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

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Abstract The mobility of butterflies determines their ability to find host plant species, and thus their potential host plant range, as well as their ability to maintain metapopulations in fragmented habitats. While butterfly movement has been extensively studied for temperate species, very little is known for tropical forest species. 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 3,705, 394 and 317 marked individuals of *Danis danis*, *Taenaris* sp. and *Parthenos aspila* respectively, with 1,031, 78 and 40 butterfly individuals recaptured at least once. Over a period of 6 weeks there were almost 22,000 individuals belonging to these three species hatching within or entering our four study plots totaling 14.58 ha in area. The most abundant species, *D. danis*, with 20,000 individuals, showed highly variable population densities during the study. The residency time in the studied plots was highest for *P. aspila* (84 days), as individual butterflies stayed mostly in a single gap; we estimated that less than 1 % of individuals disperse 1 km or more. Similar movement probability was found in *D. danis* whilst in *Taenaris* sp., 10 % of the population disperses $\geq$1 km. Movement distances of *D. danis* were more than sufficient to locate its host plant, *Derris elliptica*, which occurred in 61 % of the 20 × 20 m subplots within a 50 ha plot. Compared with temperate species, our three species have much longer life spans, but their movement patterns remain within the known mobility estimates of temperate species. The mobility of *D. danis* is close to the average for temperate Lycaenidae, while *Taenaris* sp. is more mobile and *P. aspila* less mobile than the mean for all temperate species.

Keywords Jolly–Seber · Lepidoptera · Mark-release-recapture · Melanesia · Papilionoidea

Introduction

Studies on butterfly mobility 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. 2013). This is unfortunate since mobility is a key population parameter that determines the ability of butterfly species to find their host plants. Since there are many rare plant species in tropical forests, their specialist herbivores require the ability to move over potentially large distances to find them, thus mobility 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 upon them as density dependent mortality agents (Janzen 1970; Connell 1971).

Mark-release-recapture techniques (MRR) are a good tool for studying demographic parameters of butterflies

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including population size (Nowicki et al. 2005), mobility (Baguette et al. 2011; Wang et al. 2011; Tufto et al. 2012) and longevity (Beck and Fiedler 2009; Tufto et al. 2012). 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 studies in the temperate zone focus on non-forest vegetation, particularly grasslands, and use butterfly nets, while most 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 movement, 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.

However, population size has also been only rarely studied in tropical butterflies, particularly in large undisturbed patches of forest. 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 the majority of the world's butterfly species. This bias is reflected in our poor knowledge of the population biology of tropical butterflies.

Similarly, the ecology of butterfly species is much better known for temperate than tropical species (Bonebrake et al. 2010). Crucial ecological differences between temperate and tropical regions could also shape the ecology of their butterflies. In particular, are butterfly movements and/or host specialization influenced by the higher diversity and therefore lower abundance of host plants in the tropics? Are butterfly population sizes more stable in tropical than temperate climates? Do butterfly individuals live longer in tropical than temperate areas? Here we attempt to answer these questions for understory butterflies in a lowland rainforest of Papua New Guinea. In particular, we study the three locally most abundant species, *Danis danis* (Cramer, [1775]), *Taenaris* sp. and *Parthenos aspila* Honrath, 1888 whose populations compose up to 80 % of the entire butterfly community in forest understory (Basset et al. 2011; Vlasanek et al. 2013). High density of these butterfly species allowed us to conduct a detailed population analysis, which is not usually possible for butterfly species in tropical forests.

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. 2013). 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. It is one of the most common primary forest understory butterfly species in lowland Papua New Guinea forests. For instance, it represented 9.6 % of individuals in a butterfly community in Wanang primary rainforest (Sam 2009).

Taenaris spp., Nymphalidae, is a mixture of at least two species which are 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 represented 4.3 % of all individuals in the aforementioned Wanang community (Sam 2009).

Parthenos aspila, Nymphalidae, is endemic to the northern part of mainland New Guinea and lives in and around primary forest gaps and in secondary forest. A vine from the family Cucurbitaceae has been reported as its host plant (Parsons 1999). This butterfly species represented 6.9 % of all individuals in the Wanang community (Sam 2009).

