low vegetation along roads and paths (Ehrlich & Gilbert 1973, Cook et al. 1976, de-Andrade & Freitas 2005) with the majority of studies being conducted using traps in forests and focusing on ecological topics including forest fragmentation (Uehara-Prado et al. 2007, Marin et

al. 2009), forest gap ecology (Hill et al. 2001) or selective logging (Hill et al. 1995, Lewis 2001).

Tropical – temperate comparisons of butterfly dispersal, demography and population structure are thus difficult because of methodological differences. Tropical butterfly species (adults) appear to live longer than temperate species (Scott 1973, Molleman et al. 2007, Beck & Fiedler 2009). In Heliconiinae, the life span can exceed 50 days (Ehrlich & Gilbert 1973, Cook et al. 1976) but there are observations of even longer life spans, extending to almost 300 days (Molleman et al. 2007). Our knowledge of butterfly dispersal varies greatly between temperate and tropical regions (Bonebrake et al. 2010). In temperate regions dispersal ability is known for many species and several traits affecting movements have been identified, e.g. dispersal ability is affected by butterfly density or type of habitat (Roland et al 2000). In the tropics our data on dispersal are limited mostly to the Heliconiinae group (studied along trails and roads; Ramos & Freitas 1999, de-Andrade & Freitas 2005) or to the movements between forest strata (Tangah et al. 2004). Similarly, population density is often studied in temperate regions (e.g. Vlasanek et al. 2009, Rosin et al. 2011) but tropical studies on population density are scarce and again mostly along trails and roads (Francini et al. 2005, de-Andrade & Freitas 2005).

### **Successional and disturbance gradients**

There are several ecological gradients greatly affecting the composition of butterfly communities. In addition to latitudinal gradients, requiring globally replicated study sites, there are two gradients, altitudinal and succession, which generate significant turnover of butterfly species and are replicated in virtually all tropical areas. They can be easily studied as significant environmental change along these gradients can occur across a short geographic distance, i.e. within the same regional pool of species available for the assembly of butterfly communities along these gradients.

As forest sites become more and more degraded for various reasons (selective logging, land conversion for slash and burn agriculture, pastures and plantations, and human settlements), studying the differences between primary and secondary habitats has become very popular. Generally the species richness of various taxa declines with increasing disturbance (Bowman et al. 1990, Lawton et al. 1998). Primary forest has higher plant species richness and is more complex than secondary forest and as such it allows greater coexistence of ecologically related herbivore species, the presence of

more guilds and also more specialist species on a variety of host plant species (Bowman et al. 1990). While in many focal taxa the effects of disturbance and forest conversion were obvious and trends along succession gradients clear, this was not always the case for butterflies. Some studies found butterfly diversity to be higher in primary than secondary forests (Bowman et al. 1990, Perfecto et al. 2003, Schulze et al. 2004, Veddeler et al. 2005, Barlow et al. 2007), others argued the opposite (Lawton et al. 1998, Ramos 2000). Furthermore, several studies that found higher diversity in secondary forest note that the diversity of endemic butterflies with small distribution was higher in primary forest (Hamer et al. 1997, Fermon et al. 2005, Bobo et al. 2006). These variable results are probably due to the differing spatial scales at which the research was conducted, combined with different spatial turnover of species in primary and secondary forests - studies at a larger spatial scale show higher diversity in undisturbed habitat whereas more limited studies found the opposite (Hill & Hamer 2004). DeVries et al. (1997) found that more species were present in degraded habitats and argued that this is because primary forest specialists often randomly fly out of their habitat and disperse to nearby disturbed sites. Small and medium disturbance events have a positive effect on species richness (Connell 1978). Preferences along successional gradients also differ with butterfly taxonomy, even within a single butterfly family. Hamer et al. (2003) documented that Satyrinae and Morphinae prefer shady parts of primary forest while Nymphalinae and Charaxinae (all family Nymphalidae) tend to prefer more open habitats: gaps in primary forests, and deforested habitats in the neighbourhood of human settlements. Secondary forest vegetation typically forms a small proportion, 3-5%, in natural forests, mostly in tree fall gaps. This percentage is greatly increased by selective logging. The impact of this disturbance on species richness of butterflies is often studied. Hill et al. (1995) found species richness decreased on selectively logged sites but Lewis (2001) found the opposite result. Further, selective logging and land conversion also fragments the remaining primary forest areas which may also affect butterfly species richness. As expected, fragments which are more isolated have fewer species of butterflies (Benedick et al. 2006, Uehara-Prado et al. 2007), though at least fruit feeding nymphalids are not directly endangered by fragmentation (Marin et al. 2009).

Species with optima in different parts of the secondary – primary forest succession gradient can differ in their life history strategies and other species traits. In particular, species preferring primary forest have smaller geographical ranges than those preferring secondary vegetation (Spitzer et al. 1993, Hill et al. 2001). Butterflies from



forest gaps are also better flyers and move more frequently than species from the forest understory (Hill et al 2001).

### **Altitudinal gradient**

Altitudinal gradients are amongst the steepest ecological gradients we know, as abiotic conditions change rapidly with altitude. The most important change is decreasing temperature, by 0.6 °C every 100 vertical meters in wet mountains and by 1 °C in dry air mountains (Begon et al. 2006). Humidity, precipitation, wind and soil conditions also change, but in a less predictable manner than temperature (Marrs et al. 1988, Wolf 1993). Species richness changes along altitudinal gradients (in temperate as well as tropical mountains) typically in one of several patterns: i) decreasing from low to high altitude, ii) constant species richness at lower elevations followed by decreasing number of species with increasing altitude, and iii) mid-altitudinal peak in species richness (Rahbek 2005). The existing studies on Lepidoptera are mostly from the Neotropics (Pyrzcz & Wojtusiak 2002, Brehm & Fiedler 2003, Brehm et al. 2003, Brehm et al. 2007, Pyrcz et al. 2009, Despland et al. 2012, Molina-Martinez et al in press), while the old world studies and also scattered from Europe (Gutierrez 1997, Mihoci et al. 2011), through Himalayas (Bhardwaj et al. 2012) to Australia (Ashton et al. 2011) and Papua New Guinea (Sam 2011). Results vary as some studies found decreasing pattern in species richness (Brehm & Fiedler 2003, Sam 2011, Molina-Martinez et al. in press), some a mid-altitudinal peak (Gutierrez 1997, Fleishman et al. 1998, Pyrcz & Wojtusiak 2002, Brehm et al. 2007) and some even observed that species richness increased with altitude (Brehm et al. 2003, Pyrcz et al. 2009) for particular taxa – in these cases geometrid moths and one subfamily of Nymphalidae. Factors leading to decreasing species richness with altitude include the reduction of habitable area at higher altitudes, decreasing plant (i.e. also host plant) diversity, extreme abiotic and weather conditions, and reduced primary productivity at high elevations (Lawton et al. 1987). The mid-altitudinal peak pattern could be caused by favourable conditions at middle elevations (not too high or too low temperature) and also by the mass effect as butterfly species from the lowlands meet and mix with butterfly species from highlands, therefore resulting in higher mid-elevation species diversity. Communities change rapidly along altitudinal gradients, so that the similarity between sites decreases rapidly with their altitudinal distance (Pyrzcz et al. 2009). Sam (2011), who studied a complete tropical gradient (200 - 3700 m asl.), found that an almost complete change of species (i.e., species overlap close to zero) occurred between sites separated by 2000 altitudinal meters.

## **Aims of the thesis**

In this thesis I focus on butterfly ecology in the tropical forests of New Guinea, particularly on detailed community composition, population structure and dispersal in a lowland rainforest community, extended to changes in butterfly composition along an altitudinal gradient. Methodologically, I test the feasibility of MRR studies in lowland primary forest understory; as such research has been so far missing in tropical regions. I marked all butterflies in understory habitats, including gaps, which are a natural part of primary forest. I tried to describe dispersal in relation to host plants and compare dispersal and demographic parameters with temperate species. I employed a second method, transect walking, on an altitudinal gradient in Huon Peninsula in Papua New Guinea. Focusing on primary as well as secondary sites I analyzed species richness and similarity between sites along this gradient. I also test ecological correlates for endemism in New Guinea butterflies, particularly their geographic and altitudinal range, as well as their optimum altitude.

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## Chapter I

# **Dispersal of butterflies in a New Guinea rainforest: using mark–recapture methods in a large, homogeneous habitat**

**Vlasanek, P., Sam, L., Novotny, V.**

Ecological Entomology

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Supporting information in Appendix I



## **Dispersal of butterflies in a New Guinea rainforest: using mark–recapture methods in a large, homogeneous habitat**

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### **Abstract**

1. In an intensive mark-release-recapture study of all butterfly species in a tropical rainforest understory, 5903 individuals from 90 butterfly species (from the estimated total of  $104 \pm 9$  species present in understory habitat) were marked, and 1308 recaptured at least once.

2. The study proved that mark-recapture methods are feasible in tropical rainforests, but also showed its limitations, as after 232 person-days of sampling we could only characterise dispersal for one-third of the species present.

3. The mean dispersal distance was  $184 \pm 46.1$  m per species, while for six of the 14 species studied  $>1\%$  of individuals were estimated to disperse 1 km or more. These parameters are, however, strongly dependent on the size and spatial configuration of the study plots, particularly in large homogeneous habitats. A new method proposed here to correct this bias revised the mean distance between two captures from  $135 \pm 33.6$  to  $325 \pm 87.0$  m per species.

4. These results, in combination with data from large permanent rainforest plots, suggest that most woody plant species in tropical forests are sufficiently abundant to serve as host plant species even to monophagous Lepidoptera species.

For more information:

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## Chapter II

# **Demography and mobility of three common understory butterfly species from tropical rain forest of Papua New Guinea**

**Vlasanek, P., Novotny, V.**

Submitted manuscript

Supporting information in Appendix II



## Demography and mobility of three common understory butterfly species from tropical rain forest of Papua New Guinea

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### **Abstract**

A mark-release-recapture study of the three most common butterfly species in the understory of a lowland primary rainforest in Papua New Guinea included 3705, 394 and 317 marked individuals of *Danis danis*, *Taenaris* sp. and *Parthenos aspila* respectively, with 1149 butterfly individuals recaptured at least once. There were almost 22,000 individuals belonging to these three species entering or hatching within our four study plots of area totaling 14.58 ha over a period of six weeks. The most abundant species, *D. danis*, with 20,000 individuals, showed highly variable population densities during the study. *D. danis*, *Taenaris* sp. and *P. aspila* had average daily population sizes of respectively 166.9, 16.7 and 51.4 individuals per hectare. The residency time in the studied plots was highest for *P. aspila* (84 days), as individual butterflies stay mostly in a single gap; we estimated that less than 1% of individuals disperse 1 km or more. Similar dispersal probability was found in *D. danis* whilst in *Taenaris* sp., 10% of the population disperses  $\geq 1$ km. Dispersal distances of *D. danis* were more than sufficient to locate its host plant, *Derris elliptica*, which occurred in 61% of the 20 x 20 m subplots within a 50-ha plot. We estimate that each 20 x 20 m forest plot containing the food plant produces ~100 adults of *D. danis* annually.

## **Key Words**

Papilionoidea, Melanesia, lowland rainforest, Lepidoptera, mark-release-recapture, Jolly-Seber.

## **Introduction**

Mark-release-recapture techniques (MRR) are a good tool for studying demographic parameters of butterflies including population size (Vlasanek et al. 2009; Zimmermann et al. 2011a), dispersal ability (Hanski et al. 1994; Roland et al. 2000; Baguette 2003; Zimmermann et al. 2011b) and longevity (Turner 1971; Molleman et al. 2007). There are many population studies using MRR, but these are mostly from temperate zone ecosystems and the majority is limited to a single species. Butterfly MRR data can be collected in two ways: using butterfly nets, typically in grasslands and other low vegetation, or fruit baited traps (Corbet 1942), typically in forest canopy (DeVries et al. 1997; Hill et al. 2001; Molleman et al. 2006). Interestingly, there is a dichotomy in MRR studies as most of the studies in the temperate zone focus on non-forest vegetation, particularly grasslands, and use butterfly nets, while most of the tropical studies focus on forests and use fruit traps. Unfortunately there is only one guild of butterflies - fruit feeders mainly from the family Nymphalidae - which is attracted to such traps. Further, active attraction of butterflies to traps may interfere with the assessment of their dispersal, making the use of butterfly nets preferable.

Studies in the tropics have focused mostly on community ecology of butterflies and examined their species richness and diversity (DeVries et al. 1997; Molleman et al. 2006), often in response to habitat fragmentation (Uehara-Prado et al. 2005; Benedick et al. 2006; Marin et al. 2009) or selective logging (Fermon et al. 2000; Lewis 2001), both of which are currently very serious problems in the tropics.

Studies on butterfly mobility and dispersal are rare in the tropics (Lewis 2001; Fermon et al. 2003; Francini et al. 2005; Marin et al. 2009, Marini-Filho and Martins 2010, Beirao et al. 2012; Vlasanek et al. in press). This is unfortunate since dispersal ability is a key population parameter which determines the ability of butterfly species to find their host plants. Since there are many rare plant species in tropical forests which would require good dispersal ability from their specialist herbivores, dispersal may be an important determinant of insect specialization (Dixon et al. 1987). Herbivore



specificity may in turn determine diversity of plant species since specialist herbivores can act as density dependent mortality agents for plants (Janzen 1970; Connell 1971).

Population size has also been only rarely studied in tropical butterflies, particularly in large undisturbed patches of forests. One of the few intensively studied taxa is the genus *Heliconius* Kluk, 1780, but these studies were conducted in non-forest, often disturbed habitats such as coconut plantations, or along roads and tracks, rather than in primary forests (Turner 1971; Ehrlich and Gilbert 1973; Cook et al. 1976; Ramos and Freitas 1999; de-Andrade and Freitas 2005). MRR studies from temperate ecosystems like meadows, steppes and other open habitats are almost impossible to replicate in tropical forests due to a combination of low butterfly density (Basset et al. 2011), inaccessible terrain, and a lack of dispersal barriers in large, relatively homogeneous tropical forests, which may decrease the recapture rate of butterflies. The large number of MRR studies available for the relatively few butterfly species from temperate non-forest habitats thus stands in sharp contrast with the almost complete lack of similar data from tropical forests, the habitat of a majority of the world's butterfly species. This is reflected in our poor knowledge of population biology in tropical butterflies.

Here we attempt to improve the knowledge of this neglected area by focusing on intensive research of tropical understory butterflies in a lowland rain forest of Papua New Guinea. In particular, we study three highly abundant species, *Danis danis* (Cramer, [1775]), *Taenaris* sp. and *Parthenos aspila* Honrath, 1888 whose populations compose up to 80% of all butterfly individuals in forest understory (cf. Basset et al. 2011; Vlasanek et al. in press). This allows us to conduct a detailed population analysis, which is not usually possible for butterfly species in tropical forests. Since these species are limited to the understory, we were able to use butterfly nets to catch butterflies across large forest areas, utilizing the significant man-power available to us in Papua New Guinea. This study thus serves also as a proof of concept, demonstrating the opportunities, and methodological limits, of MRR studies in tropical forest understory.

## **Materials and methods**

### *Study species*

*Danis danis*, Lycaenidae, is distributed across the mainland of New Guinea, adjacent islands, and the Cape York Peninsula in Australia (Parsons 1999). The species is restricted to the understory of primary tropical rain forests (Hill 1995; Parsons 1999;

Sam 2009; Vlasanek et al. in press). It is one of the most common primary forest understory species in lowland Papua New Guinea forests. For instance, in Sam (2009) it represented 9.6% of individuals in a butterfly community in Wanang primary rainforest. Observations of food plants are rare. Plants from the families Connaraceae (*Connarus conchocarpus*, *Rourea brachyandra*) and Fabaceae (*Derris* sp.; Orr and Kitching 2010) have been observed as larval food plants in various places of Cape York Peninsula.

*Taenaris* spp., Nymphalidae, is a mixture of at least two species which virtually impossible to distinguish in the field - *Taenaris myops* (C. & R. Felder, 1860) and *Taenaris catops* (Westwood, 1851). Both species are widespread in New Guinea, inhabiting both primary and secondary forest. Several monocotyledonous plants from the families Liliaceae, Orchidaceae, Musaceae, Arecaceae and Costaceae have been observed as food plants (Parsons 1999). These two species represent 4.3% of all individuals in an understory primary forest community (Sam 2009).

