Journal of the Lepidopterists' Society
59(2), 2005, 96–106

BIOLOGICAL TRAITS OF FRUGIVOROUS BUTTERFLIES IN A FRAGMENTED AND A CONTINUOUS LANDSCAPE IN THE SOUTH BRAZILIAN ATLANTIC FOREST

MARCIO UEHARA-PRADO [1, 2]

KEITH S. BROWN JR. [2, 3]

AND

ANDRÉ VICTOR LUCCI FREITAS [2, 4]

ABSTRACT. We test whether five biological traits of frugivorous butterflies (Lepidoptera: Nymphalidae) of the Brazilian Atlantic Forest differ between a continuous forest and an adjoining fragmented landscape. Possible fragmentation effects were detected in sex ratio and age structure, but we found no evidence that recapture rates, wing size, or damage in frugivorous butterflies were related to forest fragmentation. Among the possible explanations for the observed patterns, we suggest that 1) the landscape is sufficiently permeable and suitable for maintaining most general biological patterns in butterflies, 2) non-effects might be statistical artifacts, 3) the traits examined are usually not affected by this level of fragmentation, or 4) the most abundant frugivorous butterflies demonstrate some resistance to habitat fragmentation.

Additional key words: fruit-feeding butterflies, forest fragmentation, population biology.

An inevitable result of the expansion of human activities in forested habitats is the reduction of native vegetation and the creation of mosaics of forest remnants within an anthropic matrix. Consequently, severe ecological outcomes in the landscape may be predicted, and have been observed (Bierregaard et al. 2001). Forest fragmentation is currently one of the processes that most contributes to the increasing rates of species extinction and loss of biodiversity (Saunders et al. 1991, Tscharntke et al. 2002).

To help ensure the success of biological conservation, biologists need to understand patterns and processes of changing landscapes, as well as population responses to these large-scale modifications (Collinge 2001). Although many studies treat habitat fragmentation effects in Neotropical environments (reviews in Saunders et al. 1991, Turner 1996, Debinski & Holt 2000, Laurance et al. 2002, Tscharntke et al., 2002), few data exist for the most rich and abundant group of animals in these environments, the insects. Effects of forest fragmentation on populations of insects are still little understood, and the empirical data are diffuse and contradictory (Didham et al. 1996). Bierregaard et al. (1997) point out that basic natural history information is absent for a majority of the Neotropical fauna and is deficient even for groups considered "charismatic", such as butterflies. This scenario is even worse when focused on one of the most endangered Neotropical ecosystems, the Brazilian Atlantic Forest, where only few studies on fragmentation effects on insects have been done (eg. Tonhasca et al. 2002, Brown & Freitas 2003).

Because butterflies are short-lived organisms whose populations respond rapidly to changes in habitat quality (Brown 1991), our objective is to determine if biological traits of Atlantic Forest frugivorous butterflies (Lepidoptera: Nymphalidae) (sex ratio, recapture rates, size, incidence of damage, and age structure) differ between a continuous forest and an adjoining fragmented landscape (data on abundance distribution as well as community patterns will be reported elsewhere). These traits were chosen because they were reported in other population studies on Neotropical butterflies (e.g. Ehrlich & Gilbert 1973, Ehrlich 1984, Freitas 1993, Ramos & Freitas 1999) and are easily recorded, even if their relations to habitat fragmentation are either ambiguous (e.g. Thomas et al. 1998, Davies et al. 2000) or were not evaluated.

METHODS

Study area. The study area is located in the town of Cotia, São Paulo State, SE Brazil (23º35'S - 23º50'S, 46º45'W - 47º15'W). The altitude in the region varies from 800 to 1,000 m, with climate Cwa (humid subtropical with a dry winter, Köppen 1948). The annual mean temperature is 20.4ºC, ranging from 16.5ºC in July to 23.6ºC in February; mean annual rainfall is 1,339 mm (meteorological data for 1962-1992).

The site was originally covered with Atlantic Forest vegetation, classified as montane rainforest (Ururahy et al. 1997). Field work was done in two landscapes (Fig. 1): a continuous forest block (Morro Grande State

[1] Curso de Pós-Graduação em Ecologia, Instituto de Biologia, Universidade Estadual de Campinas CP 6109 CEP 13083-970, Campinas, São Paulo, Brazil email: muprado@yahoo.com; corresponding author
[2] Museu de História Natural e Departamento de Zoologia, Instituto de Biologia, Universidade Estadual de Campinas, CP 6109 CEP 13083-970 Campinas, São Paulo, Brazil.
[3] email: ksbrown@unicamp.br
[4] email: baku@unicamp.br

Reserve) and a mosaic of forest fragments immediately to the west. The Morro Grande State Reserve (23º39'S - 23º50'S, 46º55'W - 47º01'W) is a large block of forest (> 10,000 ha) mostly in advanced stages of succession, containing patches of well-preserved original forest. The fragmented landscape consists of a matrix formed mostly of small farms and orchards, mixed with vegetation in initial stages of regeneration (2 to 8 years) and reforestation of *Eucalyptus* and pine plantations, interspersed with about 35% natural vegetation (data from 1:10,000 aerial photographs from April, 2000).