Study site

This study was conducted in Wanang Conservation Area (5°14′S 145°05′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 (Fig. 1). Plot A (3.15 ha) was upland primary continuous forest without any creeks or gullies. Plot B (3.99 ha) and plot D (3.45 ha) were also in upland primary forest but with hills dissected by small creeks and valleys. Plot C (3.99 ha) was located in a meander of the 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. The plots were 45–682 m apart and together comprised the study area of approximately 4 × 1.5 km (Fig. 1). Each plot was divided into a 25 × 25 m grid marked with flagging tape and mapped in ArcGIS 9.3 (©ESRI, Inc.).

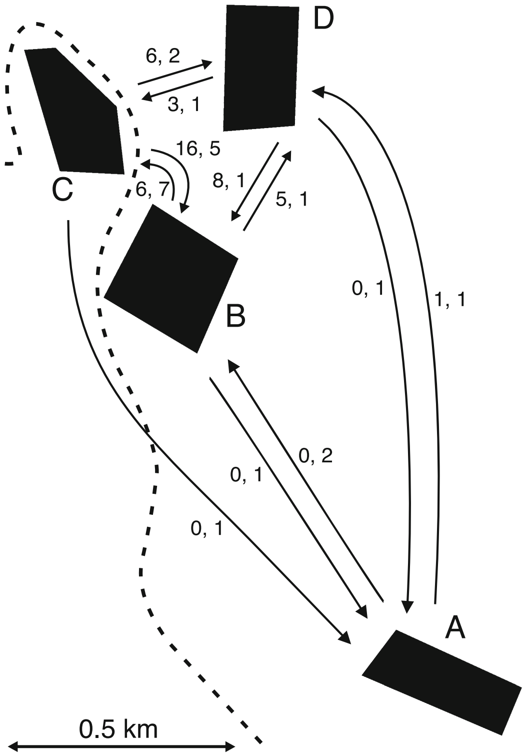

Fig. 1 Map of the study plots. *Dashed line* is the Digitam river. *Arrows* with *numbers* show the respective numbers of *D. danis* and *Taenaris* spp. individuals which moved between plots during the study. No such movement was recorded for *P. aspila*

Mark—recapture method

All understory butterflies (including the three focal species) were caught using entomological nets by evenly zigzagging through all plots. Two groups, each of which usually comprised of three people, sampled butterflies in the study plots. We also caught butterflies when moving from one plot to another (along 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 wing colour due to loss of scales) and location within the plot, recorded as coordinates of the closest point in the 25 × 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 change in protocol was a sudden rise in the abundance of *D. danis* males: their systematic collection would have distracted field workers from catching other butterfly species. The demographic parameters of *D. danis* (survival, catchability, population size) were estimated (1) for both sexes using data from regular marking and (2) for females using data from the whole study period in the study plots. Sex ratio (SR) of marked butterflies was calculated as $SR = N_{♂}/N_{♀}$. In addition we observed the oviposition behaviour of *D. danis* females from 30 November 2010 to 7 December 2010 and recorded the presence or absence of its only observed host plant, *Derris elliptica*, in 1,250 subplots, 20 × 20 m each, within a 50 ha plot.

Statistical analyses of demography

Constrained linear models (CLM), such as Jolly–Seber (JS), represent the best way to analyze MRR data (Schtickzelle et al. 2003). We used the program MARK v. 6.0 (White and Burnham 1999) with subroutine POPAN, to calculate four primary parameters: survival (φ), capture probability (p), proportional recruitment (*p*roportion *ent*ering; *pent*) and superpopulation (N). The first three parameters may be constant for sexes and time (.), sex dependent (g), factorially dependent on marking day (t), or exhibiting additive ($g + t$) or interactive ($g \times t$) patterns. The response to time can also be linear (T, $g + T$, $g \times T$) or quadratic (T^2, $g + T^2$, $g \times T^2$). 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 Akaike information criterion corrected for small sample size ($\mathrm{AIC_c}$; based on complexity, number of parameters and fitness of each model). The model with the lowest $\mathrm{AIC_c}$ is the best model and models which differ in $\mathrm{AIC_c}$ by less than 2 are comparable to each other. We started with the most complex model $\varphi(g \times t)\ p(g \times t)\ pent(g \times t)\ N(g)$ and kept simplifying it as long as AIC$_c$ kept decreasing (details in Clobert and Lebreton 1985; Lebreton et al. 1992; Schtickzelle et al. 2003). We estimated the models both for the entire study period and for the "regular marking" period, except for *D. danis* males where only regular marking period data were available.