*Parthenos aspila*, Nymphalidae, is endemic to the northern mainland of New Guinea island and lives in and around primary forest gaps and in secondary forest. The host plant has been observed to be a vine from the family Cucurbitaceae (Parsons 1999). This butterfly species represented 6.9% of all individuals in an understory primary forest community (Sam 2009).

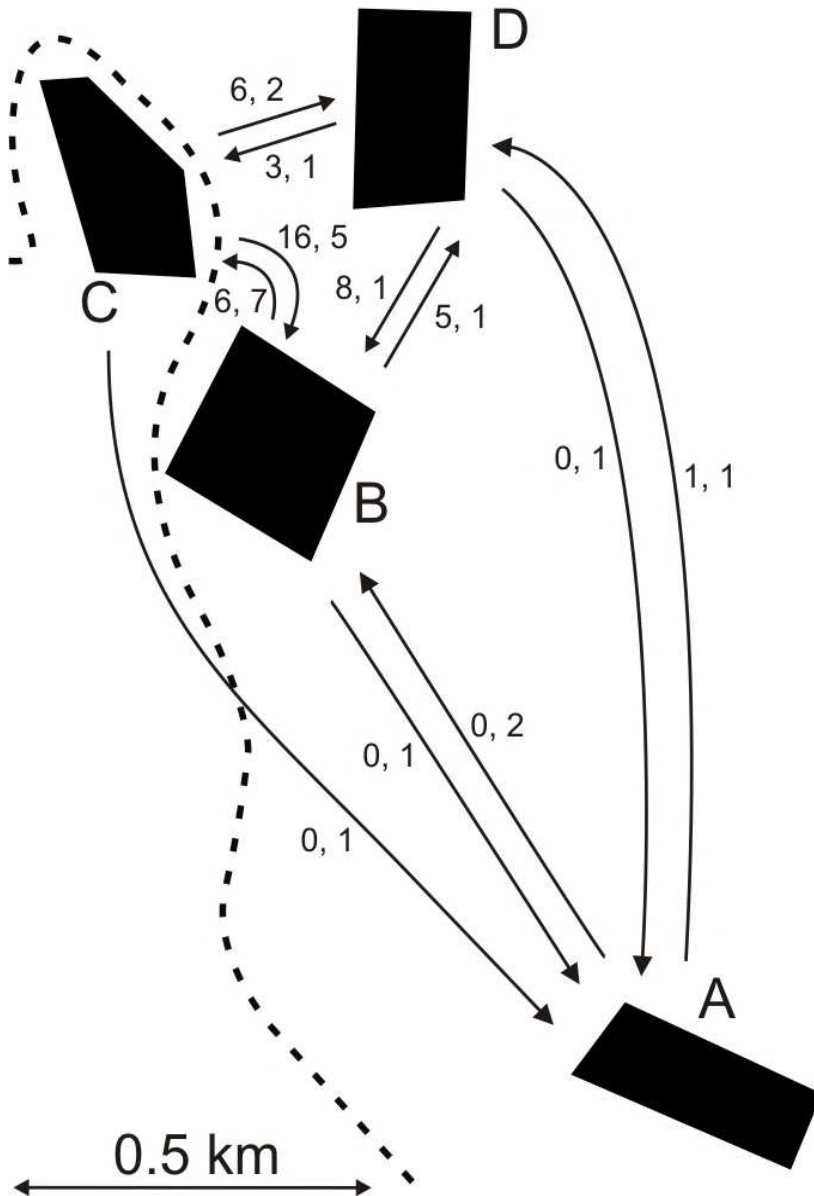
### *Study site*

This study was conducted in Wanang Conservation Area (5.23° S 145.08° E; altitude 100 m) in Madang province, Papua New Guinea during late wet season, from 25 April to 26 June 2009.

The mark-release-recapture (MRR) study was carried out in four plots which were selected as representative of the local vegetation, except the steepest parts of the terrain where it would be impossible to monitor and catch butterflies efficiently (Figure 1). Plot A (3.15 ha) was upland primary continuous forest without any creeks or gullies. Plot B (3.99 ha) was also upland primary forest with hills dissected by small creeks and valleys. Plot C (3.99 ha) was located in a meander of Digitam river, comprising regularly flooded flat areas as well as elevated terrace; the relatively undisturbed forest with closed canopy was thus flanked by more disturbed secondary vegetation along the river bank. Plot D (3.45 ha) was an upland primary forest with hills dissected by small creeks and valleys. The plots were 45 - 682 m apart and together comprised the study area of approximately 4 x 1.5 km (Figure 1). Each plot

was divided into a 25 x 25 m grid marked with flagging tape and mapped in ArcGIS 9.3 (©ESRI, Inc.).

Figure 1: Map of the study plots. Dashed line is the Digitam river. Arrows with numbers show the numbers of respectively *D. danis* and *Taenaris* sp. individuals which moved between plots during the study. No such movement was recorded for *P. aspila*.



### *Mark – recapture method*

All understory butterflies (including the three focal species) were caught using entomological nets. We were evenly zigzagging all plots. People were divided into two groups each of which usually contained three people - two who caught butterflies and one who caught butterflies and recorded them in an exercise book. We also caught butterflies when we were moving from one plot to another (on the path between them). Every butterfly was marked with a unique number and we recorded its sex, wing wear (from 1 to 4 according to loss of scales – where 1 was an almost newly hatched individual and 4 was an individual with pale colour of wings due to loss of scales) and location within the plot, recorded as coordinates of the closest point in the 25 x 25 m grid. Sampling began 25 April 2009, and males of *D. danis* were sampled until 5 June 2009 (*regular marking*). After this all other species, *D. danis* females and already marked *D. danis* males were recorded until 26 June 2009. The reason for this was a sudden rise in the abundance of males of *D. danis* which distracted field workers from catching other species of butterflies. The demographic parameters of *D. danis* (survival, catchability, population size) were estimated (i) for both sexes using data from regular marking and (ii) for females using data from whole study in the study plots. In addition we observed the oviposition behaviour of *D. danis* females from 30 November 2010 to 7 December 2010 and mapped the distribution of its only observed host plant, *Derris elliptica*, in 20 x 20 m subplots within a 50 ha plot.

### *Statistical analyses of demography*

Constrained linear models (CLM) represent the best way to analyze MRR data (Schtickzelle et al. 2003). One such model is Jolly-Seber (JS). We used program MARK v. 6.0 (White and Burnham 1999) with subroutine POPAN, which can calculate four primary parameters: survival ( $\phi$ ), capture probability ( $p$ ), proportional recruitment (*proportion entering*; *pent*) and superpopulation ( $N$ ). The first three parameters may be constant for sexes and time ( $\cdot$ ), sex dependent ( $g$ ), factorially dependent on marking day ( $t$ ), or exhibiting additive ( $g+t$ ) or interactive ( $g*t$ ) patterns. The response to time can also be linear ( $T$ ,  $g+T$ ,  $g*T$ ) or quadratic ( $T^2$ ,  $g+T^2$ ,  $g*T^2$ ). Primary parameters are used for obtaining derived parameters: daily recruitment ( $B_i$ ), daily population size ( $N_i$ ) and total population size ( $N_g$ ). CLMs are ranked following the lowest quasi-Akaike information criterion ( $AIC_c$ ; based on complexity, number of parameters and fitness of each model). The model with the lowest  $AIC_c$  is the best model and models which differ in  $AIC_c$  by 2 are comparable to each other. For further information follow e.g. Clobert and Lebreton (1985), Lebreton et al. (1992), Schtickzelle et al. (2003).

For obtaining and comparing average  $\varphi$  and  $p$  between the sexes and species we defined models with these parameters constant in time (where necessary). Then we counted residency time ( $dd$ ) and lifetime probability of capture ( $lp$ ) using as  $-\ln(\varphi)^{-1}$  and  $-\ln(p)^{-1}$  (Cook et al. 1967).

### *Analysis of mobility*

The total flight distances ( $D$ ) for each butterfly were measured, estimated as the sum of distances between the capture and all recapture points. The size and position of plots determines the proportion of dispersal events for each dispersal distance which could be detected using our sampling design. The observed frequency of dispersal distances was adjusted using these probabilities. One million points were randomly generated within a frame consisting of our four study plots. Almost 100 000 of these were inside these four plots. Each such point was assigned a random angle and distance from 20 m to 1680 m (i.e., the distance between two most distant points; 20 m increments) simulating random flight of butterflies. The probability ( $Pc$ ) of this simulated flight ending within a study plot (Supplement 1) was used to correct the observed number of individuals reaching a particular dispersal distance ( $N_{obs}$ ) as follows:  $N_{cor} = N_{obs}/Pc$ . The mean dispersal distance between two captures ( $D_{obs}$ ) calculated from the observed numbers of individuals ( $N_{obs}$ ) reaching dispersal distances of 20, 40, 60, ... m. Likewise, the corrected mean dispersal distance between two captures ( $D_{cor}$ ) was calculated using the corrected ( $N_{cor}$ ) numbers of individuals. For more information see Vlasanek et al. (in press).

We used the power law functions (inverse power function - IPF, negative exponential function - NEF) to assess the probability of movement by a butterfly over a specific distance. For IPF " $I = C \cdot D^{-m}$ ", for NEF  $I = a \cdot e^{-kD}$  where  $I$  is proportion of movements,  $D$  is distance and  $C$ ,  $m$ ,  $a$  and  $k$  are constants. (Hill et al. 1996; Fric and Konvicka 2007).

## **Results**

### *Demography*

We marked a total of 5903 butterfly individuals from 90 species. The results for all butterfly species are reported elsewhere (Vlasanek et al. in press). Here we focus on the three most abundant species, *Danis danis*, *Taenaris* sp. and *Parthenos aspila* with 3705, 394 and 317 marked individuals, respectively (Table 1). In the four study plots 118 butterfly individuals of the three studied species were captured on average each

working day (Table 2). This sample size permitted estimates of population size and other parameters, which was not possible for rarer species.

Table 1: Mark-release-recapture (MRR) data and the subset of these used to calculate demographic parameters using the program MARK. Recaptures within the same day and captures outside plots were not included in analyses. Regular marking was from 25. 4. to 5. 6. 2009. Otherwise it was from 25. 4. to 26. 6. 2009. ♂♂ and ♀♀ indicate that analyses were done separately for sexes. Some butterflies were recaptured more than once.

Plot	Marked		Recaptured		Captures	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
<b><i>Danis danis</i></b>						
MRR data	2643	1062	867	164	4653	1263
MARK - ♂♂ and ♀♀, regular marking	2362	543	682	51	3850	608
MARK - ♀♀		999		157		1186
MARK - regular marking	2905		733		4458	
<b><i>Taenaris sp.</i></b>						
MRR data	216	178	67	11	346	191
MARK - regular marking	246		50		320	
MARK	328		60		423	
<b><i>Parthenos aspila</i></b>						
MRR data	160	157	16	24	186	193
MARK - regular marking	199		25		234	
MARK	295		39		355	

In *D. danis* the sex ratio ( $SR = N_{♂♂} / N_{♀♀}$ ) of marked butterflies significantly differed from 1.0 ratio ( $SR = 2.5$ ,  $\chi^2 = 674.65$ ,  $P < 0.001$ ). For *Taenaris sp.* ( $SR = 1.2$ ,  $\chi^2 = 3.66$ ,  $P > 0.05$ ) and *P. aspila* ( $SR = 1$ ,  $\chi^2 = 0.03$ ,  $P > 0.05$ ) the sex ratio was not significantly different from 1. Data used for estimating demography parameters via the JS method are presented in Table 1. The best JS models are shown in Table 3. Capture probabilities were always factorially dependent on marking day, survival's responses to time were linear or constant. Proportional recruitment was mostly constant or response to time was quadratic. Survivals were higher than 0.9 and calculated residency time was highest for *P. aspila* - more than 80 days. Capture probabilities were lower than 0.1, highest for *D. danis*, followed by *Taenaris sp.* and finally by *P.*

*aspila*. Lifetime probability of capture ranged between 20 and 40% for the three species.

Table 2: Recapture rates measured as recaptures / captures ( $R$ ), average total flight distance ( $D$ ), average flight distance between two consecutive captures ( $D_{obs}$ ), average flight distance between two consecutive captures corrected for plot size and position ( $D_{cor}$ ), and maximum distance recorded ( $D_{max}$ ). Captures is the average total number of daily captures within the four plots. Density is average daily density per hectare based on daily population size results from MARK. Maximum, average and median of recorded values of Life span (time between the first and the last capture) are also presented. Maximum recordable life span was limited to 63 days, the duration of the study.

	$R$	$D$	$D_{obs}$	$D_{cor}$	$D_{max}$	Captures	Density	Life span
<i>Danis danis</i>	0.37	109	60.4	185.5		102	166.9	58 / 13 / 11
♂♂		117	60.3	186.8	1313			58 / 13.3 / 11
♀♀		63	60.6	173.5	630			58 / 11.8 / 10
<i>Taenaris</i> sp.	0.27	352	191.5	674.1		8	16.7	48 / 13.8 / 9
♂♂		342	169.1	537.2	2482			48 / 15.2 / 12.5
♀♀		408	392.7	947.2	1437			15 / 3.7 / 1
<i>Parthenos aspila</i>	0.16	81	60.3	103.4		7	51.4	58 / 25.5 / 22.5
♂♂		67	44	55.4	374			48 / 20.7 / 14.5
♀♀		90	71.7	121.8	313			58 / 28.8 / 28

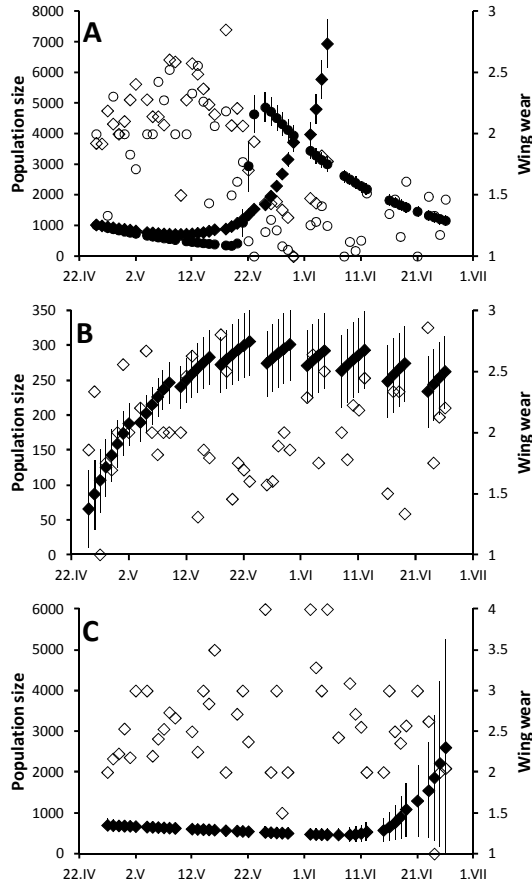
Within the four plots the estimated population size of the three focal species together during *regular marking* was ~21,000 individuals, or ~1500 individuals per hectare during our study, which included the individuals which had been there before the study started, hatched there or immigrated during the study. Daily density per hectare (based on daily population size) of *D. danis* was three times higher than for *P. aspila* and 10 times higher for *Taenaris* sp. (Table 2). The peak in population size of *D. danis* coincided with a decrease in average wing wear, presumably due to the influx of new individuals into the population. The population size grew in *Taenaris* sp. from ~50 to ~300 individuals over the course of the study. For *P. aspila* there was a similarly radical increase in population size towards the end of study, but less well documented due to large standard errors of the size estimations (Figure 2).

Table 3: Best JS models (with maximum  $\Delta AIC_c < 2$ ) from program MARK during regular marking and whole period. N.P. - number of parameters,  $\phi$  - survival,  $dd$  - residency time,  $p$  - capture probability,  $lp$  - lifetime probability of capture,  $N$  - total population size, SE - standard errors.