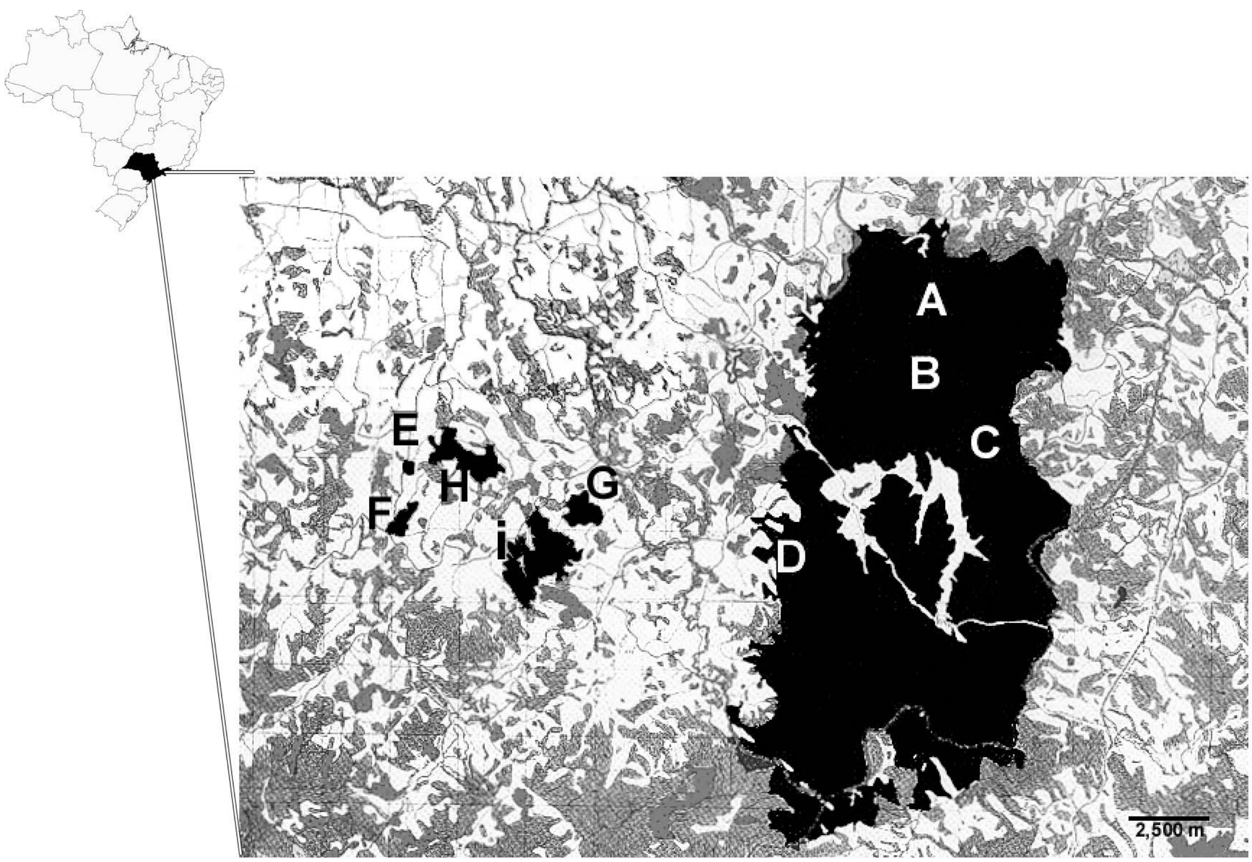
Frugivorous butterflies. Butterflies can be separated into two main guilds, considering the feeding habits of adults (DeVries 1987): 1) nectar-feeding: Papilionidae, Pieridae, Lycaenidae, Hesperiidae, and some subfamilies of Nymphalidae; 2) "frugivorous" nymphalid butterflies, mostly in the satyroid lineage (*sensu* Freitas & Brown 2004): Satyrinae, Brassolinae, Morphinae, Charaxinae, Biblidinae, and the tribe Coeini (Nymphalinae). The so-called "frugivorous butterflies", besides feeding on fermented fruits, also feed on mammal excrement, plant exudates, and carrion (DeVries 1987).

Sampling frugivorous butterflies presents some practical advantages. They can be easily captured in traps containing rotting fruit, which permits simultaneous sampling with standardized effort at different sites. After identification, the majority of the butterflies can be released unharmed and marked, so that recaptures can be evaluated with minimum handling. Moreover, the attraction of butterflies to a food resource reduces the possibility of chance capture, present in other methods (DeVries & Walla 2001, Freitas et al. 2003).

Several nymphalid species in the nectar-feeding guild (including Apaturinae, Limenitidinae and Ithomiinae) are occasionally captured with fermenting baits (DeVries et al. 1999). Since they belong to another guild and may suffer influence from flowers next to the traps, such species have not been considered in this work. A complete illustrated list of the frugivorous butterflies observed in the study area is presented by Uehara-Prado et al. (2004).

Sampling procedures. This study was carried out at nine sites in the two landscapes: four sites inside the Morro Grande State Reserve (called "control", Fig. 1 A-D) and five forest fragments of approximately 14, 29, 52, 99 and 175 ha (Fig. 1 E-I, respectively). Each site received a sampling unit (hereafter SU) of five portable bait traps. Bait traps consisted of cylinders 110 cm high x 35 cm diameter made with dark netting, with an internal cone (22 cm wide at the opening) to prevent

FIG. 1. Location of the study areas in the Morro Grande Reserve (A-D) and in the fragmented landscape (E-I). Source: Kronka et al. (1993).



butterflies from escaping. The cylinder was attached ca. 4 cm above a plywood base, on which the bait was placed (adapted from Shuey 1997).

The traps were placed linearly along pre-existing trails in the understory of each site, suspended 1.8-2.2 m above the ground, with a distance of at least 20 m between adjacent traps and at least 50 m from the forest edge. Each trap was placed in a small, partly sunny clearing large enough to allow butterflies to circle and enter without exposing the bait and butterflies to extreme heat. The average distance between traps did not differ between SUs (Kruskal-Wallis H = 12.75, p = 0.121, df = 8). The use of five spaced traps per SU aimed to average the effects of trap position and bait attractiveness on the probability of butterfly capture (DeVries & Walla 2001).

A standard mixture of mashed banana and sugar cane juice, fermented for at least 48 hours, was used as attractant. The bait was placed inside the traps in plastic pots with a perforated cover to prevent butterflies from drowning in the liquid, to avoid feeding by other insects, and to reduce evaporation (Hughes et al. 1998). The traps were checked every 48 hours, permitting an increase in the number of sample sites (Hughes et al. 1998). The baits were replaced at each visit. The traps were kept in the field 12-14 days for a total of 36,000 trap/hours, with about 10 hours of effective sampling per day. Six samplings were carried out between November 2001 and May 2002, the period most favorable for the capture of frugivorous butterflies in SE Brazil (Brown 1972).

Sampling was done with minimal collecting events to reduce the effect of individual removal over time. Before release, each butterfly received an individual alphanumeric mark made with a felt-tipped pen on the ventral surface of each hind wing (as in Freitas 1993, 1996). We registered the following data for each captured individual: sex, forewing length, wing damage (present or absent), and wing wear (a measure of age: new, intermediate or old; modified from Freitas 1993).

We used G-tests for comparing proportions and Student's t-tests for comparing wing sizes. Data for males and females of each species were analyzed separately when the sample size of each sex allowed this. When multiple comparisons were made, critical values were corrected using the sequential Bonferroni method (Rice 1989).

RESULTS

Seventy species in six subfamilies of Nymphalidae were included in the 1,810 butterflies captured (Table 1, Appendix I). In 14 species (representing 76.6 % of the sampled individuals), the sample was large enough (N > 30) to describe the chosen population measures (Appendix I). Similar analyses with the remaining species were done only when the data were pooled by subfamily.

