Journal of Tropical Ecology (1999) 15:703–722. With 4 figures

Frugivorous butterflies in Venezuelan forest fragments: abundance, diversity and the effects of isolation

GHAZALA SHAHABUDDIN[1] *and* JOHN W. TERBORGH

Nicholas School of the Environment, Duke University, Durham, NC-27708–0328, USA
(Accepted 8th April 1999)

ABSTRACT. Frugivorous butterflies were studied in a set of forested islands (0.1 to 1.15 ha) in a reservoir in eastern Venezuela to investigate the effects of fragmentation and the resulting isolation on their abundance, diversity and species composition. While some islands showed reduced abundance and species diversity in comparison to unfragmented (or control) sites, others did not. Isolation status affected both butterfly abundance and diversity. Islands located close to their colonizing sources (0.1–1 km) tended to support similar densities of butterflies but lower numbers of species in comparison to control sites. Far fragments (1–3 km from their colonizing sources) tended to harbour lower butterfly densities in comparison to control sites but undiminished numbers of species. Species composition varied significantly between control sites and islands and amongst control sites, near islands and far islands. Interspecific differences were observed in species' responses to fragmentation. Charaxines, medium-sized satyrines, morphines and brassolines may be vulnerable to extinction after habitat fragmentation while small-sized satyrines may be relatively resistant. Observations during the dry season indicate that butterfly species may exist as mainland-island metapopulations in Lago Guri, in which small habitat fragments require recolonization every year from source populations in large islands and mainland habitat.

KEY WORDS: dry forest, fragmentation, Lepidoptera, Nymphalidae, species composition, tropical

INTRODUCTION

Pioneering studies indicate that tropical butterfly communities experience changes in both diversity and composition after forest fragmentation (Brown & Hutchings 1997, Daily & Ehrlich 1995, Rodrigues *et al.* 1993). In general, butterfly taxa appear to be negatively impacted by fragmentation,

[1] Corresponding author: 6, Indraprastha Hostel, Indian Institute of Technology – Delhi Campus, Hauz Khas, New Delhi – 110016, India.

exhibiting population declines and even extinction (Lovejoy *et al.* 1986). However, the prevalence and extent of butterfly species impoverishment due to tropical forest fragmentation remains unclear because of the difficulties of discerning patterns in these immensely diverse and temporally dynamic communities (Brown & Hutchings 1997, see DeVries *et al.* 1997), the paucity of sites that have been studied and lack of sufficient replication in most cases.

Although the effects of isolation in butterfly metapopulations have been extensively studied in the temperate zone (Hanski *et al.* 1995, Hill *et al.* 1996, Lewis *et al.* 1997), we know little about the scales of isolation at which tropical butterfly communities begin to exhibit the effects of fragmentation. Specific information on the effects of isolation can give us an insight into the landscape-level implications of species loss and help design effective conservation strategies for the maintenance of invertebrate diversity in our increasingly fragmented landscapes (Didham 1997).

The present study attempts to quantitatively assess the effects of habitat fragmentation and the resulting isolation on the abundance, diversity and species composition of a tropical frugivorous butterfly community in eastern Venezuela. Specifically, the following questions are addressed in the study: (a) Is butterfly abundance and diversity significantly reduced in small habitat fragments in comparison to unfragmented forest? (b) Is the degree of faunal impoverishment on islands (with respect to both abundance and diversity) enhanced with increasing isolation from colonizing sources? and (c) Which taxa are most vulnerable to extinction in the event of habitat fragmentation?