Model	$AIC_c$	$\Delta AIC_c$	N.P.	$\phi_{\delta\delta} \pm SE$	$dd_{\delta\delta}$	$\phi_{\varphi\varphi} \pm SE$	$dd_{\varphi\varphi}$	$p_{\delta\delta} \pm SE$	$lp_{\delta\delta}$	$p_{\varphi\varphi} \pm SE$	$lp_{\varphi\varphi}$	$N_{\delta\delta} \pm SE$	$N_{\varphi\varphi} \pm SE$
<b>Danis danis, males and females, regular marking</b>													
$\phi(g^*T) p(g^*t) pent(T) N(g)$	1169.5	0	82	$0.96 \pm 0.003$	$22.44$	$0.93 \pm 0.016$	$12.97$	$0.09 \pm 0.003$	0.42	$0.01 \pm 0.002$	0.23	$10841 \pm 720$	$9196 \pm 1531$
$\phi(g^*T) p(g^*t) pent(g+T) N(g)$	1169.69	1.92	83	$0.96 \pm 0.003$	$22.39$	$0.93 \pm 0.018$	$13.62$	$0.09 \pm 0.003$	0.41	$0.02 \pm 0.003$	0.24	$10871 \pm 726$	$9136 \pm 1523$
<b>Danis danis, females</b>													
$\phi(.) p(t) pent(T^2) N(.)$	2170.4	0	54			$0.96 \pm 0.006$	$22.16$			$0.01 \pm 0.001$	0.22		$6378 \pm 703$
<b>Danis danis, regular marking</b>													
				$\phi \pm SE$		$dd$		$p \pm SE$		$lp$		$N \pm SE$	
$\phi(T^2) p(t) pent(T^2) N(.)$	1166.18	0	44	$0.98 \pm 0.002$		40		$0.08 \pm 0.003$		0.4		$17242 \pm 1693$	
$\phi(T) p(t) pent(T^2) N(.)$	1166.2	0.16	43	$0.98 \pm 0.002$		40		$0.08 \pm 0.003$		0.4		$16598 \pm 1487$	
<b>Taenaris sp., regular marking</b>													
$\phi(.) p(t) pent(T^2) N(.)$	899.9	0	40	$0.91 \pm 0.018$		11.03		$0.03 \pm 0.004$		0.28		$974 \pm 129$	
$\phi(T) p(t) pent(T^2) N(.)$	900.3	0.43	41	$0.91 \pm 0.018$		11.03		$0.03 \pm 0.004$		0.28		$946 \pm 125$	
$\phi(.) p(t) pent(.) N(.)$	900.5	0.58	38	$0.91 \pm 0.019$		10.7		$0.02 \pm 0.002$		0.24		$941 \pm 105$	
$\phi(T) p(t) pent(.) N(.)$	901.2	1.32	39	$0.91 \pm 0.019$		10.7		$0.02 \pm 0.002$		0.25		$921 \pm 106$	
<b>Taenaris sp.</b>													
$\phi(.) p(t) pent(.) N(.)$	1208.8	0	51	$0.93 \pm 0.011$		14.59		$0.04 \pm 0.005$		0.31		$1324 \pm 133$	
$\phi(T) p(t) pent(.) N(.)$	1210.3	1.5	52	$0.93 \pm 0.011$		14.59		$0.04 \pm 0.005$		0.31		$1310 \pm 135$	
<b>Parthenos aspila, regular marking</b>													
$\phi(.) p(t) pent(.) N(.)$	553.8	0	33	$0.98 \pm 0.023$		59.95		$0.02 \pm 0.003$		0.24		$758 \pm 187$	
<b>Parthenos aspila</b>													
$\phi(T) p(t) pent(T^2) N(.)$	940.2	0	51	$0.99 \pm 0.023$		84.46		$0.01 \pm 0.001$		0.22		$3137 \pm 2244$	



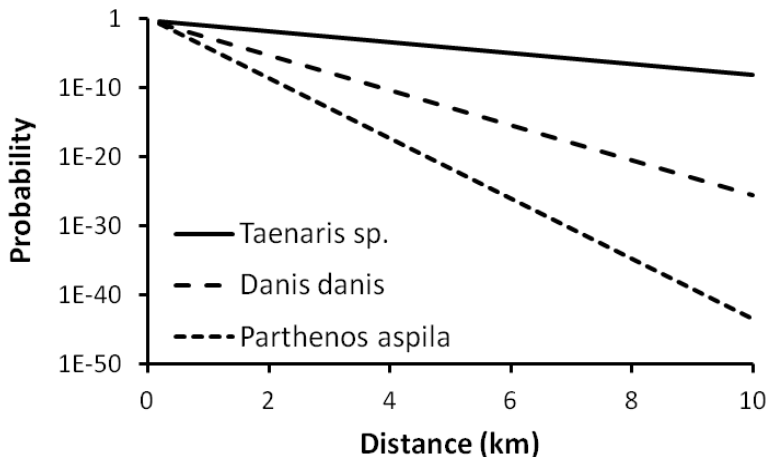
Figure 2: Daily population size of *Danis danis* (A), *Taenaris* spp. (B) and *Parthenos aspila* (C). Black symbols are population sizes, open symbols are wing wear of captured butterflies. In *Danis danis*, diamonds are males and circles are females. Note that *Danis danis* males were being captured for a shorter time than the females.



### Mobility

Less than one percent of individuals were likely to fly more than 1 km in *Danis danis* and *Parthenos aspila*, while almost 10% of individuals were likely to disperse such distances in *Taenaris* spp. (Figure 3, Supplement 2). These estimates are based on the NEF model which had better support than the IPF model (Supplement 2). Average total flight distances between two captures were 60 m for *P. aspila* and *D. danis* and 192 m for *Taenaris* sp. After correction for plot size and position, the average flight distance between two captures rose almost twice in *P. aspila* and more than three times in *D. danis* and *Taenaris* sp. (Table 2).

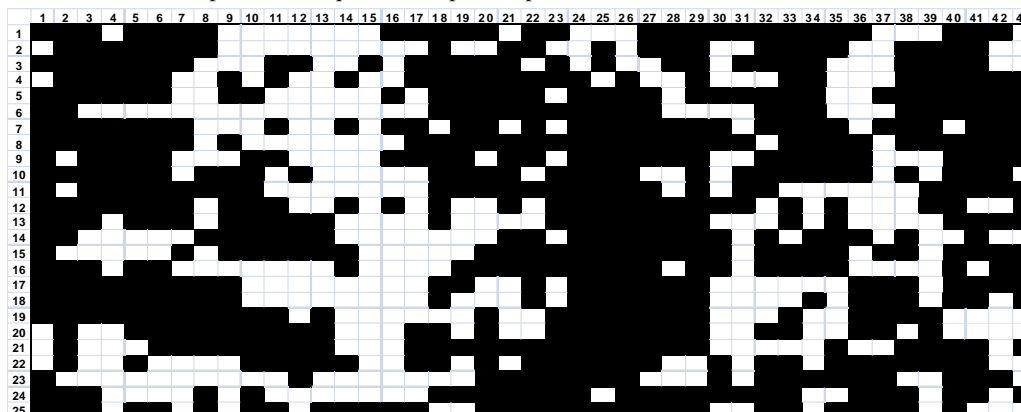
Figure 3: Probability of dispersal with distance for individual butterfly species. The fitted negative exponential function (NEF) shows highest dispersal ability for *Taenaris* sp. and lowest for *Parthenos aspila*. See Supplement 2 for parameters of individual functions.



#### Food plant of *Danis danis*

*Danis danis* females were tracked and observed flying only around three *Derris* species (Fabaceae) - *Derris oligosperma*, *D. malaccensis* and *D. elliptica*. Oviposition was not observed but caterpillars were only found on *D. elliptica*. This species was mapped in a 50-ha botany plot (20 x 20 m squares) and is a common climber in Wanang (Figure 4). Females of *Parthenos aspila* and *Taenaris* sp. were not tracked and observed due to them having much lower abundances.

Figure 4: Distribution of *Derris elliptica* (Fabaceae), a host plant of *Danis danis*, in 20 x 20 m squares within a 50 ha forest plot. Black square - host plant is present.



## Discussion

Although we conducted mark-release-recapture study of all butterflies available in understory of lowland primary forest in Papua New Guinea, with the help of numerous field assistants (Vlasanek et al. in press), only data for the three most abundant species were sufficient for population size estimates and are thus presented here. This study is pioneering because all other MRR studies in the tropics either used fruit baited traps (Hill et al. 2001; Uehara-Prado et al. 2005; Molleman et al. 2007) or caught butterflies by insect net entirely on roads, paths or trails within forest (Ehrlich and Gilbert 1973; Cook et al. 1976; Freitas et al. 2001; de-Andrade and Freitas 2005; Francini et al. 2005). There are thus no comparable mark-recapture data from a large, relatively homogeneous primary rainforest. Nevertheless it should be noted that the forest in Wanang is more suitable for such study than many other since its understory is relatively open, making walking and even running possible, thus facilitating the capture of butterflies. Further, it also seems to have a higher butterfly density than in many other tropical forests, including those in Thailand and in Panama (Basset et al. 2011).

The number of daily captures per species was similar to other studies, except for *D. danis*. South America studies of Nymphalid species from Heliconiinae and Ithomiinae reported between two and 20 daily captures, similar to our results for *Parthenos aspila* and *Taenaris* sp., but markedly lower than for *D. danis* (Freitas 1993; Freitas 1996; Freitas et al. 2001; de-Andrade and Freitas 2005; Francini et al. 2005). We cannot use these studies to compare butterfly abundance since they did not sample butterflies within study areas of defined size. Comparable studies from the Temperate zone are also rare because there are only few forest species of butterflies. For one of them, European *Parnassius mnemosyne*, Vlasanek et al. (2009) estimated daily density at 12 individuals per ha. However, this species is mostly limited to glades (= gaps) within deciduous forest (Benes et al. 2003). This preference was similar to that of *P. aspila* but not *D. danis* or *Taenaris* sp. which are more evenly distributed within the forest understory (Vlasanek et al. in press).

*D. danis* was the most abundant butterfly species during our research, being ten times more numerous than second most abundant species (*Taenaris* spp.), and representing two thirds of all captures in the entire butterfly community (Vlasanek et al. in press). In another butterfly study from the same area (Basset et al. 2012) it was also the most dominant species but represented only 17% of all individuals in counts along

transects. Kunte (2008) showed experimentally that high dominance in the community could decrease diversity in butterfly communities. The mechanism suggested in that study was competition over nectar, whilst most species in Vlasanek et al. (in press) feed on rotting fruits. It is possible that butterfly abundance is determined by host plants. High abundance of *D. danis* could also be caused by its food plant, which is common and highly poisonous (Leonard 1939), rendering larvae as well as adults unpalatable to predators (Parsons 1999).

For all three species, daily population size was highly variably in time, most clearly in *D. danis*. Seasonality is a common pattern even in the tropics, where it depends primarily on the amount of rainfall (Spitzer et al. 1993; Novotny and Basset 1998), although e.g. Molleman et al. (2006) did not find any relationship between variation in abundance (and species richness) and seasonal patterns (rainfall). The data we present here were collected during the wet season (the onset of dry season was in July). Unfortunately we do not have data about changes in the density of flowering plants or new leaves, which can be one cause of changes in daily population size (Freitas et al. 2001). In temperate areas, population sizes of univoltine and bivoltine species with discrete generations follow a similar convex trajectory in time (Vlasanek et al. 2009; Fric et al. 2010). In tropical areas such pattern can be found as well (Francini et al. 2005). Nevertheless, many species have overlapping populations throughout the year. In *Heliconius* sp., some studies have observed stable population sizes (Ehrlich and Gilbert 1973; Ramos and Freitas 1999) whilst in others population size was observed to change during the year (Cook et al. 1976; de-Andrade and Freitas 2005). In Brazil, *Heliconius* population size decreased in the dry season and peaked at the end of the wet season (Freitas et al. 2001). The population dynamics of *D. danis*, and to a lesser extent the other two species, is unusual due to the high speed of change in abundance, which suggests many individuals hatching simultaneously over the course of a few days, without any obvious environmental cue (cf. Beirao et al. 2012). Our study, limited to two months, does not allow us to test the impact of predators and parasitoids, the availability of food resources, or the weather on population changes.

Average observed life span was highest for *P. aspila*, at 26 days, as its individuals stay mostly in same gap during the whole study. *D. danis* average longevity was 13 days and *Taenaris* sp. 14 days. Estimations based on MRR data (residency time) are higher as they represent estimation of entire lifespan (from birth to death) as opposed to observed life span (from first to last capture).

Residency time of butterfly species estimated by MRR does not usually exceed 10 days in temperate regions (Davis et al. 1958; Scott 1973; Arnold 1983; Vlasanek et al. 2009) while butterflies live much longer in the tropics (Scott 1973; Freitas 1996; Molleman et al. 2007; Beck and Fiedler 2009). In Heliconiinae, life span is often longer than 20 days, sometimes even longer than 50 days (Ehrlich and Gilbert 1973; Cook et al. 1976; Ramos and Freitas 1999; de-Andrade and Freitas 2005). Interestingly, Beck and Fiedler (2009) found in their multi-species comparison that tropical species lived longer than temperate species based on the data collected in the field, but in laboratory (cage) experiments, it was temperate butterfly species which lived longer. Our data on average life span conforms to this pattern.

The dispersal abilities of tropical butterfly species have rarely been studied. Furthermore, the use of fruit-baited traps means that butterflies can be caught only at fixed points (where traps are situated) and are not released immediately after capture but often only after several hours. Data about the movements of butterflies captured using butterfly nets along trails, paths or roads are also biased if the butterflies do not live exclusively along these trails. The present study does not suffer from these problems. However, butterflies were captured within plots arbitrarily located in a homogeneous habitat, which also affects dispersal characteristics as shorter movements could be recorded more often than longer ones. Considering the probabilities of recording movements (see also Vlasanek et al. in press) we believe dispersal results are more accurate than previous studies provided.

Based on probabilities of flights over, average flight distances and also rare movements from one plot to another we found *D. danis* and *P. aspila* are much more sedentary species than *Taenaris* sp. In tropical areas, mean dispersal distances, similar to *Taenaris* spp.,  $174 \pm 25$  m based on 13 species (males and females separately) were recorded by Fermon et al. (2003), while 21 nymphalid species in Brazil had mean dispersal distance  $369 \pm 215$  m (Marini-Filho and Martins 2010). Single species studies from South America gave estimates from 140 - 280 m (Ramos and Freitas 1999; Francini et al. 2005; Beirao et al. 2012). Some tropical species are also sedentary, with short mean dispersal distance similar to *D. danis* and *P. aspila*. For instance 57 m for *Heliconius erato* (Marin et al. 2009) and 65 - 84 m for *H. ethilla* (de-Andrade and Freitas 2005). In temperate forest species, mean dispersal distances varied from 100 m for *Lopinga achine* (Konvicka et al. 2008), through 250 m for *Euphydryas maturna* (Konvicka et al. 2005) to 386 m for *Parnassius mnemosyne* (Vlasanek et al. 2009). All these results are however influenced by the length and intensity of the study and the size, shape, number and spatial configuration of suitable

habitats and study areas within these habitats (Schneider 2003). For example, in *Heliconius erato* observed mean dispersal distance differ more than four times between Ramos and Freitas (1999) and de-Andrade and Freitas (2005).

Density and movements of butterflies are influenced by density of larval food plants, and their young foliage in particular, as well as adult resources, including flowers and rotten fruits on the ground as well as in trees. These resources can vary significantly throughout the year and are difficult to map. While 1 ha plots used to study tropical forest vegetation are too small for the mapping of larval food plants, 50-ha plots from the Center for Tropical Forest Science (CTFS) network are suitable for this purpose, since their size exceeds the mean dispersal distance of most butterfly species. For instance, the mean dispersal distance of all butterfly species in our study forest in Wanang was 184 m (Vlasanek et al. in press). According to data from CTFS plots around the world most plant species have abundance higher than one individual plant per hectare, therefore a dispersal distance of 184 m is more than enough to reach their host plant. *Derris elliptica*, the host plant of *D. danis*, is present in 61% of all 20 m x 20 m squares and therefore isolation of host plants spatially is unlikely to be a limiting factor for this species. Knowing residency time and average daily density per hectare (based on MARK results), we estimate that 1523 *D. danis* butterflies are produced per hectare every year which means 100 adult individuals for every 20 m x 20 m square occupied by food plants.

In conclusion, our study shows that tropical butterflies are not demographically exceptional, except for their longer life span and overlapping generations. Their demographic parameters (daily abundance, density, movements) are similar to temperate species. *D. danis* was exceptional since it was extremely abundant and its population also showed strong short-term variability in size. Finally, *D. danis* dispersed at distances much greater than the distance to the nearest host plant individual indicating that the abundance of the host plant was probably not a limiting factor even for this monophagous specialist. However, whether this is universally true should be examined on combinations of rarer butterfly species and their rare host plants, which would be a biologically more interesting situation but also the one much more difficult to study.