TABLE 1 Species richness and abundance (individuals captured) of frugivorous butterflies subfamilies (Nymphalidae) sampled in the Morro Grande Reserve (MG) and in the fragmented landscape (FR) from November 2001 to May 2002.

Subfamily	Species richness		Individuals captured	
	MG	FR	MG	FR
Satyrinae	17	20	201	309
Biblidinae	14	17	292	583
Charaxinae	10	14	56	172
Brassolinae	10	9	105	62
Morphinae	2	2	6	15
Nymphalinae: Coeini	1	2	1	8
TOTAL	54	64	661	1,149

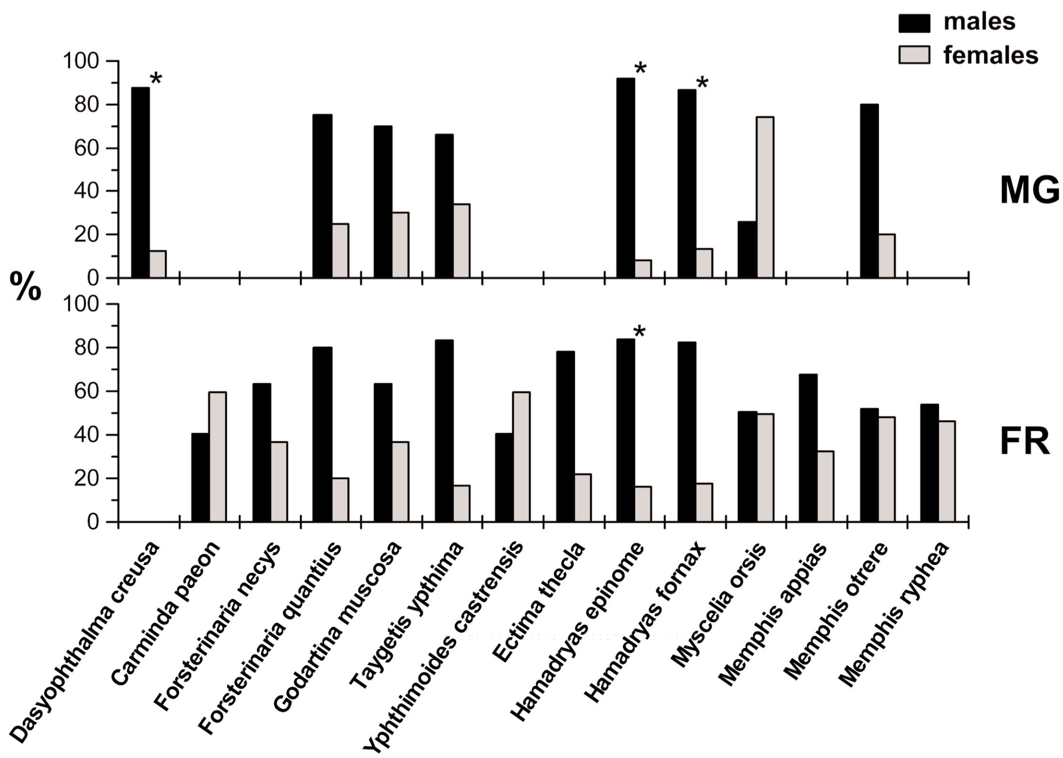
After Bonferroni's correction the sex ratio was significantly different from 1:1 in three species in the reserve and in one species in the fragments (Fig. 2). In the fragments, only *Hamadryas epinome* (Biblidinae) had a male-biased sex ratio. In the reserve, males were more abundant than females in *H. epinome*, *H. fornax*, and *Dasyophthalma creusa* (Brassolinae). When compared between landscapes, females were proportionally more abundant in the fragments (16%) than in the reserve (8%) for *H. epinome* (G = 7.31, df = 1, p = 0.007, N = 538) and proportionally more abundant in the reserve (74%) than in the fragments (50%) for *Myscelia orsis* (Biblidinae) (G = 8.07, df = 1, p = 0.005, N = 158) (critical p value = 0.007).

For both sexes of the four most abundant species and for *Dasyophthalma creusa* males, the recapture rate was similaramong landscapes (Table 2A), varying from 7.5 to 25.8 % in the fragments and from 0 to 28.2 % in the continuous landscape. When compared between landscapes (excluding *Euptychoides castrensis*, whose males were not captured in the reserve), these rates did not differ significantly (Table 2A). Likewise, there were no differences in recaptures between sexes, when each landscape was analyzed separately (Table 2B). Although individuals of some species were observed flying through the matrix in the fragmented landscape and along large roads of the Morro Grande Reserve, recaptures between SUs were not observed in any species in this study.

There were no differences in wing size between landscapes for any analyzed species (Table 3). When wing size was compared between sexes, females were significantly larger than males in 8 of the 14 analyzed species (pooled data from the two landscapes) (Table 4).

Most species showed a homogeneous age structure in both landscapes; that is, there was no predominance of

FIG. 2. Sex ratio of frugivorous butterflies (Nymphalidae) at the Morro Grande Reserve (MG) and at the fragmented landscape (FR) from November 2001 to May 2002. * = Sex ratio significantly different from 1:1 (corrected critical P-value = 0.004).



individuals in any age category. The exceptions to this pattern, all "new"-biased, were males of *Hamadryas epinome* and *Taygetis ypthima* in the reserve, and males of *H. epinome*, *Godartiana muscosa*, and *Memphis appias*, and both sexes of *Myscelia orsis* in the fragments (Table 5A). *Godartiana muscosa* (males) was the only species that showed age structure significantly different between landscapes, with more individuals in "intermediate" and "new" categories in the fragments (G = 11.29, p = 0.004, df = 2, N = 58, corrected critical p-value = 0.013). Conversely, when species were grouped by subfamily, the Satyrinae showed a predominance of individuals in "intermediate" and "old" categories in the fragments (Table 5B).

The percentage of individuals with wing damage for the nine most abundant species ranged from 0 to 30.8% in the reserve and from 4.6 to 37.5% in the fragments. Damage frequency was not different between landscapes, either when species were considered separately or grouped by subfamily (Table 6 A, B). The subfamilies showed different damage ratios, both in the reserve (G = 26.61, p < 0.001, df = 3, N = 636) and in the fragments (G = 27.83, p < 0.001, df = 3, N = 1,106), with the highest damage ratios in Brassolinae in both landscapes (corrected critical p-value = 0.013)

DISCUSSION

Population Biology. Contrary to many field studies carried out with butterfly populations (e.g., Gilbert & Singer 1975, Ehrlich 1984, Tyler et al. 1994), the sex ratio observed for most species in this study was not male-biased; recapture rates also did not differ between sexes. In most studies that sampled butterflies with nets, male-biased sex ratios result in part from differences in butterfly behaviors, with males flying in the same places frequented by lepidopterists (open tracks, with elevated light incidence and large space for flight), and females more dispersed in the habitat, searching for host plants (e.g. Ehrlich 1984, Freitas 1996, Ramos & Freitas 1999). The use of traps in the present study may minimize this bias due to the use of a food resource attractive to both sexes and independence from collector efficiency. Nonetheless, more mark-recapture studies are necessary to evaluate if, and by how much, the sex ratio is biased in different butterfly species.