The availability of a number of similar-sized habitat fragments located at varying distances from mainland colonizing sources, which were identified using observations of dispersing butterflies, enabled an explicit analysis of the role of isolation in our study system. Additionally, the relatively low species diversity of the study system allowed us to collect sufficient data for quantifying the possible effects of fragmentation on several species. Intra-annual comparisons based on systematic, phenologically matched sampling, which were repeated over three growing seasons, were expected to circumvent the problems associated with the high degree of inter-annual and seasonal variability exhibited by butterfly communities in the tropics. In several earlier studies, the presence of a terrestrial habitat matrix (in the form of secondary forest or pasture) made it difficult to clearly understand the effects of habitat fragmentation on butterfly community composition since 'matrix' butterflies frequently invade fragments (e.g. Daily & Ehrlich 1995, Lovejoy *et al.* 1986). In the current study, the separation of habitat fragments by water (see below) enabled us to distinguish clearly the effects of fragmentation on community characteristics.

STUDY SITE

The study was carried out in Lago Guri, a reservoir located in the state of Bolivar in eastern Venezuela, which was formed by the impoundment of the Caroni River

(completed in 1986). The reservoir extends from 7°N to 7°50′N and from 62°48′W to 63°W, covering *c.* 4300 km^2 in area. Lago Guri contains numerous islands ranging in size from less than a hectare to several hundred hectares, which simulate terrestrial forest fragments formed by the modification of intervening habitat by humans. The vegetation type in the area is tropical dry forest, 15–20 m in height, which consists of a mix of deciduous and semi-deciduous associations (Huber 1986). The average annual rainfall at Guri is 1100 mm (Alvarez *et al.* 1986). The rainy season, extending from May to November, alternates with a distinct dry season from December to April (Morales & Gorzula 1986). The phenology of butterfly populations in Lago Guri was found to be closely linked to that of vegetation, as would be expected in a seasonally dry forest (see DeVries 1987). Oviposition activity by butterflies begins just after the onset of the rains in mid-May, coincident with the leafing of forest vegetation. Adult butterflies begin to emerge a few weeks later and can be seen dispersing between islands from June to August. Butterflies possibly spend the dry season (December to April) as adults in reproductive diapause as observed in seasonally dry forests elsewhere (e.g. Braby 1995).

METHODS

Sampling sites

Studying the effects of habitat fragmentation preferentially requires data on the phenomenon of interest, both before and after continuous habitat is subdivided. However, in the absence of such time-series data, an alternative is to compare presently fragmented sites with continuous forest, thus making the assumption that there does not exist any spatial gradient in the habitat with respect to vegetation or microclimate that is coincident with the fragmentation process. Observations indicate that plant species occur stochastically across both islands and mainland sites, showing no systematic patterns in distribution with respect to fragmentation (G. Shahabuddin, unpubl. data).

Eleven small islands (0.1 to 1.15 ha) at varying distances from the mainland were selected, all of which were known to have been isolated since 1986. In addition, a total of nine sites on the adjoining mainland and two large islands (150–350 ha) were selected as representative of unfragmented forest and are henceforth referred to as 'control sites' (Figure 1). Over the last seven years, the two large islands were found to harbour the full complement of vertebrate fauna found on the nearby mainland and thus were justifiably used as surrogate control sites (Terborgh *et al.* 1997; G. Shahabuddin, *pers. obs.*). Of the nine control sites, six were located on the 350-ha island Danto Machado (separated by at least 200 m from each other), one on the 150-ha Isla Grande and two on the mainland (Figure 1). The study was carried out from 3 July to 8 August 1995, 13 June to 19 August 1996 and from 6 May to 17 August 1997.

Sampling methodology

The guild of frugivorous butterflies was selected for study since they are a little-known group of butterflies that may be especially vulnerable to extinction

https://doi.org/10.1017/S0266467499001121 Published online by Cambridge University Press