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## Chapter III

# **Butterfly communities along an altitudinal gradient in the tropical rainforest of Huon Peninsula, Papua New Guinea**

**Vlasanek, P., Kimbeng, F., Novotny, V.**

Manuscript

Supporting information in Appendix III



# **Butterfly communities along an altitudinal gradient in the tropical rainforest of Huon Peninsula, Papua New Guinea**

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## **Abstract**

Butterfly communities along a long primary rainforest altitudinal gradient were studied from 130 m to 2801 m asl. at approximately 500 m altitudinal increments, using three transects 300 m long at each altitude. Secondary forest was also studied at three lowest altitudes from 130 to 1276 m asl. In total 187 species were observed and total species richness along the transect was estimated at  $204 \pm 8$  species. More species were found in secondary forest (160 spp.) than in primary forest (100 spp.). Species richness in primary forest peaked at 130 m asl, then decreased with altitude. The rate of species turnover between primary forest sites separated by 500 altitudinal m was constant along the entire transect. Species turnover with altitude was higher in primary than secondary forest. The alpha and gamma diversities along the transect were much lower than along the comparable section of the Central Cordilleras transect, reflecting probably smaller area and younger geological age of the Huon Peninsula ranges.

## **Key words**

Papilionoidea, Melanesia, altitudinal gradient, Lepidoptera, transect, alpha, beta and gamma diversity.

## **Introduction**

Mountains, from foothills to summits, offer very diverse conditions within a small geographic area. The most fundamental environmental change in tropical mountains is temperature which decreases by 0.6°C for every 100 meters of elevation (Begon et al. 2006). Other environmental factors, such as precipitation, wind or soil conditions, vary with altitude as well, although less predictably (Marrs et al. 1988, Wolf 1993). Such regular changes in the environmental conditions result in the turnover of species with elevation, making altitudinal gradients globally important hotspots of biodiversity (Barthlott et al. 2007). In particular, complete tropical rainforest gradients from lowlands to alpine zone are among the most diverse regions on the planet, at least for plants (Barthlott et al. 2007).

Ecological communities are determined by regional species pools, environmental conditions, biotic interactions and dispersal. Communities along altitudinal gradients are assembled from a single regional species pool and, in addition, short geographic distances reduce the effects of dispersal. As such, altitudinal gradients are an excellent model system for studying the ecological mechanisms driving community assemblages. Finally, species' ability to respond rapidly to climate change by shifting elevation mean that altitudinal gradients are also an excellent system for observing current climate impacts (Bale et al. 2002), as well as for modelling future changes under different climate scenarios. However, base-line data on species distributions is often missing for insects in tropical rainforests, unlike their counterparts in the temperate zone (but see Chen et al. 2009).

The study of altitudinal gradients is thus one of the foci of current community ecology research. In contrast to latitudinal gradients, where species richness typically decreases uniformly from the equator to the poles (Willing et al. 2003), altitudinal gradients exhibit several patterns of alpha diversity (McCain & Grytnes 2010). Species richness either decreases with altitude, or remains constant at low altitudes before decreasing, or exhibits a mid-elevational peak. The latter pattern appears to be the most frequent, found in ~50% of all altitudinal gradient studies (Rahbek 2005). Species richness in Lepidoptera has conformed to either of the major patterns - the highest butterfly diversity was found at mid-altitudes (e.g. Fleishman et al. 1998, Pyrcz & Wojtusiak 2002), as well as decreasing from low to high altitude (Molina-Martinez in press).



The majority of focal taxa studied on altitudinal gradients have belonged to plants and vertebrates. However, butterflies are equally suitable as a model taxon since they are taxonomically well known, even in the tropics, are generally easily recognizable in the field, and their local and regional species diversity is substantial but manageable, from hundreds to a few thousand species (Parsons 1999). It is therefore rather surprising that there are not many butterfly studies along altitudinal gradients in the literature. The existing studies (butterflies and moths) are predominantly from the Neotropics (Pyrz & Wojtusiak 2002, Brehm & Fiedler 2003, Brehm et al. 2003, Brehm et al. 2007, Pyrcz et al. 2009, Despland et al. 2012, Molina-Martinez et al. in press), but also Europe (Gutierrez 1997), the Himalayas (Bhardwaj et al. 2012), Australia (Ashton et al. 2011), and Papua New Guinea (Sam 2011). They focus mostly on patterns of diversity, often in connection with species traits such as body size (Hawkins & Devries 1996). Only a few butterfly studies have included a complete (or almost complete) altitudinal rainforest gradient from lowlands (<500 m asl.) to the timber line (if present; Sam 2011, Molina-Martinez et al. in press), thus enabling an assessment of the overall contribution of altitudinal variability to butterfly species diversity to be made.

Fieldwork from altitudinal gradient studies is notoriously poorly replicated. While it is already possible to assemble dozens or even hundreds of gradient datasets for vertebrates (McCain 2005, McCain 2009), insect data are much scarcer. Furthermore, individual surveys often differ in their methodologies. Butterfly researchers benefit from having standardized transect-based survey methods (Basset et al. 2011) that can be applied consistently across different altitudinal transects. This was the case in PNG where Sam (2011) surveyed a complete rainforest transect from the lowlands (200 m asl.) to the timber line (3700 m asl.) on the Central Cordillera, the highest mountain range in PNG. The second highest mountains, also with well developed alpine zones, are on the Huon Peninsula - the Finisterre, Saruwaged, Cromwell and Rawlinson ranges, which were the subjects of our study. The Huon peninsula ranges are isolated from the Central Cordillera by a lowlands river basin (the Ramu and Markham rivers) and are therefore excellently located for testing allopatric speciation (Beehler et al. 1986).

This study describes butterfly diversity along an altitudinal gradient on the Huon Peninsula mountains and compares butterfly communities between disturbed and undisturbed forest sites at the lower altitudes.

## **Material and methods**

### *Study sites*

This study took place in the YUS Conservation Area (YUS; named after the three rivers - Yopno, Uruwa and Som) in the Huon Peninsula (Morobe Province, PNG). The YUS is the first protected area in Papua New Guinea that extends from the coast through primary forests to alpine grasslands. Fieldwork was conducted along an altitudinal transect with an altitudinal distance between sites of approximately 500 m, from 130 m asl. to 2801 m asl. There were six sites in primary forest along the transect and four sites in secondary forests - secondary forests were absent from the highest two elevations. The secondary forest sites were in various successional stages, three of which were following small-scale slash-and-burn agriculture, and the remaining site following a large gap of several ha due to tree-fall caused by strong winds. Three transects were established at each of the ten sites (excepting the 2nd site at 720 m asl., with only two transects, Table 1).

Table 1: Overview of study sites.

Site	Altitude (m)	Position	Biotope	No. of transects	No. of species	No. of individuals
Gams village	130	S5.90422 E146.85700	primary forest	3	61	908
Baiks camp	720	S5.95146 E146.84235	primary forest	3	29	91
Baiks road lower	1250	S5.96546 E146.83469	primary forest	3	17	103
Baiks road upper	1772	S5.97642 E146.83142	primary forest	3	10	66
Gormdan camp	2216	S6.00664 E146.82628	primary forest	3	6	95
Boksawin camp	2801	S6.06786 E146.87142	primary forest	3	6	51
Gams village	130	S5.90422 E146.85700	secondary habitats	3	91	858
Baiks camp	720	S5.95146 E146.84235	secondary habitats	2	70	452
Sapmanga village	835	S6.06901 E146.80919	secondary habitats	3	81	1967
Gormdan village	1276	S6.05137 E146.81740	secondary habitats	3	68	1111

### *Butterfly recording*

Fieldwork was carried out in the period from 20th January to 26th March 2011. Each 300 m long transect was surveyed 12 times during sunny weather. In primary forest sites, from 720 m to 2801 m asl., this occurred mostly in the mornings before 12pm, because in the afternoons the forests were shrouded in mist or, very frequently, it was raining. At 130 m elevation and the secondary vegetation sites, the sunny weather often persisted into the afternoon and therefore surveys could be made. Two observers (PV and FK) alternated on individual transects. Each observer walked slowly for 30 minutes to survey each transect (Pollard 1977, Caldas & Robbins 2003), recording all butterflies viewed up to 5 m in front, to the sides, and above the observer. Butterflies were identified using Parsons (1999).

### *Statistical analyses*

The program EstimateS 8.2.0 (Colwell 2006) was used to compute rarefaction curves (Colwell et al. 2004), Chao's (Chao 1) species richness (Chao 1984) and Chao-Sorensen's abundance based similarity index (Chao et al. 2005). The whole dataset was analysed to obtain species richness in the entire area, and also separately for primary and secondary sites; each of the 29 transects was considered a sample. Chao-Sorensen's abundance based similarity index between elevations was calculated using pooled transects from each site and forest type.

Canonical correspondence analysis (CCA) was employed to characterize habitat and altitudinal preference for each butterfly species, using the program Canoco 4.5 (Ter Braak & Smilauer 2002) with down-weighting of rare species. Separate analyses were performed for the entire transect and for sites between 130 and 1250 (1275) m asl. where both forest types were available. We excluded the second, incompletely sampled site at 720 m asl. (Baiks camp) from this analysis.

Altitudinal and geographic ranges were obtained for each species from Parsons (1999). Geographical range was classified as i) endemic to Papua New Guinea, ii) New Guinea and nearby islands, iii) Australian region, iv) Australian plus Indo-Malayan region, and v) Australasian tropics or greater.

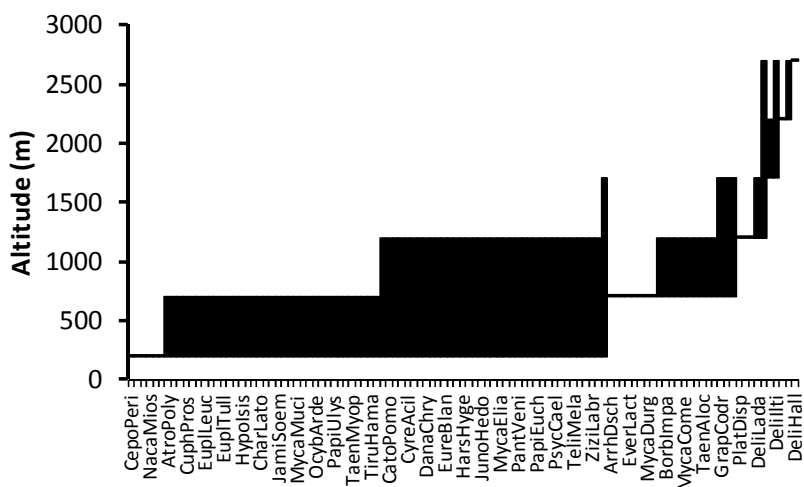
## **Results**

A total of 5702 butterflies belonging to 187 species were recorded, including 100 species in primary forest and 160 species in secondary habitats, from 29 transects at 10 study sites. Most species belonged to the families Nymphalidae (40%) and Lycaenidae (30%), followed by Hesperidae, Pieridae and Papilionidae (14%, 8% and 7%, respectively; Supplement 1). No species inhabited the entire primary forest gradient.

*Ornithoptera priamus* was found in four successive primary sites (it's range is therefore at least 1500 m). *Hasora discolor* was found at the 720 m asl. secondary site and the 2216 m asl primary site. Similarly *Udara drucei* was found at the 1276 m asl. secondary site and the 2801 m asl primary site. Therefore, both species have an altitudinal range of at least 1500 m as well. *Delias iltis*, *Mycalesis barbara*, *Pithecopis dionisius* and *Tellervo zoilus* were found in three primary sites (range 1000 m). 32 species ranged from 130 to 1276 m asl. in secondary sites (Figure 1, Supplement 1).

The total number of potential species inhabiting the transect was estimated at  $204 \pm 8$  species, based on the Chao 1 estimator. Species accumulation curves for primary and secondary forests were similar to one another (Figure 2).

Figure 1: Observed altitudinal ranges of common species (with 10 or more individuals). Altitudes are rounded to 200, 700, 1200, 1700, 2200 and 2700 m asl.



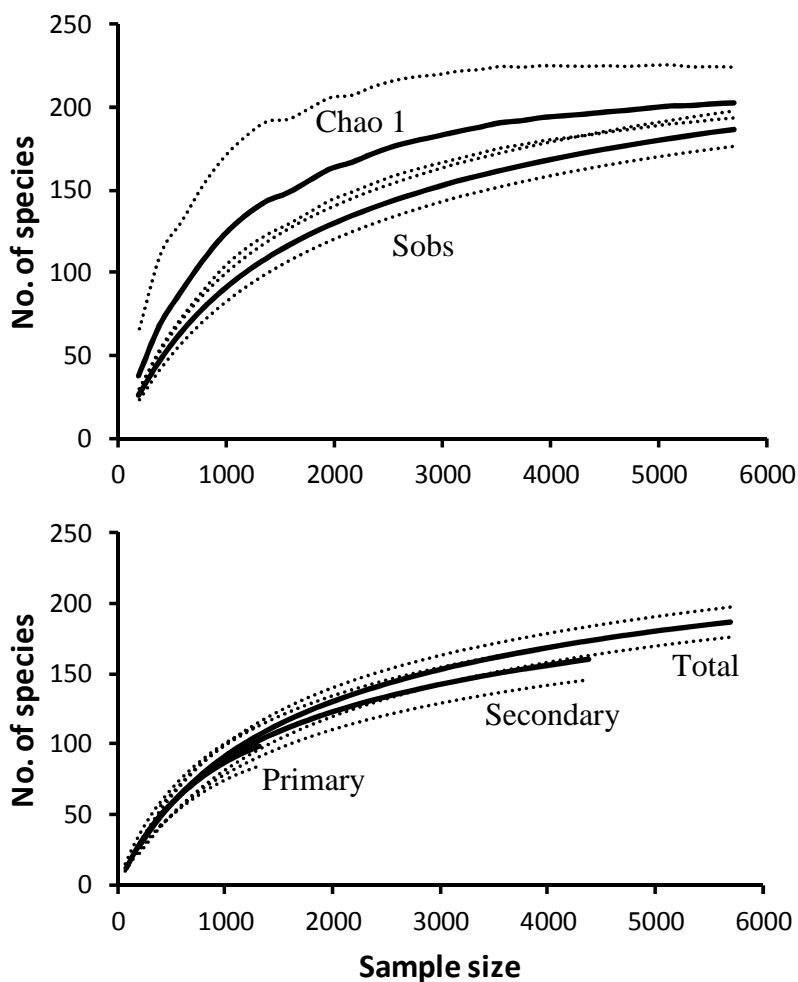
Both species richness and abundance decreased with altitude in both habitats. In primary forest 908 individuals were observed at the lowest site but only 51 - 103 individuals were observed at higher elevations. Abundances in secondary habitats were consistently higher than those in primary forest (Figure 3).

The proportion of shared species between adjacent pairs of sites in primary forest was independent of altitude (Jaccard index; Pearson  $r = -0.0381$ ,  $p = 0.951$ ,  $N = 5$ , Figure 4b), similarly the proportion of species unique to the lower altitude (Pearson  $r = -0.8134$ ,  $p = 0.094$ ,  $N = 5$ ), but the proportion of species unique to the higher altitude increases significantly with altitude (Pearson  $r = 0.9227$ ,  $p = 0.026$ ,  $N = 5$ ).

Community similarity based on species abundance decreased with altitudinal distance. At low altitudinal distances (500 & 1000 m), similarity between secondary forest sites is higher than those between primary forest sites (Figure 5).