The recapture rates found in this study - always less than 30% in both landscapes - might be attributed to particular characteristics of each species, such as large population size, flight ability, relatively short life span, or

TABLE 2 Recapture of frugivorous butterflies species (Nymphalidae) in the Morro Grande Reserve (MG) and in the fragmented landscape (FR) from November 2001 to May 2002. **A**. Comparisons among landscapes. **B**. Comparisons among sexes. BRA = Brassolinae, SAT = Satyrinae, BIB = Biblidinae, Subf = Subfamily.

A) Species	Subf.	Sex	Morro Grande Reserve		Fragmented landscape		MG x FR	
			Capture	Recapture (%)	Capture	Recapture (%)	G-test	*P*
Dasyophthalma creusa	BRA	♂	33	1 (3.03)	18	3 (16.7)	2.50	0.114
Godartiana muscosa	SAT	♂	26	6 (23.1)	31	8 (25.8)	0.06	0.815
		♀	9	2 (22.2)	18	2 (11.1)	0.02	0.899
Hamadryas epinome	BIB	♂	163	46 (28.2)	283	60 (21.2)	2.76	0.097
		♀	15	2 (13.3)	48	8 (16.7)	0.09	0.763
Myscelia orsis	BIB	♀	28	1 (3.6)	51	4 (7.8)	0.55	0.460

B) Species	Subf.	Morro Grande Reserve		Fragmented landscape	
		G-test	*P*	G-test	*P*
Godartiana muscosa	SAT	0.00	0.960	1.54	0.215
Euptychoides castrensis	SAT	-	-	0.02	0.876
Hamadryas epinome	BIB	1.69	0.194	0.53	0.467
Myscelia orsis	BIB	-	-	1.39	0.239

TABLE 3 Wing size of frugivorous butterflies (Nymphalidae) sampled in the Morro Grande Reserve and in the fragmented landscape from November 2001 to May 2002: comparisons among landscapes. Abbreviations as in Table 2 legend. CHA = Charaxinae. * Corrected critical *P*-value = 0.004

Species	Subf.	Sex	Morro Grande Reserve			Fragmented landscape			MG x FR		
			$\bar{x}$ (mm)	SE	N	$\bar{x}$ (mm)	SE	N	*t*-test	df	*P**
Dasyophthalma creusa	BRA	♂	45.44	0.24	39	45.44	0.27	25	0.02	55.4	0.991
Forsterinaria necys	SAT	♂	24.00	0.62	7	24.04	0.28	26	0.06	8.6	0.956
Forsterinaria quantius	SAT	♂	25.19	0.22	26	25.13	0.69	8	0.09	8.5	0.95
Godartiana muscosa	SAT	♂	22.33	0.35	30	23.58	0.37	36	2.45	63.9	0.017
		♀	23.91	0.60	11	25.87	0.34	23	2.86	16.8	0.011
Taygetis ypthima	SAT	♂	36.65	0.27	31	35.78	0.28	9	2.23	24.7	0.035
Euptychoides castrensis	SAT	♀	20.20	0.37	5	19.51	0.19	47	1.64	6.3	0.151
Hamadryas epinome	BIB	♂	36.06	0.15	156	35.95	0.09	262	0.62	258.8	0.534
		♀	37.67	0.29	15	36.96	0.20	47	2.03	28.7	0.052
Hamadryas fornax	BIB	♂	36.62	0.26	26	36.46	0.25	28	0.42	51.8	0.680
		♀	37.75	0.48	4	36.80	0.20	5	1.83	4.1	0.140
Myscelia orsis	BIB	♂	24.60	0.65	10	25.58	0.15	57	1.46	9.9	0.178
		♀	27.27	0.29	30	27.13	0.26	53	0.35	58.5	0.730

territoriality. In the present work, it is not possible to identify which of these factors could account for the observed pattern. Recapture rates may also be a result of the capture method employed, which may have been "traumatic" for certain species. Morton (1982) found that handling changed recapture rates in four of the five species studied, all captured with nets. Mallet et al. (1987) demonstrated that capture and handling reduce the tendency of *Heliconius* butterflies to return to the capture site in the days following marking, while maintaining their presence in another part of their living area. However, Hughes et al. (1998) found no evidence for either 'trap-happiness' or 'trap-recognition' for frugivorous butterflies in Costa Rica. In the present

Table 4. Wing size of frugivorous butterflies (Nymphalidae) sampled in the Morro Grande Reserve and in the fragmented landscape from November 2001 to May 2002: comparisons among sexes (both landscapes pooled). Bold numbers represent significant *p* values (after Bonferroni's correction). Abbreviations as in Table 2 legend. CHA = Charaxinae. *Corrected critical *P*-value = 0.004

Species	Subf	♂			♀			♂ x ♀		
		x (mm)	SE	N	x (mm)	SE	N	*t*-test	df	*P**
Dasyophthalma creusa	BRA	45.44	0.17	64	52.25	0.47	8	14.01	9.3	**< 0.001**
Moneuptychia paeon	SAT	19.89	0.36	12	18.79	0.18	19	0.32	16.65	0.378
Forsterinaria necys	SAT	24.03	0.25	33	25.47	0.31	15	3.62	32.7	**0.001**
Forsterinaria quantius	SAT	25.09	0.26	34	26.55	0.37	11	3.25	20.9	**0.004**
Godartiana muscosa	SAT	23.02	0.27	66	25.24	0.34	34	5.18	73.3	**< 0.001**
Taygetis ypthima	SAT	36.70	0.38	40	37.89	0.34	18	2.32	51.22	0.012
Euptychoides castrensis	SAT	18.63	0.26	27	19.58	0.18	52	3.04	50.6	**0.004**
Ectima thecla	BIB	21.68	0.24	25	21.56	0.34	9	0.30	16.41	0.383
Hamadryas epinome	BIB	35.99	0.08	418	37.13	0.17	62	6.08	90.7	**< 0.001**
Hamadryas fornax	BIB	36.54	0.18	54	37.22	0.28	9	2.07	15.8	0.055
Myscelia orsis	BIB	25.43	0.16	67	27.30	0.23	83	6.57	139.8	**< 0.001**
Memphis appias	CHA	29.95	0.47	19	31.40	1.06	10	1.26	12.64	0.116
Memphis otrere	CHA	30.00	0.81	16	32.27	0.53	15	2.34	25.5	0.027
Memphis ryphea	CHA	29.82	0.62	22	31.88	0.28	17	3.03	29.02	**0.003**

study, the long time between visits to the traps (48 hours) along with butterfly handling might have contributed to many individuals acquiring aversion to the trap ('trap shyness').