For comparing average φ and p between the sexes and species we defined models with these parameters constant in time. Then we counted residency time (time from birth or immigration to death or emigration; *rt*) and lifetime probability of capture (within four study plots; *lp*) as $-\ln(\varphi)^{-1}$ and $-\ln(p)^{-1}$, respectively (Cook et al. 1967). Additionally we counted maximum, average and median life span as the time between the first and the last capture.

Analysis of mobility

The total flight distance (D_i) was measured for each butterfly individual i as the sum of distances between the capture and all recapture points (d). Maximum distance recorded (D_{max}) is the highest D_i value for each species. The size and position of plots determines the proportion of movement events for each movement distance which could be detected using our sampling design. The observed frequency of movement distances was adjusted using these probabilities. For this analysis we used distance d (e.g., for an individual caught 4 times we used all three recorded distances). One million points were randomly generated within a simulated forest space including our four study plots. Almost 100,000 of these were inside the four plots. Each such point was assigned a random angle and given distance from 20 m to 1,680 m (i.e., the distance between two most distant points from our study plots; in 20 m increments), simulating random flight of butterflies. Analyses were done separately for 20, 40, 60, … and 1,680 m. The probability (Pc) of this simulated flight ending within a study plot [Electronic Supplementary Material (ESM) S1] was used to correct the number of individuals observed as reaching a particular movement distance (N_{obs}) as follows: $N_{cor} = N_{obs}/Pc$. The mean movement distance between two captures ($\overline{D}_{obs}$) was calculated from the observed numbers of individuals (N_{obs}) reaching movement distances of 20, 40, 60, … m. Likewise, the corrected mean movement distance between two captures ($\overline{D}_{cor}$) was calculated using the corrected (N_{cor}) numbers of individuals (see also Baker et al. 1995; Vlasanek et al. 2013).

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 $I = C \times D^{-m}$, for NEF $I = a \times e^{-k \times D}$ where I is proportion of movements, D is distance and C, m, a and k are constants.

Results

Demography

We marked a total of 3,705, 394 and 317 butterfly individuals belonging to *Danis danis*, *Taenaris* sp. and *Parthenos aspila*, respectively (Table 1). The results for all butterfly species are reported elsewhere (Vlasanek et al. 2013). Population size and other parameters could be estimated for the three focal species, sampled as 118 individuals per day in our study plots (Table 2), but not for rarer species.

The sex ratio of marked butterflies significantly differed from 1.0 in *D. danis* ($SR = 2.5$, $\chi^2 = 674.65$, $P < 0.001$), but not in *Taenaris* sp. ($SR = 1.2$, $\chi^2 = 3.66$, $P > 0.05$) or *P. aspila* ($SR = 1.0$, $\chi^2 = 0.03$, $P > 0.05$). Data used for estimating demography parameters by the JS method are presented in Table 1. The best JS models are shown in Table 3. Capture probabilities were mostly factorially dependent on marking day, while response of survival to time was linear, quadratic or constant. The response of proportional recruitment to time was constant or quadratic. Survival probabilities were >0.9 for all three studied species. The calculated residency time was highest for *P. aspila*, >80 days. Capture probabilities were <0.1 in all three species, highest for *D. danis*, followed by *Taenaris* sp. and *P. aspila*. Lifetime probability of capture ranged between 20 and 40 % for the three species.

The estimated population size of the three focal species together during *regular marking* was approximately 21,000 individuals within the four plots, or approximately 1,500 individuals per hectare, during our study. This included the individuals that had been there before the study started, hatched there or immigrated during the study period. The peak in population size of *D. danis* coincided with a decrease in average wing wear caused by influx of new individuals into the population. The population size in *Taenaris* sp. grew from approximately 50 to approximately 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 reliably documented due to large standard errors of the population size estimations (Fig. 2).