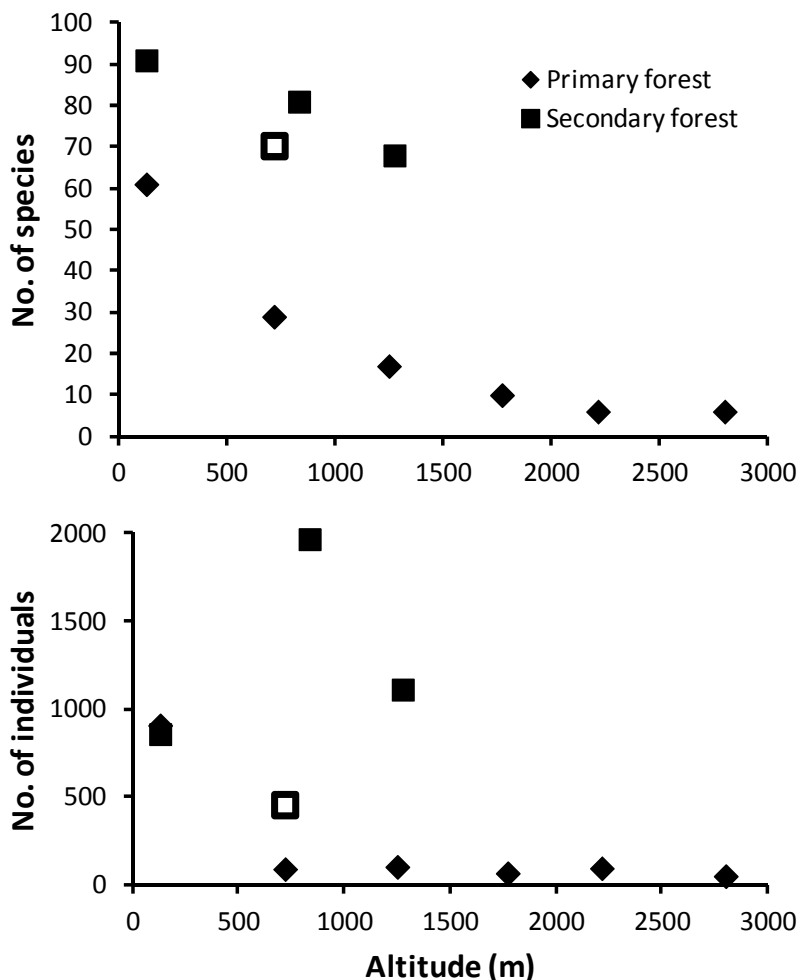
Species composition was analysed using CCA with the first axis representing altitude and the second axis habitat type. These two axes explained 20.8% of species variability: the first axis explained 11.8% and the second axis 9% of the variation (Figure 6). Both axes were significant (Monte Carlo test,  $F = 3.408$ ,  $P = 0.001$ ).

Figure 2: A - Species accumulation curves (with 95% confidence intervals; dotted lines) for observed (Sobs) and estimated (Chao 1) species richness in the YUS. B - Species accumulation curves for observed species richness in primary and secondary forest and total.



The altitudinal ranges of endemic species were smaller than the more wide-ranging species. Similarly, the mean mid-point altitude for endemic species was at a higher altitude compared with other species (Figure 7). There is a logarithmic relationship between regional (whole of Papua New Guinea) and local species richness. (Figure 8).

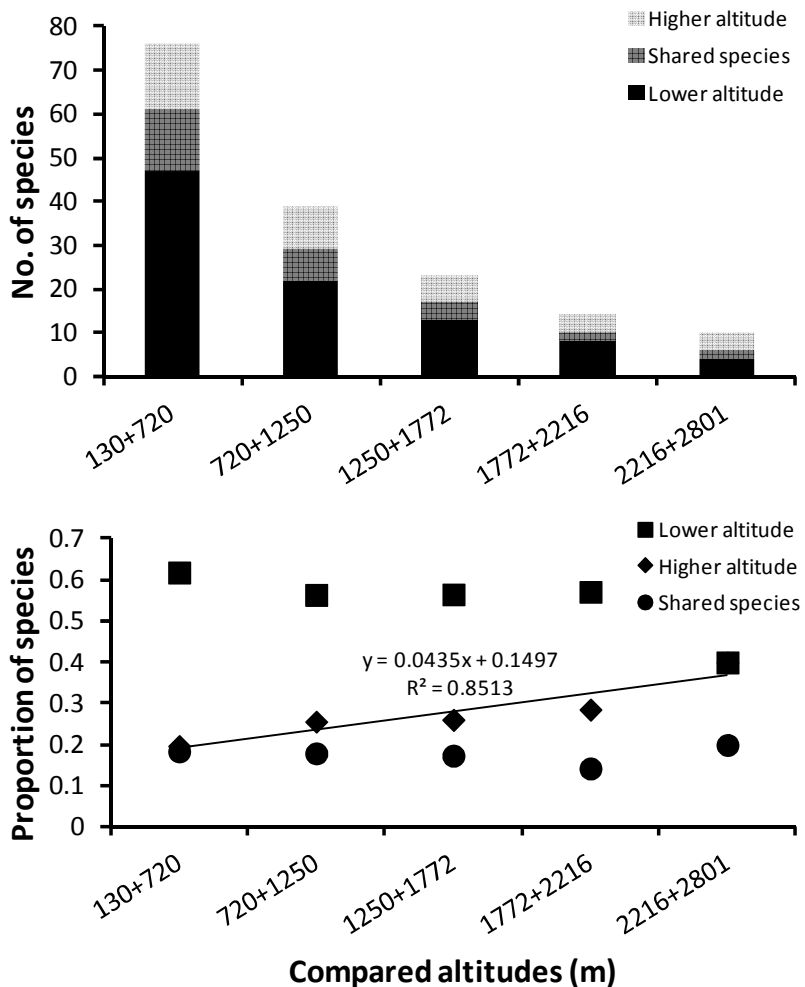
Figure 3: Number of species and individuals at 10 study sites. Empty square is an additional secondary site at 720 m asl.



## Discussion

Our observed transect-wide diversity converged on the diversity estimated by Chao1 and was thus reliable. At the same time, the observed number of species (187) was markedly lower than the 273 species observed by Sam (2011) in the Central Cordillera of PNG. Sam (2011) also observed a rapid decline in species richness between 1200 m (125 species) and 1700 m asl. (35 species) for both primary and secondary forest habitats. We observed the greatest decline in species between 130 and 720 m asl (in primary forest only).

Figure 4: Overlaps in species composition of butterfly communities between primary forest sites in absolute numbers of species (A) and their relative proportions (B).



Species richness in primary forest sites decreased with altitude, as was the case along Neotropical and PNG altitudinal gradients focusing on butterflies (Sam 2011, Molina-Martinez et al. in press), and several, but not all, subtaxa of geometrid moths (Brehm & Fiedler 2003). However, lepidopteran studies are not uniform, and other patterns of species richness have been observed. Several studies found the peak of species richness at mid elevations. For example, Fleishman et al. (1998) studied montane butterfly communities (from 1972 m to 3272 m asl.) and observed that species richness peaked at around 2300 m asl. A high altitude study on pronophiline butterflies (Pyrzcz & Wojtusiak 2002) revealed a similar pattern. Brehm et al. (2007) surveyed geometrid moths along a complete volcano gradient and also observed a mid altitudinal peak in species richness. Gutierrez (1997), studying butterflies, observed a mid altitude peak as well as a gradually decreasing pattern dependent on the geographical orientation of sites (i.e., northern slope versus sheltered gorge). Interestingly, Brehm & Fiedler (2003) and Pyrcz et al. (2009) both observed that species richness increased with altitude, but both studies were completed on shortened gradients (1040 - 2677 m and 1600 - 2600 m asl., respectively). Additionally, the subfamilies they studied (geometrid moths or nymphalid butterflies) are not representative for butterflies or Lepidoptera overall.

Figure 5: Chao-Sorensen's abundance based similarity index for both habitats.

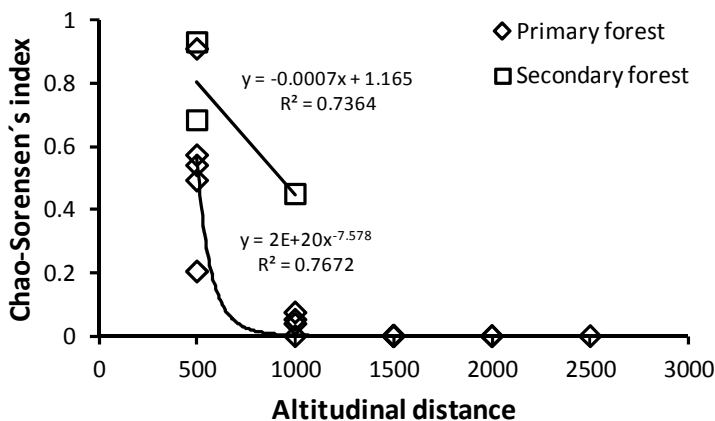




Figure 6: First two axes from CCA analysis with all 29 transects. Black diamonds are transects from undisturbed forest and open diamonds are transects from disturbed forests. Transects from same sites are grouped together. The first axis correlates with altitude, the second with disturbance.

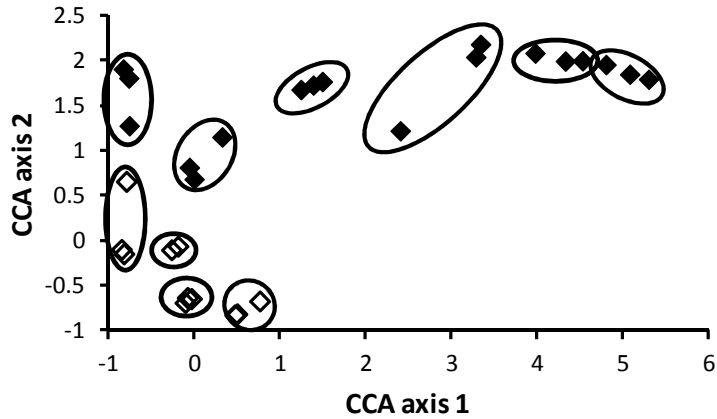
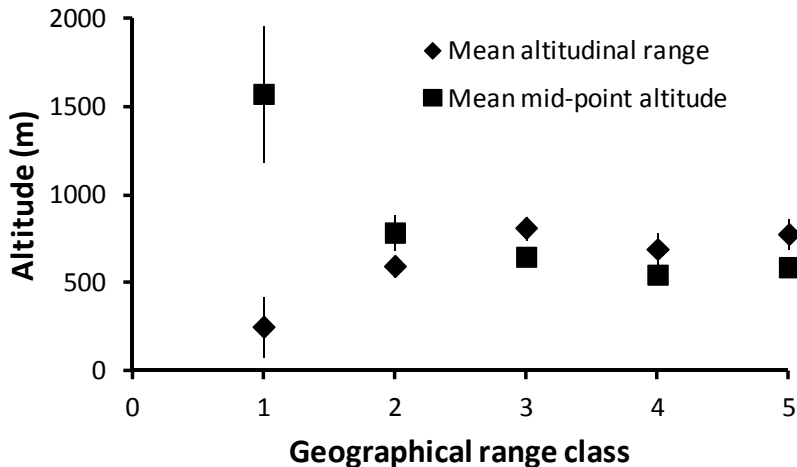
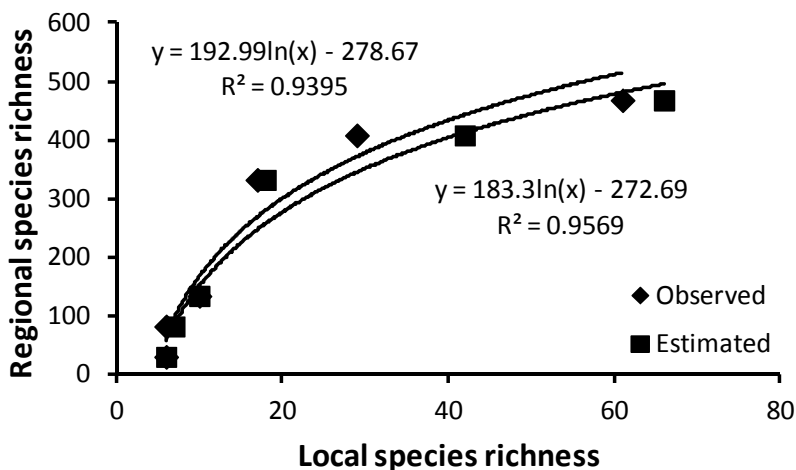


Figure 7: Relationship of common species ( $\geq 10$  individuals) between Geographical range class and mean altitudinal range or mean mid-point altitude with standard errors of the mean.



Lawton et al. (1987) gave four explanations for decreasing species richness at higher altitudes: reduction of habitat area, reduction of resources (host plants), reduction of primary productivity and adverse environment conditions in high altitudes. Temperature influences species richness (Menendez et al. 2007) and even abundance (Pollard 1988). In tropical butterflies, Molina-Martinez et al. (in press) found that temperature (followed by humidity) explained most of the variation in butterfly species richness along an altitudinal gradient.

Figure 8: Relationship between local species richness, observed and estimated (Chao 1; species numbers from primary sites) and regional species richness (species available in Papua New Guinea).



The difference in species richness between primary and secondary sites is striking. It is known that small- or medium-scale disturbance has a positive effect on diversity (Connell 1978). In the tropics there are studies supporting both higher diversity in primary forests (Perfecto et al. 2003, Schulze et al. 2004, Veddeler et al. 2005, Barlow et al. 2007) and higher diversity in secondary habitats (Lawton et al. 1998, Ramos 2000). Hamer et al. (1997), Fermon et al. (2005) and Bobo et al. (2006) observed the highest species richness in secondary sites, but claimed that endemic species with limited geographical ranges have higher diversity in primary forest. The different results could have been caused by differential sampling effort as large scale studies show a higher species diversity in undisturbed forest whereas small-scale studies tend to show the opposite (Hill & Hamer 2004). This idea is supported by our results as the species accumulation curves for primary and secondary forest are similar, but the former's curve is shortened due to a much smaller number of individuals present per forest area compared with secondary habitats. In primary forests there are natural secondary habitats such as gaps or clearings, canopy or river banks, which play a significant role in defining the total species richness (Vlasanek et al. in press). In such habitats, probably all the species found in our anthropogenic secondary sites occur, but in much smaller numbers and hence it is difficult to record them there.

In contrast to Sam (2011), who found that similarities between adjacent sites linearly decreased with altitude, we observed steady similarity values along the whole

gradient. According to the unified theory of biodiversity (Hubbel 2001), between-site similarity should linearly decrease with the log of distance. Sam (2011), in agreement with this study, found decreasing similarity with increasing altitudinal distance between two communities. Studies on Pronophilina butterflies from Ecuador (Pyrzcz et al. 2009) and Venezuela (Pyrzcz & Wojtusiak 2002) observed the same pattern, but on very short gradients (800 - 1000 m long).

The mean altitudinal range was narrower for endemic species than for widespread species (as observed by Sam 2011) and the mean mid-point altitude was higher for endemic species. This means that endemic species not only have a limited geographical range, but they have a limited altitudinal range in addition. Also, endemic species seem to prefer to inhabit higher elevations, contrary to the ubiquitous and widespread species living in lower altitudes.

In conclusion, this work is one of only a few butterfly studies spanning an almost complete altitudinal gradient. It is evident that butterfly communities are changing rapidly along the gradient and that butterfly species diversity in the Huon Peninsula is poorer than that of a comparable gradient in the Central Cordilleras of PNG.

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## **Summary**



## Summary

A mark-release-recapture study of butterflies within a lowland primary rainforest analysed butterfly dispersal within a large continuous rainforest habitat and, for the most common species, related it to host plant abundance. The study analysed population size and dispersal for the 14 most common species. A new method was developed to estimate dispersal measured in a network of fixed study plots within a large homogeneous habitat. Butterfly dispersal was characterized by recapture rate (lower recapture rate means better dispersal), mean dispersal distance, and a negative exponential function of dispersal probability with distance. These dispersal parameters were tested against the species' gap and succession preference, geographical and altitudinal range and body size. The recapture rate increased from secondary to primary forest. Even in primary forest, only five from 90 species were limited to the shady understory. Most species were more or less concentrated in gaps. The dispersal ability of most butterfly species was sufficient to track their host plants even at the density of only single plant individual per hectare. At least 1% of individuals dispersed 1 km or more in six out of 14 species studied. The three most abundant species were analyzed in as much detail as the data allowed in order to compute demographic parameters such as survival and population size. Ten times more individuals were marked for the most abundant species (*Danis danis* (Lycaenidae)) than for the second and third most abundant species (*Taenaris* sp. and *Parthenos aspila* (Nymphalidae)). There were almost 22,000 individuals belonging to these three species within the study plots (14.58 ha) during 6 weeks of the study. The average daily population size was 235 individuals per hectare. In the middle of study, many individuals of *Danis danis* hatched in synchrony, raising the daily population size more than 5 times within a few days. *Parthenos aspila* individuals stayed mostly in same gap, the other two species lived mostly in the shady understory. That could be one reason for the extraordinary long residence time of *Parthenos aspila* in comparison to the other two species. The dispersal ability of *Parthenos aspila* and *Danis danis* was low, not even 1% of the population could reach 1 km. In *Taenaris* sp. I found that 10% of population could travel more than 1 km. Due to high abundance of *Danis danis*, host plant could be tracked. Host plant density was high in relation to *Danis danis* dispersal ability. I estimated that each 20 x 20 m forest plot containing the food plant produced ~100 adults of *D. danis* annually. Apart from their extraordinary residence times tropical butterflies seem to be similar to temperate species in many ways. My results show that tropical and temperate butterfly species are demographically similar, including their dispersal behaviour. However, tropical

butterflies tend to have overlapping generations and longer life spans than temperate species.