In many cases, we observed frugivorous butterflies flying through the matrix and along the main open roads in the Reserve. Thus, the lack of recaptures between SUs could be a result of large numbers of butterflies present in the study area together with the small probability of recaptures of the individuals, not a result of the impermeability of the matrix or low mobility of these butterflies.

The regularity of age structure probably reflects continuous reproduction with overlapping generations in the majority of the analyzed species (unpublished data). As new individuals are continuously being added to the population, the presence of all ages, from 'new' to 'old' is expected. For species in which individuals are added at a greater rate, the accumulation of individuals of the 'new' category would be proportionally greater than the others, as observed in some cases (Table 5; see also Freitas 1993).

The higher wing damage rates of the subfamily Brassolinae may reflect only their large size, characteristic of many species of this subfamily. A simple explanation would be that these individuals are more damaged because they collide more often with the vegetation. The same trait may make them both conspicuous targets for predators and more likely to escape a predator attack. Another explanation for the large damage rates would be the aggressiveness of some species (Brown 1992, Freitas et al. 1997, Srygley & Penz 1999).

Fragmentation effects. The sex ratio of the two most abundant species in both landscapes, *Hamadryas epinome* and *Myscelia orsis*, showed different patterns between the landscapes; *H. epinome* showed a higher proportion of females in the fragments, whereas in *M. orsis* more females were recorded in the reserve. Some studies have shown that density of males, quantity of host plant, and reduction or increase of competitors and predators can result in biased sex ratios (Shapiro 1970, Blau 1980, Peterson 1997).

The large number of Satyrinae in 'intermediate' and 'old' age categories in the fragments indicates some fragmentation effect on the wing wear in this subfamily. Possible explanations could be that individuals in the fragments age faster, live longer, or both. Another explanation could be the increase in individual activity in fragmented landscapes. This increase may be related to a higher light incidence and consequently higher temperature in the fragments, a well-known fragmentation effect (see Turton & Freiburger 1997). Because most satyrines in the study sites fly in the lower forest strata, an increase in temperature and light level associated with fragmentation could be more important for the individuals of this subfamily. The pattern observed in *G. muscosa*, with individuals tending to 'new' in the fragments is divergent in the subfamily Satyrinae, and should be studied in more detail.

We detected possible effects of forest fragmentation only in sex ratio and age structure; we found no

TABLE 5. Age structure of frugivorous butterflies (Nymphalidae) sampled in the Morro Grande Reserve and in the fragmented landscape from November 2001 to May 2002. A. Males vs. females. B. Comparison among landscapes, pooled by subfamilies. Bold numbers represent significant p values (after Bonferroni's correction). Abbreviations as in Tab. 2 legend. Int = Intermediate, CHA = Charaxinae. ° Corrected critical *P*-value: Fragments = 0.01; Reserve = 0.005; °° Corrected critical *P*-value = 0.013

A) Species	Subf.	Sex	Morro Grande Reserve					Fragmented landscape				
			New	Int	Old	G-test	*P*°	New	Int	Old	G-test	*P*°
Dasyophthalma creusa	BRA	♂	8	22	9	4.27	0.118	7	13	7	1.23	0.540
		♀	6	0	0	-	-	-	-	-	-	-
Moneuptychia paeon	SAT	♂	1	0	0	-	-	2	4	7	1.53	0.466
		♀	-	-	-	-	-	10	8	1	5.35	0.069
Forsterinaria necys	SAT	♂	4	2	2	-	-	9	13	4	2.64	0.267
		♀	-	-	-	-	-	10	5	0	-	-
Forsterinaria quantius	SAT	♂	19	6	2	9.07	0.011	2	5	1	-	-
		♀	1	6	2	-	-	2	0	0	-	-
Godartiana muscosa	SAT	♂	4	13	5	2.78	0.249	20	15	1	13.33	**0.001**
		♀	4	7	0	-	-	7	12	3	3.02	0.221
Taygetis ypthima	SAT	♂	27	2	6	15.67	**<0.001**	7	3	0	-	-
		♀	13	4	1	7.01	0.030	0	0	0	-	-
Euptychoides castrensis	SAT	♂	-	-	-	-	-	7	11	15	1.51	0.469
		♀	2	2	1	-	-	13	26	0	35.44	**< 0.001**
Memphis appias	CHA	♂	0	0	1	-	-	18	2	1	13.01	**0.002**
		♀	-	-	-	-	-	3	5	2	-	-
Memphis otrere	CHA	♂	1	0	3	-	-	7	7	1	3.58	0.167
		♀	1	0	0	-	-	9	3	2	2.86	0.239
Memphis ryphea	CHA	♂	-	-	-	-	-	15	4	3	5.56	0.062
		♀	1	0	0	-	-	14	3	1	8.27	0.016
Ectima thecla	BIB	♂	0	0	0	-	-	23	2	0	-	-
		♀	2	0	0	-	-	7	0	0	-	-
Hamadryas epinome	BIB	♂	99	46	28	22.84	**< 0.001**	197	61	36	72.38	**< 0.001**
		♀	14	1	0	-	-	46	2	0	-	-
Hamadryas fornax	BIB	♂	23	3	0	-	-	17	11	0	-	-
		♀	0	0	0	-	-	3	3	0	-	-
Myscelia orsis	BIB	♂	8	1	1	-	-	43	12	2	27.04	**< 0.001**
		♀	16	12	4	4.30	0.117	30	21	4	12.99	**< 0.001**

B) Subfamily	Morro Grande Reserve			Fragmented landscape			MG x FR	
	New	Int	Old	New	Int	Old	G-test	*P*°°
Brassolinae	39	39	18	15	25	17	4.11	0.128
Satyrinae	114	57	26	116	137	48	18.77	**< 0.001**
Charaxinae	39	5	9	103	40	24	5.93	0.052
Biblidinae	180	70	35	403	125	47	5.27	0.072