Mobility

Less than one percent of individuals in *Danis danis* and *Parthenos aspila* were likely to fly more than 1 km, while

Table 1 Mark-release-recapture (MRR) data and the subset of data (MARK) used to calculate demographic parameters using the program MARK

Plot	Marked		Recaptured		Captures	
	♂	♀	♂	♀	♂	♀
Danis danis						
MRR data	2,643	1,062	867	164	4,653	1,263
MARK— ♂ and ♀, regular marking	2,362	543	682	51	3,850	608
MARK— ♀, full study		999		157		1,186
MARK—regular marking	2,905		733		4,458	
Taenaris sp.						
MRR data	216	178	67	11	346	191
MARK—regular marking	246		50		320	
MARK—full study	328		60		423	
Parthenos aspila						
MRR data	160	157	16	24	186	193
MARK—regular marking	199		25		234	
MARK—full study	295		39		355	

Recaptures within the same day and captures outside plots were not included in analyses. Regular marking was from 25 April to 5 June 2009, full study from 25 April to 26 June 2009. ♂ and ♀ indicate that analyses were done separately for sexes. Some butterflies were recaptured more than once

Table 2 Recapture rates measured as recaptures/captures (R), average total flight distance ($\overline{D}$), mean movement distance between two captures ($\overline{D}_{obs}$), mean movement distance between two captures corrected for plot size and position ($\overline{D}_{cor}$), and maximum distance recorded (D_{max})

	R	$\overline{D}$	$\overline{D}_{obs}$	$\overline{D}_{cor}$	D_{max}	Captures	Life span Max/average/median
Danis danis	0.37	109	60.4	185.5		102	58/13.0/11.0
♂		117	60.3	186.8	1,313		58/13.3/11.0
♀		63	60.6	173.5	630		58/11.8/10.0
Taenaris sp.	0.27	352	191.5	674.1		8	48/13.8/9.0
♂		342	169.1	537.2	2,482		48/15.2/12.5
♀		408	392.7	947.2	1,437		15/3.7/1.0
Parthenos aspila	0.16	81	60.3	103.4		7	58/25.5/22.5
♂		67	44.0	55.4	374		48/20.7/14.5
♀		90	71.7	121.8	313		58/28.8/28.0

Captures is the average total number of daily captures within the four plots. 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

almost 10 % of individuals were likely to disperse such distances in *Taenaris* spp. (Table 4). These estimates are based on the NEF model which had better support than the IPF model (Table 4). Mean total movement distance between two captures was 60 m for *P. aspila* and *D. danis* and 192 m for *Taenaris* sp. After correction for plot size and position, the mean movement distance between two captures rose almost twice in *P. aspila* and more than three times in *D. danis* and *Taenaris* sp. (Table 2). Movement distances (total and between two captures) are compared with results of 42 studies on temperate butterfly species (Fig. 3, ESM S2). We compared our results with all species, forest species, Lycaenidae and Nymphalidae. *Taenaris* sp. is in most cases above 95 % confidence intervals. *Parthenos aspila* is also beyond the 95 % confidence intervals but contrary to *Taenaris* sp. it is below it. Movement distances (both total and between two capture movement distances) of *Danis danis* is average within Lycaenidae group.

Food plant of *Danis danis*

Forty two *Danis danis* females were tracked and their behavior observed. Individual females were tracked from 4 min to almost 5 h, together 54 h and 40 min. They were mostly resting in shade on leaves and only 8 were observed flying around three *Derris* species (Fabaceae)—*Derris oligosperma*, *D. malaccensis* and *D. elliptica*. Oviposition was not observed but caterpillars were later found only on *D. elliptica*. Mapping of this plant species in a 50 ha

Table 3 Best JS models (with $\Delta AIC_c < 2$) from program MARK during *regular marking* and whole period

Model	AIC_c	ΔAIC_c	NP	$\varphi_♂ \pm$ SE	$rt_♂$	$\varphi_♀ \pm$ SE	$rt_♀$	$p_♂ \pm$ SE	$lp_♂$	$p_♀ \pm$ SE	$lp_♀$	$N_♂ \pm$ SE	$N_♀ \pm$ SE
Danis danis, males and females, regular marking													
$\varphi(g \times T)\ p(g \times t)\ pent(T)\ N(g)$	11,695.0	0.00	82	0.96 ± 0.003	22.44	0.93 ± 0.016	12.97	0.09 ± 0.003	0.42	0.01 ± 0.002	0.23	10,841 ± 720	9,196 ± 1,531
$\varphi(g \times T)\ p(g \times t)\ pent(g + T)\ N(g)$	11,696.9	1.92	83	0.96 ± 0.003	22.39	0.93 ± 0.018	13.62	0.09 ± 0.003	0.41	0.02 ± 0.003	0.24	10,871 ± 726	9,136 ± 1,523
Danis danis, females													
$\varphi(.)\ p(t)\ pent(T^2)\ N(.)$	2,170.4	0.00	54			0.96 ± 0.006	22.16			0.01 ± 0.001	0.22		6,378 ± 703