The altitudinal gradient study was a transect study encompassing an almost complete rainforest altitudinal gradient, from 130 to 2801 m asl. in the Huon Peninsula. It is compared with a parallel study by Sam (2011) from the Central Cordillera, an adjacent montane range of similar topography but much greater geological age. The butterfly communities on Huon Peninsula ranges are poorer than in the Central Cordilleras. That could be because the Huon Peninsula is smaller and isolated from the Central Cordilleras, and thus has a limited pool of montane butterflies. In total there were 187 species along the transect, mostly from the family Nymphalidae. Species richness decreased with altitude while beta diversity remained constant, as the proportion of shared species between adjacent sites 500 altitudinal metres apart ranged from 15 - 20% in all cases. Similarity between secondary forest sites vertically separated by 500 m and 1000 m was higher than between primary sites. The importance of secondary habitats for species richness was confirmed not only in lowland MRR study (where most species have some preference for gaps) but also in altitudinal gradient, as diversity was higher in secondary habitats than in primary forest sites.

## **References**

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# **Appendix I**

Supporting information for Chapter I



Supplement 1: Butterfly species caught in and around the study plots. A, B, C, D - captures from inside the plot; A1, B1, C1, D1 - within 25 m from the plot; A2, B2, C2, D2 - on paths connecting different plots, farther than 25 m from any plot. *Taenaris* sp. is a mixture of at least two species - *T. catops* and *T. myops*.

Plot	A	A <sup>1</sup>	A <sup>2</sup>	B	B <sup>1</sup>	B <sup>2</sup>	C	C <sup>1</sup>	C <sup>2</sup>	D	D <sup>1</sup>	D <sup>2</sup>	Total
<b>Hesperiidae</b>													
<i>Hasora subcaelestis</i> Rothschild, 1916							1						1
<i>Chaetocneme critomedia</i> (Guérin-Méneville, [1831])				1									1
<i>Notocrypta renardi</i> Oberthür, 1878)	1			1			3			1			6
<i>Tagiades japetus</i> (Stoll, [1781])										1			1
<i>Toxidia inornata</i> (Butler, 1883)	1						1						2
<b>Papilionidae</b>													
<i>Atrophaneura polydorus</i> (Linnaeus, 1763)	9		1	7			1			4			22
<i>Graphium agamemnon</i> (Linnaeus, 1758)	4	1		2			1			2			10
<i>Graphium aristeus</i> (Stoll, [1780])												1	1
<i>Graphium wallacei</i> (Hewitson, [1858])								1					1
<i>Ornithoptera paradisea</i> Staudinger, 1893	1			6						1			8
<i>Papilio aegaeus</i> Donovan, 1805	37		5	16			5	1		8			72
<i>Papilio ambrax</i> Boisduval, 1832	29	1		7		1	4		1	12	1		56
<i>Papilio euchenor</i> Guérin-Méneville, 1829	1		1	4						3			9
<i>Papilio ulysses</i> Linnaeus, 1758			1										1
<b>Pieridae</b>													
<i>Appias cf. ada</i> (Stoll, [1781])									1				1
<i>Appias celestina</i> (Boisduval, 1832)			1										1
<i>Cepora abnormis</i> (Wallace, 1867)		1					5						6
<i>Delias aruna</i> (Boisduval, 1832)	1												1
<i>Delias mysis</i> (Fabricius, 1775)	2						1			1			4
<i>Elodina andropis</i> Butler, 1876	9		4	5			7		1	1			27
<i>Eurema blanda</i> (Boisduval, 1836)					1							1	2
<i>Eurema puella</i> (Boisduval, 1832)	20		3	9		1	8	1	1	14			57
<b>Lycanidae</b>													
<i>Amblypodia annetta</i> Staudinger, [1888]							1	2					3
<i>Arhopala thamyras</i> (Linnaeus, 1764)	1			1						2			4
<i>Candalides helenita</i> (Semper, [1879])	1									1			2
<i>Danis danis</i> (Cramer, [1775])	1458	35	131	1790	2	84	767	39	282	1306	13	9	5916
<i>Danis glaucopsis</i> (Grose-Smith, 1894)	49	1	1	35			14		2	29	1		132
<i>Dicallaneura decorata</i> (Hewitson, 1862)				2									2
<i>Dicallaneura ribbei</i> Röber, 1886	4						1			1			6
<i>Epimastidia inops</i> (C. & R. Felder, 1860)	1												1
<i>Hypochrysops heros</i> (Grose-Smith, 1894)				1									1
<i>Hypochrysops chrysargyra</i> Grose-Smith & Kirby, 1895	1												1
<i>Hypolycaena phorbis</i> (Fabricius, 1793)										2			2
<i>Ionolyce helicon</i> (Felder, 1860)	4			2									6
<i>Jamides aetherialis</i> (Butler, 1884)							3						3

<i>Jamides aleuas</i> (C. & R. Felder, 1865)	1									1	
<i>Jamides amarauge</i> Druce, 1891				1		1				2	
<i>Jamides coritus</i> (Guérin-Méneville, 1829)	6	1	2	13	3	8	2	3		38	
<i>Jamides cytus</i> (Boisduval, 1832)	1			4		3		4		12	
<i>Nacaduba cyanea</i> (Cramer, [1775])	16		2	27	1	14	1	5	9	1	76
<i>Nacaduba pactolus</i> (Felder, 1860)	1					1		1			3
<i>Philiris cf. moira</i> (Grose-Smith, 1899)									1		1
<i>Pithecopis dionisius</i> (Boisduval, 1832)	8	2	1	4					6	1	22
<i>Psychonotis caelius</i> (C. & R. Felder, 1860)	1								1		2
Nymphalidae											
<i>Apaturina erminea</i> (Cramer, [1779])	2			1		1	2				6
<i>Cethosia cydippe</i> (Linnaeus, 1767)	21		1	37	2	17	1		13		92
<i>Cirrochroa regina</i> C. & R. Felder, [1867]	99		4	24		19	2		24		172
<i>Cupha prosope</i> (Fabricius, 1775)	16			2	1	7			9		35
<i>Cyrestis acilia</i> (Godart, [1824])				2		2	1			2	7
<i>Cyrestis achates</i> Butler, 1865			1						1		2
<i>Doleschallia nacar</i> (Boisduval, 1832)	1			2	1	1			1		6
<i>Doleschallia noorna</i> Grose-Smith & Kirby, 1889	7					2	2		2		13
<i>Elymnias cybele</i> C. & R. Felder, 1860	9			5		1			1		16
<i>Euploea netscheri</i> Snellen, 1889	3			2		1	3		1		10
<i>Euploea stephensii</i> C. & R. Felder, [1865]				2		1					3
<i>Euploea wallacei</i> C. & R. Felder, 1860				3			7	2			12
<i>Harsiesis hygea</i> (Hewitson, 1863)					1						1
<i>Hypolimnas alimena</i> (Linnaeus, 1758)									1		1
<i>Hypolimnas bolina</i> (Linnaeus, 1758)	1								1		2
<i>Hypolimnas deois</i> Hewitson, 1858	4			12		4	1	1	4	1	27
<i>Hyantis hodeva</i> Hewitson, [1862]	3	2					1	1	1		8
<i>Hypocysta isis</i> Fruhstorfer, 1894	1					1					2
<i>Charaxes latona</i> Butler, 1865			1			2					3
<i>Junonia erigone</i> (Cramer, [1775])	1			3							4
<i>Lamprolenis nitida</i> Godman & Salvin, [1881]	25			6	1	9			5		46
<i>Lexias aeropa</i> (Linnaeus, 1758)	6		2	7		3	1	1	3		23
<i>Melanitis constantia</i> (Cramer, [1777])	2			1					1		4
<i>Morphopsis albertisi</i> Oberthür, 1880	3					1	4	4	2		14
<i>Mycalesis duponcheli</i> (Guérin-Méneville, [1838])	3		1	14		1			1	2	22
<i>Mycalesis durga</i> Grose-Smith & Kirby, 1892	5										5
<i>Mynes geoffroyi</i> (Guérin-Méneville, [1830])			1	1		1			2		5
<i>Mycalesis mehadeva</i> (Boisduval, 1832)	35		5	15	1	7	1	1	22	1	88
<i>Mycalesis mucia</i> Hewitson, 1862	10			7		8		1			26
<i>Mycalesis phidon</i> Hewitson, [1862]				2		4					6
<i>Mycalesis terminus</i> (Fabricius, 1775)	1										1
<i>Neptis nausicaa</i> de Nicéville, 1897	25		1	14		1			10		51
<i>Neptis satina</i> Grose-Smith, 1894	6		1	13		6			3		29
<i>Parthenos aspila</i> Honrath, 1888	101		2	115	3	90	5	9	50	4	379



<i>Pantoporia consimilis</i> (Boisduval, [1832])	34		2	6			4		2	9	1		58
<i>Pantoporia venilia</i> (Linnaeus, 1758)				4									4
<i>Prothoe australis</i> (Guérin-Méneville, [1831])	23	1	6	13		1	10	5	4	4	2	1	70
<i>Taenaris bioculatus</i> (Guérin-Méneville, [1830])	15		1	12			11		2	2			43
<i>Taenaris dimona</i> (Hewitson, 1862)	7		3	11			3		4	3		1	32
<i>Taenaris gorgo</i> (Kirsch, 1877)	2			4									6
<i>Taenaris sp.</i>	133	5	45	114	0	6	99	8	33	91	2	1	537
<i>Tellervo nedusia</i> (Geyer, 1832)	19		4	29		2	29	1		39	3	2	128
<i>Terinos tethys</i> Hewitson, 1862	2			2									4
<i>Vagrans egista</i> (Cramer, [1780])	3						1		1			1	6
<i>Vindula arsinoe</i> (Cramer, [1777])			2						1				3
<i>Yoma algina</i> (Boisduval, 1832)				5			6	1	1				13
Total	2296	50	236	2428	3	109	1203	91	364	1719	28	24	8551
Number of species	61			54			53			51			

Supplement 2: Butterfly species with  $\geq 15$  captures. Count of total captures, marked and recaptured individuals. R - recapture rate (recaptures / captures); D<sub>avg</sub> - mean dispersal distance in meters; D<sub>obs</sub> - mean dispersal distance between two captures in meters; D<sub>cor</sub> - mean dispersal distance between two captures adjusted for plots' positions; Gap% - gap preference (proportion of captures in gaps); CCA – distribution optimum along succession gradient from secondary forests (low CCA values) to primary forests (high CCA values); Geo - geographical range (1 - endemic for New Guinea and associated islands; 2 – also in Australian tropics); Altitude - Altitudinal range in PNG in meters; Size - wing span in mm.

Species	Total	Marked	Recaptured	R	D <sub>avg</sub>	Median	D <sub>obs</sub>	D <sub>cor</sub>	Gap%	CCA	Geo.	Altitude	Size
<i>Danis danis</i>	5916	3703	1031	0.37	108.7	71	60.4	185.5	1	0.98	2	1000	44
<i>Taenaris sp.</i>	537	394	78	0.27	351.6	181.5	191.5	674.1	4	0.95	2	1500	87
<i>Parthenos aspila</i>	379	317	40	0.16	80.5	64	60.3	103.4	60	0.13	1	800	88.5
<i>Cirrochroa regina</i>	172	151	18	0.12	104.3	45	99.0	211.4	63	0.67	2	1200	63.5
<i>Danis glaucopis</i>	132	108	17	0.18	63.4	47	55.8	59.9	8	1.17	1	200	40
<i>Tellervo nedusia</i>	128	83	27	0.35	146.7	124	87.0	154.3	2	1.11	1	1000	42.5
<i>Cethosia cydippe</i>	92	67	17	0.27	135.6	118	94.8	190.1	58	0.68	2	2300	78
<i>Mycalesis mehadewa</i>	88	84	4	0.05	35.8	29	50.0	53.3	43	0.93	1	480	43.5
<i>Nacaduba cyanea</i>	76	76	0	0.00	NA	NA	NA	NA	17	1.20	2	1400	35
<i>Papilio aegaeus</i>	72	64	8	0.11	203.8	107.5	194.3	757.3	22	0.44	2	1600	106.5
<i>Prothoe australis</i>	70	64	5	0.09	193.8	109	188.0	616.8	17	1.87	1	1200	72.5
<i>Pantoporia consimilis</i>	58	56	1	0.03	NA	NA	NA	NA	79	0.43	2	1200	41
<i>Eurema puella</i>	57	52	3	0.09	86	26	64.0	77.3	23	0.03	2	1500	48.5
<i>Papilio ambrax</i>	56	45	6	0.20	648.5	636	361.8	1040.7	36	0.84	2	1200	80
<i>Neptis nausicaa</i>	51	44	6	0.14	648.2	635	565.7	1084.6	35	0.00	1	200	57
<i>Lamprolenis niida</i>	46	23	12	0.50	128.1	119.5	64.5	108.3	0	1.93	1	1500	61.5
<i>Taenaris bioculatus</i>	43	37	4	0.14	82.3	89	70.0	85.0	7	1.19	1	1200	79
<i>Jamides coritus</i>	38	36	2	0.05	NA	NA	NA	NA	21	0.71	1	1000	37.5
<i>Cupha prosope</i>	35	33	2	0.06	NA	NA	NA	NA	60	0.04	2	1200	56
<i>Taenaris dimona</i>	32	31	1	0.03	NA	NA	NA	NA	3	1.15	1	1200	84
<i>Neptis satina</i>	29	29	0	0.00	NA	NA	NA	NA	31	0.58	1	1200	57.5
<i>Elodina andropis</i>	27	26	1	0.04	NA	NA	NA	NA	30	0.26	1	0	43
<i>Hypolimnias deois</i>	27	25	1	0.07	NA	NA	NA	NA	81	0.02	1	1500	43
<i>Mycalesis mucia</i>	26	18	5	0.31	74.2	80	51.4	91.9	58	1.17	1	800	52
<i>Lexias aeropa</i>	23	22	1	0.04	NA	NA	NA	NA	13	2.47	2	1500	73.5
<i>Atrophaneura polydorus</i>	22	21	1	0.05	NA	NA	NA	NA	18	NA	2	1000	85
<i>Mycalesis duponcheli</i>	22	17	3	0.23	38	24	40	40	45	1.10	1	1200	55
<i>Pithecopis dionisius</i>	22	20	2	0.09	NA	NA	NA	NA	23	0.62	2	1800	31

<i>Elymias cybele</i>	16	10	2	0.38	NA	NA	NA	NA	56	2.44	1	500	77.5
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Supplement 3: Probability of an individual butterfly dispersing a particular distance estimated for well sampled butterfly species from regression-based models (IPF and NEF) with  $c$  and  $z$  as fitted parameters and coefficient of determination ( $R^2$ ). Values in bold style show better fit of IPF or NEF. Probability ( $p$ ): \*\*\* < 0.001 < \*\* < 0.01 < \* < 0.05 < n.s.