TABLE 6 Wing damage in frugivorous butterflies (Nymphalidae) in the Morro Grande Reserve and in the fragmented landscape sampled from November 2001 to May 2002. A. Most abundant species. B. Data pooled by subfamily. Abbreviations as in Tab. 2 legend. * Corrected critical *P*-value = 0.004. ** Corrected critical *P*-value = 0.013

A) Species	Subf	Sex	% damaged (n)		MG x FR	
			MG	FR	G-test	*P**
Dasyophthalma creusa	BRA	♂	5.9 (39)	5.9 (27)	0.00	0.982
Forsterinaria necys	SAT	♂	25.0 (8)	7.7 (26)	1.53	0.216
Forsterinaria quantius	SAT	♂	11.1 (27)	37.5 (8)	2.65	0.104
Godartiana muscosa	SAT	♂	18.2 (33)	13.9 (36)	0.24	0.627
		♀	10.0 (11)	4.6 (22)	0.25	0.616
Taygetis ypthima	SAT	♂	5.7 (35)	30.0 (10)	3.85	0.500
Euptychoides castrensis	SAT	♀	20.0 (5)	12.5 (48)	0.20	0.655
Hamadryas epinome	BIB	♂	28.0 (175)	21.0 (296)	2.99	0.084
		♀	13.3 (15)	8.3 (48)	0.31	0.580
Hamadryas fornax	BIB	♂	30.8 (26)	25.0 (28)	0.22	0.636
Myscelia orsis	BIB	♂	0.0 (10)	13.8 (58)	2.72	0.099
		♀	21.9 (32)	19.3 (57)	0.08	0.772

B) Subfamily	% damaged (n)		MG x FR	
	MG	FR	G-test	*P***
Brassolinae	41.7 (96)	45.6 (57)	0.23	0.634
Satyrinae	14.2 (197)	14.4 (306)	0.00	0.959
Charaxinae	19.0 (58)	24.0 (167)	0.63	0.428
Biblidinae	23.5 (285)	18.4 (576)	3.04	0.081

evidence that recapture rates, wing size, or damage in frugivorous butterflies are related to fragmentation. Among the possible explanations for the observed pattern, we suggest that 1) even though the environment was modified more than 100 years ago, due to land-use rules of the region the landscape continues to be sufficiently permeable and suitable for maintaining most general biological patterns for long periods of time in butterflies; 2) many of the non-effects found in this study could be statistical artifacts, due to the conservative analyses we used; 3) most of the traits chosen in this study are usually not affected by this level of fragmentation, or 4) the commonest frugivorous butterflies could be in some degree resistant to habitat fragmentation (at least for the traits used in this study).

Frugivorous butterflies are easy (and inexpensive) to sample and identify, are potentially 'charismatic' to nonscientists and could be used in monitoring programs by nonspecialists. However, basic natural history studies on this group are virtually absent for the Brazilian Atlantic Forest species. The data presented here should serve as a guideline for future work, either with population biology or with fragmentation effects in this butterfly group.

ACKNOWLEDGEMENTS

This study was conducted as part of an MSc project on Ecology in the Universidade Estadual de Campinas (Unicamp). We would like to thank W. W. Benson for critically reading the manuscript. The Companhia de Saneamento Básico do Estado de São Paulo (Sabesp), represented by José Roberto Náli, and the Instituto Florestal de São Paulo facilitated field work in Morro Grande. We would like to thank Jean Paul Metzger for the opportunity to take part in his project and Jean Paul Metzger and Luciana Alves for helping in diverse phases of the work and providing data on landscape and vegetation of the region. The Meteorological station of Eletropaulo - Eletricidade de São Paulo S.A. provided climatic data. MU-P and AVLF also thank the Fundação de Amparo a Pesquisa do Estado de São Paulo (FAPESP) for fellowships (00/14717-4 to MU-P; 00/01484-1 and 04/05269-9 to AVLF), and the United States National Science Foundation (NSF DEB-0316505 to AVLF). This research is part of two Biota/FAPESP thematic projects: 98/05101-8 and 99/05123-4.

LITERATURE CITED

BIERREGAARD JR, R. O., W. F.LAURANCE, J. W. SITES, A. J. LYNAM, R. K. DIDHAM, M. ANDERSEN, C. GASCON, M. D. TOCHER, A. P. SMITH, V. M. VIANA, T. E. LOVEJOY, K. E. SIEVING, E. A. KRAMER, C. RESTREPO & C. MORITZ. 1997. Key priorities for the study of fragmented tropical ecosystems, pp 515-525. *In* Laurance, W. F. & R. O. Bierregaard (eds.), Tropical forest remnants: ecology, management, and conservation of fragmented communities. University of Chicago Press, Chicago & London.

BIERREGAARD JR., R. O., W. F. LAURANCE, C. GASCON, J., BENITEZ-MALVIDO, P. M. FEARNSIDE, C. R. FONSECA, G. GANADE, J. R. MALCOLM, M. B. MARTINS, S. MORI, M. OLIVEIRA, J. RANKIN-DE

MÉRONA, A. SCARIOT, W SPIRONELLO. & B. WILLIAMSON. 2001. Principles of forest fragmentation and conservation in the Amazon, pp. 371-385. *In* Bierregaard, R. O., C. Gascon, T. E. Lovejoy & Mesquita, R. (eds.), Lessons from Amazonia: the ecology and conservation of a fragmented forest. Yale University Press, New Haven.

BLAU, W. S. 1980. The effect of environmental disturbance on a tropical butterfly population. Ecology 61:1005-1012.

BROWN Jr., K. S. 1972. Maximizing daily butterfly counts. J. Lepid. Soc. 26: 183-196.

——. 1991. Conservation of neotropical environments: insects as indicators, pp. 349-404. *In* Collins, N. M. & Thomas, J. A. (eds.), The conservation of insects and their habitats. Academic Press, London.

——. 1992. Borboletas da Serra do Japi: diversidade, habitats, recursos alimentares e variação temporal, pp. 142-186. *In* Morellato, L. P. C. (ed.), História natural da Serra do Japi: ecologia e preservação de uma área florestal no sudeste do Brasil. Editora Unicamp, Campinas.

——. & A. V. L. FREITAS. 2003. Butterfly communities of urban forest fragments in Campinas, São Paulo, Brazil: structure, instability, environmental correlates, and conservation. J. Insect Conserv. 6:217-231.

COLLINGE, S. K. 2001. Introduction: spatial ecology and biological conservation. Biol. Cons. 100:1-2.