Model	AIC_c	ΔAIC_c	NP	$\varphi \pm$ SE	rt	$p \pm$ SE	lp	$N \pm$ SE
Danis danis, regular marking								
$\varphi(T^2)\ p(t)\ pent(T^2)\ N(.)$	11,661.8	0.00	44	0.98 ± 0.002	40.00	0.08 ± 0.003	0.40	17,242 ± 1,693
$\varphi(T)\ p(t)\ pent(T^2)\ N(.)$	11,662.0	0.16	43	0.98 ± 0.002	40.00	0.08 ± 0.003	0.40	16,598 ± 1,487
Taenaris sp., regular marking								
$\varphi(.)\ p(t)\ pent(T^2)\ N(.)$	899.9	0.00	40	0.91 ± 0.018	11.03	0.03 ± 0.004	0.28	974 ± 129
$\varphi(T)\ p(t)\ pent(T^2)\ N(.)$	900.3	0.43	41	0.91 ± 0.018	11.03	0.03 ± 0.004	0.28	946 ± 125
$\varphi(.)\ p(t)\ pent(.)\ N(.)$	900.5	0.58	38	0.91 ± 0.019	10.70	0.02 ± 0.002	0.24	941 ± 105
$\varphi(T)\ p(t)\ pent(.)\ N(.)$	901.2	1.32	39	0.91 ± 0.019	10.70	0.02 ± 0.002	0.25	921 ± 106
Taenaris sp.								
$\varphi(.)\ p(t)\ pent(.)\ N(.)$	1,208.8	0.00	51	0.93 ± 0.011	14.59	0.04 ± 0.005	0.31	1,324 ± 133
$\varphi(T)\ p(t)\ pent(.)\ N(.)$	1,210.3	1.50	52	0.93 ± 0.011	14.59	0.04 ± 0.005	0.31	1,310 ± 135
Parthenos aspila, regular marking								
$\varphi(.)\ p(t)\ pent(.)\ N(.)$	553.8	0.00	33	0.98 ± 0.023	59.95	0.02 ± 0.003	0.24	758 ± 187
Parthenos aspila								
$\varphi(T)\ p(t)\ pent(T^2)\ N(.)$	940.2	0.00	51	0.99 ± 0.023	84.46	0.01 ± 0.001	0.22	3,137 ± 2,244

NP number of parameters, φ survival, *rt* residency time, *p* capture probability, *lp* lifetime probability of capture, *N* total population size, *SE* standard errors

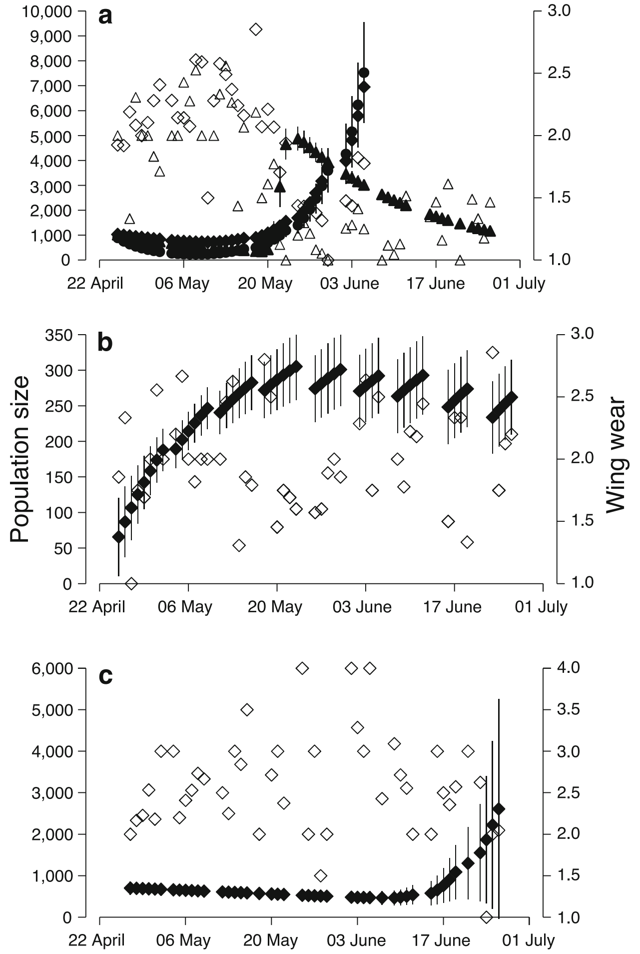

Fig. 2 Daily population size of *Danis danis* (**a**), *Taenaris* spp. (**b**) and *Parthenos aspila* (**c**). *Black symbols* are population sizes, *open symbols* are wing wear of captured butterflies. In *Danis danis*, *diamonds* are males and *circles* (complementary results to males) and *triangles* (results from best model for whole study period) are females. Note that *Danis danis* males were captured for a shorter time than females. *Vertical lines* on the *black symbols* represent standard errors (SE)