Species	IPF/NEF	0.2 km	0.5 km	1 km	5 km	10 km	$c$	$z$	$R^2$	F	p
<i>Danis danis</i>	IPF	0.14880	0.01796	0.00363	8.8E-05	1.8E-05	0.004	-2.31	0.932	218.8 (1,16)	***
	NEF	0.19441	0.03397	0.00186	1.5E-13	3.5E-26	0.622	-5.82	<b>0.940</b>	249.9 (1,16)	***
♂♂	IPF	0.16259	0.02043	0.00425	0.00011	2.3E-05	0.004	-2.26	0.928	205.8 (1,16)	***
	NEF	0.21212	0.03817	0.00219	2.6E-13	9.9E-26	0.665	-5.72	<b>0.940</b>	249 (1,16)	***
♀♀	IPF	0.07689	0.01164	0.00279	0.00010	2.4E-05	0.003	-2.06	<b>0.988</b>	473.2 (1,6)	***
	NEF	0.12957	0.01161	0.00021	2.2E-18	7.6E-36	0.647	-8.04	0.894	50.6 (1,6)	***
<i>Taenaris sp.</i>	IPF	0.51808	0.19859	0.09614	0.01784	0.00864	0.096	-1.05	0.881	148.1 (1,20)	***
	NEF	0.49744	0.28842	0.11627	8.1E-05	9.2E-09	0.715	-1.82	<b>0.961</b>	489.5 (1,20)	***
♂♂	IPF	0.50054	0.18483	0.08699	0.01512	0.00711	0.087	-1.09	0.898	150.1 (1,17)	***
	NEF	0.48440	0.28041	0.11275	7.7E-05	8.5E-09	0.697	-1.82	<b>0.934</b>	238.5 (1,17)	***
♀♀	IPF	0.48938	0.28845	0.19338	0.07641	0.05123	0.193	-0.58	0.865	38.51 (1,6)	***
	NEF	0.61513	0.40012	0.19538	0.00063	4.9E-07	0.819	-1.43	<b>0.958</b>	137 (1,6)	***
<i>Tellervo nedusia</i>	IPF	0.25040	0.08120	0.03464	0.00479	0.00204	0.035	-1.23	<b>0.895</b>	42.46 (1,5)	**
	NEF	0.34462	0.13792	0.02997	1.5E-07	3.5E-14	0.635	-3.05	0.709	12.19 (1,5)	*
♂♂	IPF	0.18958	0.04752	0.01668	0.00147	0.00052	0.017	-1.51	0.841	21.16 (1,4)	*
	NEF	0.22027	0.00700	2.2E-05	2.4E-25	2.6E-50	2.195	-11.50	<b>0.971</b>	134.6 (1,4)	***
♀♀	IPF	0.42864	0.20122	0.11356	0.03009	0.01698	0.114	-0.83	<b>0.922</b>	35.22 (1,3)	**
	NEF	0.60704	0.31077	0.10181	1.4E-05	1.9E-10	0.949	-2.23	0.885	23.16 (1,3)	*
<i>Parthenos aspila</i>	IPF	0.12090	0.02387	0.00699	0.00040	0.00012	0.007	-1.77	0.959	94.26 (1,4)	***
	NEF	0.18261	0.00902	6.0E-05	2.3E-22	3.9E-44	1.356	-10.03	<b>0.972</b>	138.4 (1,4)	***
♂♂	IPF	0.15570	0.04424	0.01707	0.00187	0.00072	0.017	-1.37	<b>0.979</b>	91.51 (1,2)	*
	NEF	0.23046	0.02571	0.00066	1.3E-16	1.8E-32	0.994	-7.31	0.888	15.77 (1,2)	n.s.
♀♀	IPF	0.14572	0.03253	0.01046	0.00075	0.00024	0.011	-1.64	0.935	42.9 (1,3)	**
	NEF	0.19088	0.00765	3.6E-05	8.5E-24	4.4E-47	1.630	-10.72	<b>0.991</b>	340.4 (1,3)	***
<i>Cethosia cydippe</i>	IPF	0.26959	0.09003	0.03927	0.00572	0.0025	0.039	-1.20	0.863	31.6 (1,5)	**
	NEF	0.36922	0.05074	0.00186	6.0E-15	2.6E-29	1.387	-6.62	<b>0.973</b>	178.8 (1,5)	***
♂♂	IPF	0.24125	0.08488	0.03852	0.00615	0.00279	0.039	-1.14	0.899	26.73 (1,3)	*
	NEF	0.33404	0.04850	0.00195	1.3E-14	1.4E-28	1.209	-6.43	<b>0.959</b>	69.57 (1,3)	**
♀♀	IPF	0.70262	0.25691	0.12002	0.02050	0.00958	0.120	-1.10	<b>0.993</b>	140.3 (1,1)	n.s.
	NEF	0.74459	0.21575	0.02737	1.8E-09	2.0E-18	1.701	-4.13	0.967	29.06 (1,1)	n.s.
<i>Danis glaucopsis</i>	IPF	0.14076	0.04029	0.01564	0.00174	0.00067	0.016	-1.37	<b>0.981</b>	105.8 (1,2)	**
	NEF	0.15454	0.00722	4.4E-05	8.0E-23	5.3E-45	1.191	-10.21	0.867	13.3 (1,2)	n.s.
<i>Cirrochroa regina</i>	IPF	0.30741	0.10144	0.04385	0.00625	0.0027	0.044	-1.21	<b>0.952</b>	79.18 (1,4)	***

	NEF	0.29025	0.04561	0.00209	4.0E-14	1.6E-27	0.997	-6.17	0.946	69.64 (1,4)	**
<i>Lamprolenis nitida</i>	IPF	0.26992	0.09424	0.04251	0.00670	0.00302	0.043	-1.15	0.838	20.73 (1,4)	*
	NEF	0.33901	0.02983	0.00052	4.4E-18	1.1E-35	1.714	-8.10	<b>0.976</b>	165.6 (1,4)	***
<i>Papilio ambrax</i>	IPF	0.72733	0.54929	0.44419	0.27127	0.21937	0.444	-0.31	0.833	10 (1,2)	n.s.
	NEF	0.88495	0.68605	0.44883	0.01506	0.00022	1.049	-0.85	<b>0.947</b>	36 (1,2)	*
<i>Papilio aegaeus</i>	IPF	0.37556	0.19090	0.11442	0.03486	0.02089	0.114	-0.74	<b>0.997</b>	1256 (1,4)	***
	NEF	0.47576	0.23826	0.07525	7.4E-06	7.3E-11	0.754	-2.31	0.874	27.8 (1,4)	**
<i>Neptis nausicaa</i>	IPF	0.71046	0.45447	0.32413	0.14788	0.10547	0.324	-0.49	0.746	11.74 (1,4)	*
	NEF	0.80253	0.59126	0.35533	0.00605	3.7E-05	0.984	-1.02	<b>0.765</b>	12.98 (1,4)	*
<i>Prothoe australis</i>	IPF	0.45874	0.25269	0.16094	0.05647	0.03596	0.161	-0.65	0.976	81.23 (1,2)	*
	NEF	0.61219	0.28589	0.08036	3.1E-06	9.6E-12	1.102	-2.54	<b>0.978</b>	86.71 (1,2)	*
<i>Mycalesis mucia</i>	IPF	0.32447	0.15256	0.08620	0.02290	0.01294	0.086	-0.82	0.993	141.9 (1,1)	n.s.
	NEF	0.24858	0.01591	0.00016	2.0E-20	2.5E-40	1.554	-9.16	<b>0.996</b>	226.9 (1,1)	*
<i>Taenaris bioculatus</i>	IPF	0.22727	0.07774	0.03453	0.00525	0.00233	0.035	-1.17	0.790	3.767 (1,1)	n.s.
	NEF	0.14309	0.00224	2.2E-06	1.8E-30	1.4E-60	2.289	-13.86	<b>0.898</b>	8.767 (1,1)	n.s.



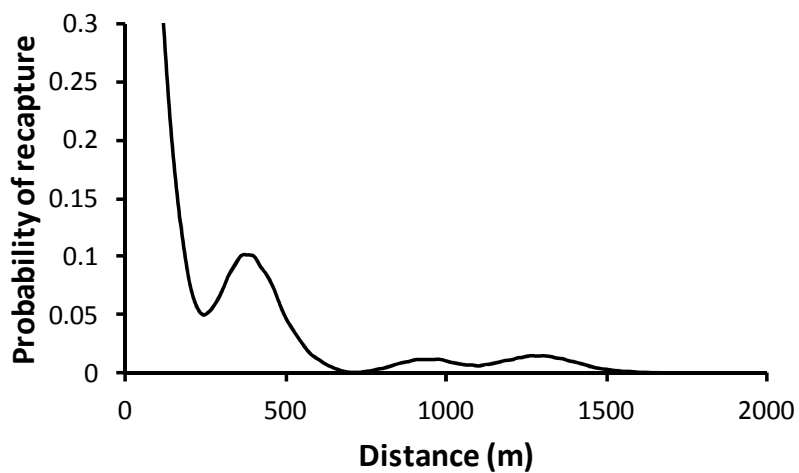
## **Appendix II**

Supporting information for Chapter II





Supplement 1: Recapture probability of a butterfly captured within the four plots and flying a given distance in a random direction.



Supplement 2: Probability of an individual butterfly dispersing a particular distance estimated from regression-based models (IPF and NEF) with  $c$  and  $z$  as fitted parameters and coefficient of determination (R2). Values in bold style show better fit of IPF or NEF. Probability (p): \*\*\* < 0.001 < \*\* < 0.01 < \* < 0.05 < n.s.

Species	IPF/NEF	0.2 km	0.5 km	1 km	5 km	10 km	$c$	$z$	R2	F	p
<i>Danis danis</i>	IPF	0.14880	0.01796	0.00363	8.8E-05	1.8E-05	0.004	-2.31	0.932	218.8 (1,16)	***
	NEF	0.19441	0.03397	0.00186	1.5E-13	3.5E-26	0.622	-5.82	<b>0.940</b>	249.9 (1,16)	***
♂♂	IPF	0.16259	0.02043	0.00425	0.00011	2.3E-05	0.004	-2.26	0.928	205.8 (1,16)	***
	NEF	0.21212	0.03817	0.00219	2.6E-13	9.9E-26	0.665	-5.72	<b>0.940</b>	249 (1,16)	***
♀♀	IPF	0.07689	0.01164	0.00279	0.00010	2.4E-05	0.003	-2.06	<b>0.988</b>	473.2 (1,6)	***
	NEF	0.12957	0.01161	0.00021	2.2E-18	7.6E-36	0.647	-8.04	0.894	50.6 (1,6)	***
<i>Taenaris</i> <i>sp.</i>	IPF	0.51808	0.19859	0.09614	0.01784	0.00864	0.096	-1.05	0.881	148.1 (1,20)	***
	NEF	0.49744	0.28842	0.11627	8.1E-05	9.2E-09	0.715	-1.82	<b>0.961</b>	489.5 (1,20)	***
♂♂	IPF	0.50054	0.18483	0.08699	0.01512	0.00711	0.087	-1.09	0.898	150.1 (1,17)	***
	NEF	0.48440	0.28041	0.11275	7.7E-05	8.5E-09	0.697	-1.82	<b>0.934</b>	238.5 (1,17)	***
♀♀	IPF	0.48938	0.28845	0.19338	0.07641	0.05123	0.193	-0.58	0.865	38.51 (1,6)	***
	NEF	0.61513	0.40012	0.19538	0.00063	4.9E-07	0.819	-1.43	<b>0.958</b>	137 (1,6)	***
<i>Parthenos</i> <i>aspila</i>	IPF	0.12090	0.02387	0.00699	0.00040	0.00012	0.007	-1.77	0.959	94.26 (1,4)	***
	NEF	0.18261	0.00902	6.0E-05	2.3E-22	3.9E-44	1.356	10.03	<b>0.972</b>	138.4 (1,4)	***
♂♂	IPF	0.15570	0.04424	0.01707	0.00187	0.00072	0.017	-1.37	<b>0.979</b>	91.51 (1,2)	*
	NEF	0.23046	0.02571	0.00066	1.3E-16	1.8E-32	0.994	-7.31	0.888	15.77 (1,2)	n.s.
♀♀	IPF	0.14572	0.03253	0.01046	0.00075	0.00024	0.011	-1.64	0.935	42.9 (1,3)	**
	NEF	0.19088	0.00765	3.6E-05	8.5E-24	4.4E-47	1.630	10.72	<b>0.991</b>	340.4 (1,3)	***

## **Appendix III**

Supporting information for Chapter III



Supplement 1: List of observed species. Geo is geographical range class; 1) endemic to Papua New Guinea, 2) New Guinea and nearby islands, 3) Australian region, 4) Australian plus Indo-Malayan region, and 5) Australasian tropics or greater.

Species	Shortcut	Geo	Known altitude		Observed altitude		Total
			Min	Max	Min	Max	
<u>Hesperiidae</u>							
<i>Arrhenes dschilus</i> (Plötz, 1885)	ArrhDsch	3	0	1600	700	700	6
<i>Arrhenes marnas</i> (C. Felder, 1860)	ArrhMarn	2	0	1600	200	1200	58
<i>Borbo cinnara</i> (Wallace, 1866)	BorbCinn	5	0	800	700	700	7
<i>Borbo impar</i> (Mabille, 1883)	BorbImpa	3	0	1200	700	1200	10
<i>Cephrenes trichopepla</i> (Lower, 1908)	CephTric	3	?	?	700	700	2
<i>Hasora discolor</i> (C. & R. Felder, 1859)	HasoDisc	3	0	1600	700	2200	2
<i>Kobrona idea</i> Evans, 1949	KobrIdea	2	0	1200	700	1200	8
<i>Kobrona wama</i> (Plötz, 1885)	KobrWama	2	0	1200	700	1200	2
<i>Mimene kolbei</i> (Ribbe, 1899)	MimeKolb	2	0	1200	700	700	1
<i>Notocrypta maria</i> Evans, 1949	NotoMari	2	500	1800	1200	1200	3
<i>Notocrypta renardi</i> (Oberthür, 1878)	NotoRena	2	0	1800	200	700	24
<i>Ocybadistes ardea</i> Bethune-Baker, 1906	OcybArde	4	0	1000	200	700	45
<i>Ocybadistes walkeri</i> Heron, 1894	OcybWalk	4	0	1300	700	700	2
<i>Pelopidas agna</i> (Moore, 1866)	PeloAgn	5	0	1600	1200	1200	1
<i>Pelopidas lyelli</i> (Rothschild, 1915)	PeloLyel	3	0	800	700	700	1
<i>Pelopidas mathias</i> (Fabricius, 1789)	PeloMath	5	0	200	200	1200	3
<i>Sabera caesina</i> (Hewitson, 1866)	SabeCaes	4	0	1000	200	700	4
<i>Suniana sunias</i> (C. Felder, 1860)	SuniSuni	3	0	2592	200	1200	125
<i>Tagiades nestus</i> (C. Felder, 1860)	TagiNest	3	0	800	200	200	18
<i>Tagiades trebellius</i> (Höpffer, 1874)	TagiTreb	4	0	1200	200	700	16
<i>Taractrocera ilia</i> Waterhouse, 1932	Tarallia	3	0	1500	200	200	4
<i>Telicota angiana</i> Evans, 1934	TeliAngi	2	700	2000	200	700	2
<i>Telicota ixion</i> Evans, 1949	TeliIxio	2	0	1500	1700	1700	1
<i>Telicota melanion</i> (Mabille, 1878)	TeliMela	2	0	800	200	1200	16
<i>Telicota sadrella</i> Parsons, 1986	TeliSadr	2	0	200	700	700	2
<i>Toxidia inornata</i> (Butler, 1883)	ToxiInor	3	0	2000	700	1200	15
<u>Papilionidae</u>							
<i>Atrophaneura polydorus</i> (Linnaeus, 1763)	AtroPoly	3	0	1000	200	700	8
<i>Graphium agamemnon</i> (Linnaeus, 1758)	GrapAgam	5	0	1200	200	700	8
<i>Graphium codrus</i> (Cramer, 1777)	GrapCodr	4	0	1300	700	1700	5
<i>Graphium sarpedon</i> (Linnaeus, 1758)	GrapSarp	5	0	1500	200	700	5
<i>Graphium wallacei</i> (Hewitson, 1858)	GrapWall	2	0	1200	700	700	4

<i>Graphium weiskei</i> (Ribbe, 1900)	GrapWeis	2	500	3420	2700	2700	3
<i>Ornithoptera chimaera</i> (Rothschild, 1904)	OrniChim	2	1200	2800	1700	1700	2
<i>Ornithoptera priamus</i> (Linnaeus, 1758)	OrniPria	3	0	2000	200	1700	21
<i>Papilio aegeus</i> Donovan, 1805	PapiAege	3	0	1600	200	1200	77
<i>Papilio ambrax</i> Boisduval, 1832	PapiAmbr	3	0	1200	200	1200	35
<i>Papilio demoleus</i> Linnaeus, 1758	PapiDemo	5	0	200	700	700	1
<i>Papilio euchenor</i> Guérin-Ménéville, 1830	PapiEuch	3	0	1600	200	1200	26
<i>Papilio ulysses</i> Linnaeus, 1758	PapiUlys	3	0	1600	200	700	9
<i>Troides oblongomaculatus</i> (Goeze, 1779)	TroiOblo	2	0	800	200	200	3