DAVIES, K. F., C. R. MARGULES & J. F. LAWRENCE. 2000. Which traits of species predict population declines in experimental forest fragments? Ecology 81:1450-1461.

DEBINSKI, D. M. & R. D. HOLT. 2000. A survey and overview of habitat fragmentation experiments. Cons. Biol. 14:342-355.

DEVRIES, P. J. 1987. The butterflies of Costa Rica and their natural history: Papilionidae, Pieridae, and Nymphalidae. Princeton University Press, Princeton. 327 pp.

——, T. R. WALLA & H. F. GREENEY. 1999. Species diversity in spatial and temporal dimensions of a fruit-feeding butterfly community from two Ecuadorian rainforests. Biol. J. Linn. Soc. 68:333-353.

——. & T. R. WALLA. 2001. Species diversity and community structure in Neotropical fruit-feeding butterflies. Biol. J. Linn. Soc. 74:1-15.

DIDHAM, R. K., J. GHAZOUL, N. E. STORK & A. J. DAVIS. 1996. Insects in fragmented forests: a functional approach. TrEE. 11:255-260.

EHRLICH, P. R. 1984. The structure and dynamics of butterfly populations, pp. 25-40. *In* Vane-Wright R. I. & P. R. Ackery (eds.), The Biology of Butterflies. Academic Press, London.

——. & L. E. GILBERT. 1973. Population structure and dynamics of the tropical butterfly *Heliconius ethilla*. Biotropica 5:69-82.

FREITAS, A. V. L. 1993. Biology and population dynamics of *Placidula euryanassa*, a relict ithomiine butterfly (Lepidoptera: Ithomiinae). J. Lepid. Soc. 47:87-105.

——. 1996. Population biology of *Heterosais edessa* (Nymphalidae: Ithomiinae). J. Lepid. Soc. 50:273-289.

——, W. W. BENSON, O. J. MARINI-FILHO & R. M. CARVALHO. 1997. Territoriality by the dawn's early light: the Neotropical butterfly *Caligo idomenaeus* (Nymphalidae: Brassolinae). J. Res. Lepid. 34:14-20.

——, R. B. FRANCINI & K. S. BROWN JR. 2003. Insetos como indicadores ambientais, pp. 125-151. *In* Cullen Jr., L., C. Valladares-Pádua & R. Rudran (eds.), Métodos de estudos em biologia da conservação e manejo da vida silvestre. Editora da UFPR, Fundação O Boticário de Proteção à Natureza, Curitiba.

——. & K. S. BROWN JR. 2004. Phylogeny of the Nymphalidae (Lepidoptera). Syst. Biol. 53:363-383.

GILBERT, L. E. & M. C. SINGER. 1975. Butterfly ecology. Annu. Rev. Ecol. Syst. 6: 365-397.

HUGHES, J. B., G. C. DAILY & P. R. EHRLICH. 1998. Use of bait traps for monitoring of butterflies (Lepidoptera: Nymphalidae). Rev. Biol. Trop. 46:697-704.

KÖPPEN, W. 1948. Climatologia. Fondo de Cultura Económica, México. 478 pp.

KRONKA, F. J. N., C. K. MATSUKUMA, M. A. NALON, H. D. CALIL, M. ROSSI, I. F. A. MATTOS & A. A. B. PONTINHA. 1993. Inventário Florestal do Estado de São Paulo. SMA/CINP/Instituto Florestal, São Paulo. 199 pp.

LAURANCE, W. F., T. E. LOVEJOY, H. L. VASCONCELOS, E. M. BRUNA, R. K. DIDHAM, P. C. STOUFFER, C. GASCON, R. O. BIERREGAARD JR, S. G. LAURANCE & E. SAMPAIO. 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. Cons. Biol. 16:605-618.

MALLET, J., J. T. LONGINO, D. MURAWSKI, A. MURAWSKI & A. SIMPSON DE GAMBOA. 1987. Handling effects in *Heliconius*: where do all the butterflies go? J. Anim. Ecol. 56:377-386.

MORTON, A. C. 1982. The effects of marking and capture on recapture frequencies of butterflies. Oecologia 53:105-110.

PETERSON, M. A. 1997. Host plant phenology and butterfly dispersal: causes and consequences of uphill movement. Ecology 78:167-180.

RICE, W. W. 1989. Analyzing tables of statistical tests. Evolution 43:223-225.

RAMOS, R. R. & A. V. L. FREITAS. 1999. Population biology and wing color variation in *Heliconius erato phyllis* (Nymphalidae). J. Lepid. Soc. 53:11-21.

SAUNDERS, D. A., R. J. HOBBS & C. R. MARGULES. 1991. Biological consequences of ecosystem fragmentation: a review. Cons. Biol. 5:18-32.

SHUEY, J. A. 1997. An optimized portable bait trap for quantitative sampling of butterflies. Trop. Lepid. 8:1-4.

SHAPIRO, A. M. 1970. The role of sexual behavior in density-related dispersal of pierid butterflies. Amer. Nat. 104:367-372.

SRYGLEY, R. B. & C. M. PENZ 1999. Lekking in neotropical owl butterflies, *Caligo illioneus* and *C. oileus* (Lepidoptera : Brassolinae). J. Insect Behav. 12:81-103.

THOMAS C. D., J. K. Hill & O. T. Lewis. 1998. Evolutionary consequences of habitat fragmentation in a localized butterfly. J. Anim. Ecol. 67:485-497.

TONHASCA, A., J. L. BLACKMER & G.S. ALBUQUERQUE. 2002. Abundance and diversity of euglossine bees in the fragmented landscape of the Brazilian Atlantic forest. Biotropica 34:416-422.

TSCHARNTKE, T., I. STEFFAN-DEWENTER, A. KRUESS, C. THIES. 2002. Characteristics of insect populations on habitat fragments: a mini review. Ecol. Res. 17:229-239.

TURNER, I. M. 1996. Species loss in fragments of tropical rain forest: a review of the evidence. J. Appl. Ecol. 33:200-209.

TURTON, S. M. & H.J. FREIBURGER. 1997. Edge and aspect effects on the microclimate of a small tropical forest remnant on the Atherton Tableland, northeast Australia, pp. 45-54. *In* Laurance, W. F. & R. O. Bierregaard (eds.), Tropical forest remnants: ecology, management, and conservation of fragmented communities. University of Chicago Press, Chicago & London.

TYLER, H. A., K.S. BROWN JR. & K. H. WILSON. 1994. Swallowtail butterflies of the Americas. A study in biological dynamics, ecological diversity, biosystematics and conservation. Scientific Publishers, Gainesville. 376 pp.