botany plot revealed it as a common climber in Wanang (ESM S3).

Discussion

Previous 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 along 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 an understory of a large, relatively homogeneous primary rainforest. Nevertheless it should be noted that the forest in Wanang is more suitable for such a study than many other tropical forests since its understory is relatively open, thus facilitating the capture of butterflies. Further, it also seems to have a higher butterfly density than many other tropical forests, including those in Thailand and Panama (Basset et al. 2011).

Kunte (2008) showed experimentally that high dominance could decrease diversity in butterfly communities. The mechanism suggested in that study was competition over nectar, whilst most species in our understory community feed on rotting fruits (Vlasanek et al. 2013). *Danis danis* was ten times more numerous than the second most abundant species (*Taenaris* sp.), and represented two-thirds of all captures in the entire butterfly community (Vlasanek et al. 2013). 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. It is also possible that butterfly abundance is determined by larval host plants. The high abundance of *D. danis* in our study could be a result of its abundant food plant, which, in addition to being common, is highly poisonous (Leonard 1939), rendering larvae and adults unpalatable to predators (Parsons 1999). Furthermore, not all plant species enjoy the same level of protection by predators and parasitoids of their herbivores (Barbosa et al. 2001; Lill et al. 2002), so it is possible that *D. danis* benefits from exploiting plant species, *Derris* sp., which are less frequented by its natural enemies.

Seasonality is common even in the tropics, where fluctuations in abundance are driven primarily by rainfall (Wolda 1988; Spitzer et al. 1993), although e.g., Molleman et al. (2006) did not find any relationship between seasonal patterns of rainfall and variation in abundance and species richness. For all three species, daily population size was highly variable in time, especially in *D. danis*. 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 on changes in the density of flowering plants or new leaves, which can cause changes in daily population size (Freitas et al. 2001). In temperate areas, population sizes of univoltine and bivoltine species with discrete generations follow a well defined convex trajectory in time. In tropical areas such patterns can also be found (Francini et al. 2005), but overlapping populations of many species open possibilities for greater variability in population dynamics. In *Heliconius* spp., some studies observed stable population sizes (Ehrlich and Gilbert 1973; Ramos and Freitas 1999) whilst others found changing population size throughout 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* are unusual because the high rate of change in abundance suggests many individuals hatching

Table 4 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 (R^2)

Species	IPF/NEF	0.2 km	0.5 km	1 km	5 km	10 km	*c*	*z*	R^2	*F*	*P*
Danis danis	IPF	0.149	0.018	0.004	<0.001	<0.001	0.004	−2.31	0.932	218.8 (1, 16)	***
	NEF	0.194	0.034	0.002	<0.001	<0.001	0.622	−5.82	**0.940**	249.9 (1, 16)	***
♂	IPF	0.163	0.020	0.004	<0.001	<0.001	0.004	−2.26	0.928	205.8 (1, 16)	***
	NEF	0.212	0.038	0.002	<0.001	<0.001	0.665	−5.72	**0.940**	249.0 (1, 16)	***
♀	IPF	0.077	0.012	0.003	<0.001	<0.001	0.003	−2.06	**0.988**	473.2 (1, 6)	***
	NEF	0.130	0.012	<0.001	<0.001	<0.001	0.647	−8.04	0.894	50.6 (1, 6)	***
Taenaris sp.	IPF	0.518	0.199	0.096	0.018	0.009	0.096	−1.05	0.881	148.1 (1, 20)	***
	NEF	0.497	0.288	0.116	<0.001	<0.001	0.715	−1.82	**0.961**	489.5 (1, 20)	***
♂	IPF	0.501	0.185	0.087	0.015	0.007	0.087	−1.09	0.898	150.1 (1, 17)	***
	NEF	0.484	0.280	0.113	<0.001	<0.001	0.697	−1.82	**0.934**	238.5 (1, 17)	***
♀	IPF	0.489	0.288	0.193	0.076	0.051	0.193	−0.58	0.865	38.5 (1, 6)	***
	NEF	0.615	0.400	0.195	0.001	<0.001	0.819	−1.43	**0.958**	137.0 (1, 6)	***
Parthenos aspila	IPF	0.121	0.024	0.007	<0.001	<0.001	0.007	−1.77	0.959	94.3 (1, 4)	***
	NEF	0.183	0.009	<0.001	<0.001	<0.001	1.356	−10.03	**0.972**	138.4 (1, 4)	***
♂	IPF	0.156	0.044	0.017	0.002	0.001	0.017	−1.37	**0.979**	91.5 (1, 2)	*
	NEF	0.230	0.026	0.001	<0.001	<0.001	0.994	−7.31	0.888	15.8 (1, 2)	n.s.
♀	IPF	0.146	0.033	0.010	0.001	<0.001	0.011	−1.64	0.935	42.9 (1, 3)	**
	NEF	0.191	0.008	<0.001	<0.001	<0.001	1.630	−10.72	**0.991**	340.4 (1, 3)	***