### Pieridae

<i>Catopsilia pomona</i> (Fabricius, 1775)	CatoPomo	5	0	1200	200	1200	19
<i>Catopsilia scylla</i> (Linnaeus, 1763)	CatoScyl	5	0	500	200	700	2
<i>Cepora perimale</i> (Donovan, 1805)	CepoPeri	4	0	1200	200	200	10
<i>Delias hallstromi</i> Sanford & Bennett, 1955	DeliHall	1	2600	3500	2700	2700	19
<i>Delias iltis</i> Ribbe, 1900	Delillti	1	1400	2740	1700	2700	37
<i>Delias ladas</i> Grose-Smith, 1894	DeliLada	2	400	1800	1200	1700	33
<i>Delias meeki</i> Rothschild, 1904	DeliMeek	1	1500	2400	2200	2200	14
<i>Delias mira</i> Rothschild, 1904	DeliMira	2	1800	2400	2200	2700	48
<i>Delias nais</i> Jordan, 1912	DeliNais	2	1000	2000	1700	2200	60
<i>Elodina andropis</i> Butler, 1876	ElodAndr	2	0	1200	1200	1200	3
<i>Elodina hypatia</i> C. & R. Felder, 1865	ElodHypa	2	0	1200	200	700	597
<i>Eurema blanda</i> (Boisduval, 1836)	EureBlan	4	0	1600	200	1200	123
<i>Eurema hecabe</i> (Linnaeus, 1758)	EureHeca	5	0	2000	200	1200	305
<i>Eurema laeta</i> (Boisduval, 1836)	EureLaet	5	0	1200	700	700	1
<i>Eurema puella</i> (Boisduval, 1832)	EurePuel	3	0	1500	200	1200	34

### Lycaenidae

<i>Arhopala leander</i> Evans, 1957	ArhoLean	2	0	1200	700	700	1
<i>Arhopala madytus</i> Fruhstorfer, 1914	ArhoMady	3	0	1200	200	200	2
<i>Arhopala meander</i> Boisduval, 1832	ArhoMean	2	0	500	200	200	3
<i>Caleta mindarus</i> (C. & R. Felder, 1865)	CaleMind	2	0	800	200	200	3
<i>Catochrysops panormus</i> (C. Felder, 1860)	CatoPano	5	0	1200	200	700	14
<i>Catochrysops strabo</i> (Fabricius, 1793)	CatoStra	5	0	200	1200	1200	2
<i>Catopyrops ancyra</i> (C. Felder, 1860)	CatoAncy	4	0	1600	200	700	12
<i>Danis danis</i> (Cramer, 1775)	DaniDani	3	0	1000	700	700	1
<i>Dicallaneura decorata</i> (Hewitson, 1862)	DicaDeco	2	0	1600	700	700	2
<i>Epimastidia inops</i> (C. & R. Felder, 1860)	EpimInop	2	0	2000	700	700	1
<i>Erysichton lineata</i> (Murray, 1874)	ErysLine	3	0	1600	700	1200	5

<i>Erysichton palmyra</i> (C. Felder, 1860)	ErysPalm	3	0	1600	1200	1200	2
<i>Euchrysops cnejus</i> (Fabricius, 1798)	EuchCnej	4	0	1600	200	1200	113
<i>Everes lacturnus</i> (Godart, 1824)	EverLact	5	0	1700	700	700	9
<i>Hypochlorosis ancharia</i> (Hewitson, 1869)	HypoAnch	2	0	660	200	700	31
<i>Hypochrysops geminatus</i> Sands, 1986	HypoGemi	2	200	1800	1200	1200	1
<i>Hypolycaena danis</i> (C. & R. Felder, 1865)	HypoDani	3	0	1600	700	1200	2
<i>Hypolycaena phorbas</i> (Fabricius, 1793)	HypoPhor	3	0	1400	200	200	2
<i>Jamides amaraugae</i> Druce, 1891	JamiAmar	3	0	1600	200	700	27
<i>Jamides bochus</i> (Stoll, 1782)	JamiBoch	4	?	?	200	700	60
<i>Jamides coritus</i> (Guérin-Méneville, 1831)	JamiCori	2	0	1000	200	200	1
<i>Jamides nemophilus</i> (Butler, 1876)	JamiNemo	3	0	1000	200	200	1
<i>Jamides soemias</i> Druce, 1891	JamiSoem	3	0	1500	200	700	63
<i>Lampides boeticus</i> (Linnaeus, 1767)	LampBoet	5	0	1600	700	1200	2
<i>Leptotes plinius</i> (Fabricius, 1793)	LeptPlin	5	0	600	700	700	1
<i>Luthrodes cleotas</i> (Guérin-Méneville, 1831)	LuthCleo	2	0	800	200	200	1
<i>Nacaduba berenice</i> (Herrich-Schäffer, 1869)	NacaBere	4	0	1600	200	200	7
<i>Nacaduba hermus</i> (C. Felder, 1860)	NacaHerm	4	1200	1400	1200	1200	2
<i>Nacaduba lucana</i> Tite 1963	NacaLuca	1	?	?	200	200	41
<i>Nacaduba major</i> Rothschild, 1915	NacaMajo	2	600	1300	1200	1200	1
<i>Nacaduba mallicollo</i> Druce, 1892	NacaMall	1	?	?	200	200	3
<i>Nacaduba mioswara</i> Tite, 1963	NacaMios	2	?	?	200	200	20
<i>Nacaduba ruficirca</i> Tite, 1963	NacaRufi	2	600	2600	200	1200	5
<i>Paraduba metriodes</i> (Bethune-Baker, 1911)	ParaMetr	2	0	1400	700	700	2
<i>Philiris agatha</i> (Grose-Smith, 1899)	PhilAgat	2	0	1800	1200	1200	1
<i>Philiris albihumerata</i> Tite, 1963	PhilAlbi	2	0	1500	700	700	2
<i>Philiris caelestis</i> Sands, 1979	PhilCael	1	300	1470	1200	1200	2
<i>Philiris dinawa</i> (Bethune-Baker, 1908)	PhilDina	1	180	1600	700	700	1
<i>Philiris fulgens</i> (Grose-Smith & Kirby, 1897)	PhilFulg	3	0	1600	1200	1200	1
<i>Philiris harterti</i> (Grose-Smith, 1894)	PhilHart	2	0	1300	700	1200	2
<i>Philiris helena</i> (Snellen, 1887)	PhilHele	2	0	1200	200	700	14
<i>Philiris luscenscens</i> Tite, 1963	PhilLusc	2	0	1000	700	700	1
<i>Philiris oreas</i> Tite, 1963	PhilOrea	2	?	760	1200	1200	1
<i>Philiris refusa</i> (Grose-Smith, 1894)	PhilRefu	2	0	1300	700	700	3
<i>Philiris tombara</i> Tite, 1963	PhilTomb	2	0	1000	700	1200	2
<i>Pistoria nigropunctata</i> (Bethune-Baker, 1908)	PistNigr	2	1400	1800	1200	1200	1
<i>Pithecopus dionisius</i> (Boisduval, 1832)	PithDion	3	0	1800	200	1200	117
<i>Praetaxila hunttei</i> (Sharpe, 1903)	PraeHunt	2	600	1600	1200	1200	5
<i>Praetaxila satraps</i> (Grpse-Smith, 1894)	PraeSatr	2	0	1600	1200	1200	3
<i>Prosotas nora</i> (C. Felder, 1860)	ProsNora	5	0	800	200	1200	7

<i>Psychonotis caelius</i> (C. & R. Felder, 1860)	PsycCael	3	0	1600	200	1200	12
<i>Psychonotis hebes</i> (Druce, 1904)	PsycHebe	2	0	1800	1200	1200	4
<i>Udara dilecta</i> (Moore, 1879)	UdarDile	5	300	2200	1200	1200	2
<i>Udara drucei</i> (Bethune-Baker, 1906)	UdarDruc	2	1200	1400	1200	2700	7
<i>Udara owgarra</i> (Bethune-Baker, 1906)	UdarOwga	2	1200	1800	2700	2700	3
<i>Zizina labradus</i> (Godart, 1824)	ZiziLabr	5	0	2600	200	1200	374
<i>Zizula hylax</i> (Fabricius, 1775)	ZizuHyla	5	0	1600	200	1200	206

### Nymphalidae

<i>Acraea meyeri</i> Kirsch, 1877	AcraMeye	2	0	1800	700	1200	4
<i>Apaturina erminea</i> (Cramer, 1779)	ApatErmi	3	0	1000	200	200	2
<i>Cethosia cydippe</i> (Linnaeus, 1763)	CethCydi	3	0	2300	200	1200	91
<i>Cirrochroa regina</i> C. & R. Felder, 1865	CirrRegi	3	0	1200	200	1200	6
<i>Cupha prosope</i> (Fabricius, 1775)	CuphPros	3	0	1200	200	700	8
<i>Cyrestis acilia</i> (Godart, 1819)	CyreAcil	3	0	2000	200	1200	39
<i>Cyrestis achates</i> Butler, 1865	CyreAcha	2	0	1200	200	1200	4
<i>Danaus affinis</i> (Fabricius, 1775)	DanaAffi	5	0	1500	200	1200	221
<i>Danaus chrysippus</i> (Linnaeus, 1758)	DanaChry	5	0	2500	200	1200	4
<i>Doleschallia nacar</i> (Boisduval, 1832)	DoleNaca	2	0	1200	200	700	17
<i>Doleschallia noorna</i> Grose-Smith & Kirby, 1893	DoleNoor	2	0	800	200	1200	3
<i>Elymnias cybele</i> (C. Felder, 1860)	ElymCybe	2	0	500	200	1200	35
<i>Erycinidia gracilis</i> Rothschild & Jordan, 1905	ErycGrac	2	1500	2400	1200	1200	3
<i>Euploea leucostictos</i> (Gmelin, 1790)	EuplLeuc	3	0	1200	200	700	32
<i>Euploea netscheri</i> Snellen, 1889	EuplNets	2	0	800	200	700	23
<i>Euploea stephensii</i> C. & R. Felder, 1865	EuplStep	2	0	1200	200	700	21
<i>Euploea tulliolus</i> (Fabricius, 1793)	EuplTull	4	0	1200	200	700	28
<i>Euploea wallacei</i> C. & R. Felder, 1860	EuplWall	2	0	1700	700	700	12
<i>Harsiesis hygea</i> (Hewitson, 1863)	HarsHyge	2	0	1200	200	1200	248
<i>Hyantis hodeva</i> Hewitson, 1862	HyanHode	2	0	1600	700	700	3
<i>Hypocysta isis</i> Grose-Smith, 1894	HypoIsis	2	0	1200	200	700	27
<i>Hypolimnas alimena</i> (Linnaeus, 1758)	HypoAlim	3	0	1200	200	1200	19
<i>Hypolimnas bolina</i> (Linnaeus, 1764)	HypoBoli	5	0	1500	200	700	14
<i>Hypolimnas deois</i> (Hewitson, 1858)	HypoDeoi	2	0	1500	200	1200	29
<i>Hypolimnas pithoeka</i> Kirsch, 1877	HypoPith	3	0	1000	1200	1200	1
<i>Charaxes latona</i> Butler, 1865	CharLato	3	0	1200	200	700	9
<i>Junonia erigone</i> (Cramer, 1775)	JunoErig	4	0	1600	200	200	2
<i>Junonia hedonia</i> (Linnaeus, 1764)	JunoHedo	4	0	1200	200	1200	170
<i>Junonia vilida</i> (Fabricius, 1787)	JunoVili	4	0	2400	200	1200	66



<i>Lamprolenis nitida</i> Godman & Salvin, 1880	LampNiti	2	0	1500	700	700	7
<i>Melanitis amabilis</i> (Boisduval, 1832)	MelaAmab	3	0	1500	200	1200	41
<i>Melanitis leda</i> (Linnaeus, 1758)	MelaLeda	5	0	1500	200	700	12
<i>Morphopsis albertisi</i> Oberthür, 1880	MorpAlbe	2	0	2200	1200	1200	2
<i>Mycalesis aethiops</i> Butler, 1868	MycaAeth	2	0	1800	200	200	1
<i>Mycalesis asophis</i> Hewitson, 1862	MycaAsop	2	0	200	700	700	2
<i>Mycalesis barbara</i> Grose-Smith, 1894	MycaBarb	2	600	2000	700	1700	228
<i>Mycalesis comes</i> Grose-Smith, 1894	MycaCome	2	0	1150	700	1200	47
<i>Mycalesis discobolus</i> Fruhstorfer, 1906	MycaDisc	2	800	2500	1700	1700	2
<i>Mycalesis duponcheli</i> (Guérin-Méneville, 1831)	MycaDupo	2	0	1200	200	700	5
<i>Mycalesis durga</i> Grose-Smith & Kirby, 1892	MycaDurg	2	0	1000	700	700	5
<i>Mycalesis elia</i> Grose-Smith, 1894	MycaElia	4	0	1800	200	1200	197
<i>Mycalesis mehadeva</i> (Boisduval, 1832)	MycaMeha	2	0	480	700	700	11
<i>Mycalesis mucia</i> Hewitson, 1862	MycaMuci	2	0	800	200	700	7
<i>Mycalesis perseus</i> (Fabricius, 1775)	MycaPers	4	0	1500	700	1200	2
<i>Mycalesis phidon</i> Hewitson, 1862	MycaPhid	2	0	1700	200	1200	138
<i>Mycalesis sirius</i> (Fabricius, 1775)	MycaSiri	3	0	1200	200	700	3
<i>Mycalesis terminus</i> (Fabricius, 1775)	MycaTerm	3	0	1600	200	700	108
<i>Mynes geoffroyi</i> (Guérin-Méneville, 1831)	MyneGeof	3	0	1200	700	1200	8
<i>Neptis brebissonii</i> (Boisduval, 1832)	NeptBreb	2	0	1200	700	700	1
<i>Neptis praslini</i> (Boisduval, 1832)	NeptPras	3	0	1200	200	200	1
<i>Orsotriaena medus</i> (Fabricius, 1775)	OrsoMedu	4	0	1200	200	700	36
<i>Pantoporia consimilis</i> (Boisduval, 1832)	PantCons	3	0	1200	200	700	49
<i>Pantoporia venilia</i> (Linnaeus, 1758)	PantVeni	3	0	1600	200	1200	27
<i>Parantica melusine</i> (Grose-Smith, 1894)	ParaMelu	2	50	2200	700	700	1
<i>Parantica weiskei</i> (Rothschild, 1901)	ParaWeis	2	1500	2500	2200	2200	1
<i>Phaedyma shepherdii</i> (Moore, 1858)	PhaeShep	3	0	1200	200	700	3
<i>Platythyma dispar</i> Joicey & Talbot, 1922	PlatDisp	2	1250	2000	1200	1200	7
<i>Platythyma septentrionalis</i> Nieuwenhuis & Howarth, 1969	PlatSept	1	1470	1580	1200	1200	13
<i>Prothoe australis</i> (Guérin-Méneville, 1831)	ProtAust	2	0	1200	200	200	2
<i>Symbrenthia hippoclus</i> (Cramer, 1779)	SymbHippo	5	0	1500	700	1200	4
<i>Taenaris alocus</i> Brooks, 1950	TaenAloc	1	0	2200	700	1200	27
<i>Taenaris artemis</i> (S. C. Snellen van Vollenhoven, 1860)	TaenArte	3	0	800	200	200	1
<i>Taenaris bioculatus</i> (Guérin-Méneville, 1830)	TaenBioc	2	0	1200	200	200	1
<i>Taenaris catops</i> (Westwood, 1851)	TaenCato	3	0	1500	200	1200	70
<i>Taenaris dimona</i> (Hewitson, 1862)	TaenDimo	2	0	1200	700	1200	11
<i>Taenaris dioptrica</i> (S. C. Snellen van Vollenhoven, 1860)	TaenDiop	2	0	900	200	200	1

<i>Taenaris myops</i> (C. & R. Felder, 1860)	TaenMyop	2	0	1300	200	700	29
<i>Taenaris schoenbergi</i> (Fruhstorfer, 1893)	TaenScho	2	320	2500	700	1700	28
<i>Tellervo nedusia</i> (Geyer, 1832)	TellNedu	2	0	1000	200	700	10
<i>Tellervo zoilus</i> (Fabricius, 1775)	TellZoil	3	0	2000	200	1200	49
<i>Terinos tethys</i> Hewitson, 1862	TeriTeth	2	0	200	700	700	1
<i>Tirumala hamata</i> (Macleay, 1827)	TiruHama	5	0	1700	200	700	58
<i>Vindula arsinoe</i> (Cramer, 1777)	VindArsi	3	0	1500	200	200	7
<i>Yoma algina</i> (Boisduval, 1832)	YomaAlgi	3	0	1300	200	700	166
<i>Ypthima arctoa</i> (Fabricius, 1775)	YpthArct	4	0	1600	200	1200	27

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