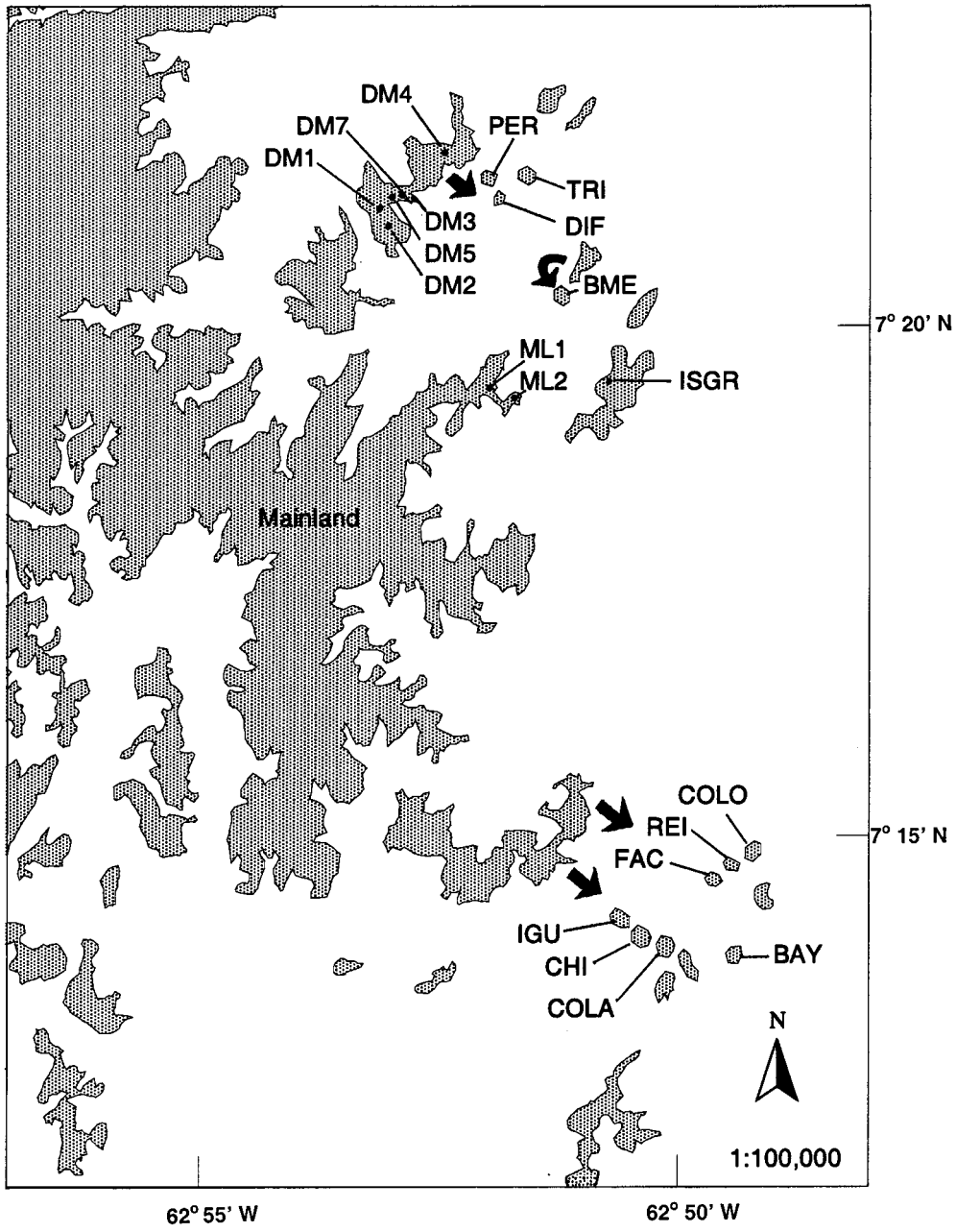

Figure 1. Location of study sites in Lago Guri, Venezuela. Thick arrows indicate the pathways of butterfly flight observed during June and July of 1996. Refer to Table 2 for full site names.

https://doi.org/10.1017/S0266467499001121 Published online by Cambridge University Press

in the event of habitat fragmentation (Brown & Hutchings 1997, Rodrigues *et al*. 1993). In addition, frugivorous butterflies feed obligately on ripe and rotten fruit, and therefore can be efficiently censused using the bait-trapping method (see below).