Values in bold style show better fit of IPF or NEF. Probability (*P*): *** <0.001; ** <0.01; * <0.05; n.s. >0.05

simultaneously over the course of a few days, without any obvious environmental cue (cf. Beirao et al. 2012). Our study, limited to 2 months, does not allow us to test the impact of the weather or the availability of food resources, or predators and parasitoids. When attacked by herbivores, plants produce volatile compounds that attract predators and parasitoids (Dicke et al. 1990). This system can reduce the number of herbivores by more than 90 % (Kessler and Baldwin 2001). Synchronized populations may suffer less from parasitism if they are able to saturate their parasitoid populations.

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) 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, for some individuals 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 that tropical species lived longer than temperate species based on the data collected in the field, while temperate species live longer in laboratory (cage) experiments. Our data on average life span and residency time support the idea that tropical butterfly species are long lived creatures whose life-span easily exceeds 10 days. This underestimates the actual life span as our study was conducted in a homogeneous habitat that made it easy for butterflies to enter or leave our study plots. However, high values of survival suggest that emigration from study plots was very low.

The mobility of tropical butterfly species has 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. Data on 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 movement characteristics since shorter movements can be recorded much more reliably than longer ones. This problem, common to other MRR studies, has been corrected for here so that we believe our movement results to be more accurate than those provided by previous studies.

In fragmented habitats butterflies tend to stay in suitable patches (Brakefield 1982; Conradt et al. 2001) or even to return to the original capture site (Keller et al. 1966). Based on movement probabilities, short average flight distances, and low frequency of movements from one plot to another, we found *D. danis* and *P. aspila* are much more sedentary species than *Taenaris* sp. Habitat preference may play a role in this lack of mobility. In *P. aspila* higher sedentarity is probably caused by a strong preference to gaps, which in primary forest are often separated by natural barriers of vegetation growth, preventing butterflies from easily