UEHARA-PRADO, M., A. V. L. FREITAS, R. B. FRANCINI & K. S. BROWN JR. 2004. Guia das Borboletas Frugívoras da Reserva Estadual do Morro Grande e região de Caucaia do Alto, Cotia (São Paulo). Biota Neotropica 4:1-25. http://www.biotaneotropica.org.br/v4n1/pt/abstract?inventory+BN00504012004 (accessed 15 January 2005).

URURAHY, J. C., J. E. R. COLLARES, M. M. SANTOS & R. A. A. BARRETO. 1987. Vegetação, pp. 553-611. *In* Projeto RADAMBRASIL, Vol. 32, fls. SF 23-24 (Rio de Janeiro e Vitória). Ministério das Minas e Energia, Brasília.

Received for publication 13 July 2004; revised and accepted 31 March 2005

Appendix I. Frugivorous butterfly (Nymphalidae) sampled in the Morro Grande Reserve and in the fragmented landscape from November 2001 to May 2002. MOR = Morphinae, BRA = Brassolinae, SAT = Satyrinae, BIB = Biblidinae, CHA = Charaxinae, COE = Nymphalinae, Coeini. nd = individuals whose sex could not be determined (abdomen missing due to predation in traps).

		Morro Grande Reserve				Fragmented landscape			
Species	Subf.	♂	♀	nd	Total	♂	♀	nd	Total
Morpho achilles	MOR	0	0	1	1	0	5	0	5
Morpho catenarius	MOR	3	1	1	5	7	1	2	10
Caligo arisbe	BRA	1	4	1	6	3	0	0	3
Caligo beltrao	BRA	3	0	0	3	1	0	0	1
Caligo eurilochus	BRA	1	0	0	1	4	0	0	4
Caligo illioneus	BRA	1	0	0	1	0	0	0	0
Dasyophthalma creusa	BRA	42	8	0	50	29	0	2	31
Dasyophthalma rusina	BRA	0	0	1	1	0	0	0	0
Eriphanes reevesi	BRA	12	7	1	20	2	3	0	5
Narope cyllarus	BRA	0	0	0	0	1	0	0	1
Opoptera aorsa	BRA	1	2	0	3	2	1	0	3
Opoptera syme	BRA	10	0	1	11	10	2	1	13
Opsiphanes invirae	BRA	7	0	2	9	1	0	0	1
Archeuptychia cluena	SAT	11	2	1	14	5	2	1	8
Moneuptychia griseldis	SAT	0	0	0	0	0	2	0	2
Moneuptychia paeon	SAT	1	0	0	1	13	19	3	35
Eteona tisiphone	SAT	1	1	0	2	1	5	0	6
"Euptychia" pronophila	SAT	0	0	0	0	0	1	0	1
Forsterinaria necys	SAT	8	0	0	8	26	15	3	44
Forsterinaria quantius	SAT	27	9	2	38	8	2	0	10
Godartiana muscosa	SAT	31	11	2	44	23	36	1	60
Hermeuptychia hermes	SAT	1	0	0	1	6	0	1	7
Moneuptychia soter	SAT	0	1	0	1	6	2	2	10
Pareuptychia ocirrhoe	SAT	0	0	0	0	1	0	0	1
Paryphthimoides phronius	SAT	0	1	0	1	1	0	0	1
Splendeuptychia ambra	SAT	6	1	0	7	0	0	0	0
Splendeuptychia doxes	SAT	2	1	0	3	11	7	2	20
Splendeuptychia hygina	SAT	6	0	0	6	0	0	0	0
Taygetis acuta	SAT	8	1	0	9	1	0	0	1
Taygetis ypthima	SAT	35	19	2	56	10	2	1	13
Taygetis laches	SAT	3	0	1	4	1	0	0	1
Taygetis virgilia	SAT	0	1	0	1	1	0	0	1
Yphthimoides angularis	SAT	0	0	0	0	1	0	0	1
Euptychoides castrensis	SAT	0	5	0	5	33	48	5	86
Callicore sorana	BIB	0	0	0	0	1	0	0	1
Catonephele acontius	BIB	0	1	0	1	0	0	0	0
Catonephele numilia	BIB	3	3	0	6	6	1	0	7

APPENDIX 1. continued

Species	Subf.	Morro Grande Reserve				Fragmented landscape			
		♂	♀	nd	Total	♂	♀	nd	Total
Diaethria candrena	BIB	0	1	0	1	0	1	0	1
Diaethria clymena	BIB	0	0	0	0	1	1	1	3
Ectima thecla	BIB	0	2	0	2	25	7	1	33
Epiphile huebneri	BIB	0	0	0	0	4	0	0	4
Epiphile orea	BIB	0	4	0	4	4	4	0	8
Eunica eburnea	BIB	1	0	0	1	0	0	0	0
Hamadryas amphinome	BIB	3	0	0	3	10	2	0	12
Hamadryas arete	BIB	1	0	0	1	3	2	0	5
Hamadryas epinome	BIB	174	15	5	194	294	48	4	346
Hamadryas februa	BIB	3	0	0	3	4	1	0	5
Hamadryas feronia	BIB	0	0	0	0	2	1	0	3
Hamadryas fornax	BIB	26	4	0	30	28	6	0	34
Hamadryas iphthima	BIB	2	0	0	2	3	0	0	3
Myscelia orsis	BIB	11	32	0	43	58	55	2	115
Paulogramma pyracmon	BIB	0	0	0	0	1	1	0	2
Temenis laothoe	BIB	1	0	0	1	1	0	0	1
Consul fabius	CHA	0	0	0	0	1	1	0	2
Hypna clytemnestra	CHA	3	5	1	9	8	9	0	17
Memphis appias	CHA	1	0	0	1	21	10	0	31
Memphis arginussa	CHA	3	0	0	3	4	3	0	7
Memphis morvus	CHA	0	0	0	0	3	0	1	4
Memphis otrere	CHA	4	1	0	5	15	14	0	29
Memphis philumena	CHA	0	1	0	1	1	0	0	1
Memphis ryphea	CHA	0	1	0	1	22	19	1	42
Prepona amphimachus	CHA	14	2	0	16	5	0	1	6
Prepona chalciope	CHA	1	1	1	3	7	8	0	15
Prepona demophon	CHA	5	1	0	6	6	2	0	8
Prepona demophoon	CHA	0	0	0	0	3	0	0	3
Prepona pylene	CHA	0	0	0	0	1	0	0	1
Zaretis itys	CHA	3	7	1	11	1	5	0	6