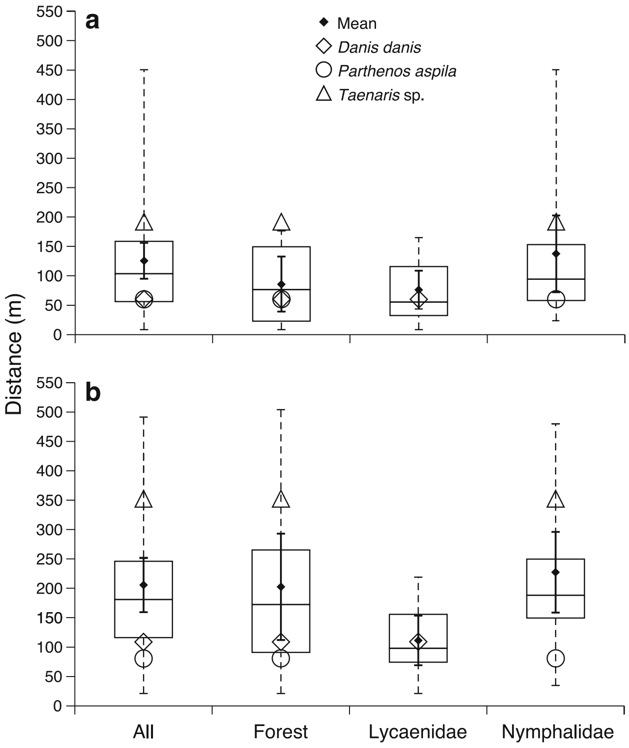

Fig. 3 Box plots for **a** movement distance between captures and **b** total movement distance for 46 temperate butterfly species (data from ESM S2) compared to our three tropical forest species. *Box plots* show three quartiles and minimums and maximums (*dashed lines*). Means are shown with 95 % confidence intervals. When there were more values for one species, the mean value was used. All results ($n = 38$ and $n = 32$ for movement distance between captures and total movement distance, respectively), forest species ($n = 8$ and $n = 12$), Lycaenidae ($n = 11$ and $n = 9$), Nymphalidae ($n = 14$ and $n = 15$)

moving between them. In *D. danis* high sedentarity may be explained by territoriality (in males; it mostly perched on tips of leaves, lurking for females) or the use of restricted home ranges, so far very rarely observed in butterflies. Home range behaviour is exhibited by the genus *Maculinea* (Hovestadt and Nowicki 2008; Korosi et al. 2008) in order to enhance the survival of its myrmecophilous larvae; which benefit from a home range overlapping the radius of an ant colony. But this strategy is not limited to parasitic species; *Heliconius* butterflies also exhibit home range behavior, even in non-fragmented habitats (Turner 1971; Ehrlich and Gilbert 1973), but establish their home range later in life, travelling the greatest distances soon after eclosure (Mallet 1986). Alternatively, low mobility may simply be a suitable response to a high density of both host plants and sexual partners experienced by *D. danis*.

There are only several studies which have measured movement of tropical butterflies, mostly in Central and South America. Movement distances (total and between two captures) ranged from several tens to 400 meters (Ramos and Freitas 1999; Fermon et al. 2003; de-Andrade and Freitas 2005; Francini et al. 2005; Marin et al. 2009; Beirao et al. 2012). One multi-species study reported on average of 369 ± 215 m for 21 nymphalid species (Marini-Filho and Martins 2010). In temperate regions there are dozens of studies measuring movement of butterflies, ranging from several meters to several hundred meters (see ESM S2). Compared to these studies *P. aspila* seems to be relatively sedentary and *Taenaris* sp. relatively mobile. Mobility was not correlated with size in butterfly species in Wanang Conservation Area (Vlasanek et al. 2013), but such correlations exist elsewhere (Sekar 2012). Movement behaviour of butterflies may be influenced by the abundance, fragmentation and spatial distribution of their habitats, larval host plant species, or adult food resources (Schneider 2003). Thus, even the same species may behave differently, depending on its circumstances. For example, movement distance of *Heliconius erato* differed by a factor of four between Ramos and Freitas (1999) and de-Andrade and Freitas (2005).

Tropical vegetation typically has more species at lower population densities than temperate zone vegetation (Wright 2002). As a result, tropical butterflies, particularly those from highly diverse rainforests, should disperse more, or have broader host plant ranges, than temperate species.

Population studies using MMR for adult butterflies are typically completely disconnected from studies of their caterpillars and host plants. As a result, very few mobility parameters have been matched with estimates of the minimum movement required to locate host plants. Such studies are particularly difficult in complex tropical habitats. The mapping of plant resources has to be done on an appropriate spatial scale in order to match movement distances of butterfly species. While the 1 ha plots often used to study tropical forest vegetation are too small for 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 movement distance of most butterfly species. For instance, the mean movement distance of all butterfly species in our study forest in Wanang was 184 m (Vlasanek et al. 2013). *Derris elliptica*, the host plant of *D. danis*, was present in 61 % of all 20 × 20 m squares and therefore spatial isolation of host plants was unlikely to be a limiting factor for this species.

In conclusion, our study shows that tropical butterflies differ from temperate species with their longer life span and overlapping generations. *Danis danis* was exceptional by its high abundance and high short-term population variability. Finally, *D. danis* travelled distances much greater than the distance to the nearest host plant individual, indicating that host plant abundance was probably not a limiting factor even for this monophagous specialist.

However, whether this is universally true needs further investigation, particularly on rare butterfly species that feed on a narrow range of rare host plants, a potentially interesting biological scenario, but a more demanding one than our *D. danis* feeding on *Derris*.

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