A reference collection of frugivorous butterflies was made in May 1995, before systematic sampling started. Specimens were identified using DeVries (1987) and D'Abrera (1984). We also used comparisons with museum specimens and consulted experts in Smithsonian Institution, USA; Allyn Museum of Entomology, USA; and Universidad Central, Venezuela for confirming identifications. Apart from two morphospecies belonging to Satyrinae that could be identified only to genus level, all others were identified to the species level.

Sampling of butterflies was carried out using two to five 'sampling sessions' (days) at every site in a given year. At every site, the intervals between sampling sessions varied from 7–10 d. In a single sampling session, butterflies were trapped using either five or 10 Van Someren–Rydon bait-traps (DeVries 1987). The bait-traps were hung 2–3 m above the ground in a consistent crosswise arrangement, over an area of *c*. 1200 m^2. The area over which the traps were arranged at each study site is henceforth referred to as the 'trapping zone'. Observations indicated that the probability of butterflies entering the trapping zone from outside it, during the 4–6 h of trapping, was negligible (G. Shahabuddin, unpubl. data). Thus 1200 m^2 was considered to be the effective sampling area at each site. The traps were baited with rotten plantains and rum and left for 4–6 h between 09h30 and 15h30. At the end of each sampling session, all butterflies caught in the traps were identified, counted and released. A few butterflies could not be identified during the sampling sessions and were therefore collected.

It was assumed that the number of captures of each species at a given site was indicative of its local population density. Mark-recapture experiments on both islands and control sites indicated that the frequency of recaptures was low, *c*. 2% 7–9 d after release (G. Shahabuddin, unpubl. data). Since the interval between sampling sessions at each site was always seven days or more, the possibility of capturing the same butterfly during two consecutive sessions was negligible.

The number and identity of sites, number of sampling sessions, number of traps used and period of sampling varied from year to year (see Table 1).

Table 1. Details of the three data sets used in the study of the butterfly communities of Lago Guri islands, Venezuela.

Year	Period of sampling	Number of sampling sessions	Trapping duration (h)	Traps used per session	Number of controls, near and far islands sampled
1995	July, August	5	6	5	4 control, 3 near
1996	June, July, August	4	4	10	4 control, 4 near, 5 far
1997	July, August	2	5	10	4 control, 6 far

https://doi.org/10.1017/S0266467499001121 Published online by Cambridge University Press

However, the sampling methodology was consistent within each year. Thus statistical analysis was carried out separately for each year, ensuring equal sampling effort across sampled sites in any given year. Three data sets (one each for 1995, 1996 and 1997) were compiled by adding together butterfly captures from equal numbers of phenologically-matched sampling sessions carried out over all the sites sampled in a given year. A subsample of three control sites and three islands were additionally sampled on a single day during the dry season of 1997 (May) to assess the phenological variation in butterfly abundance, if any.

Measuring island isolation and area

To ascertain the colonizing sources for the study islands, so that isolation could be quantified, 14 observation points were established in various portions of the lake, around the two major clusters of study islands. In 1996, each point was surveyed for dispersing butterflies 2–3 times during the peak flight season, for 0.5–2 h from an anchored boat. All butterflies flying within 10 m on either side of the boat, were counted and their direction of flight was noted. The distance between each study island and its primary colonizing source (found out as described above) was then estimated from a map of Lago Guri prepared by Electrificacion del Caroni (EDELCA), the Venezuelan hydroelectric company that manages the operation of the Raul Leoni dam. The colonizing sources for some islands were larger islands while others appeared to be colonized from mainland sources (Figure 1). Ascertaining the actual colonizing sources for the study fragments thus took into account any stepping-stone colonization that may be taking place in the island system (MacArthur & Wilson 1967). Islands located between 0.1–1 km from a colonizing source were operationally considered as near islands and those between 1 and 3 km, as far islands (Figure 1). Areas of islands were estimated by mapping the perimeter of each island using a compass (Suunto KB-14) and distance-measuring electronic meter (Sonin Combo Pro). Table 2 gives the area and isolation of each study site.

Statistical analysis

Total butterfly abundances were compared between control sites and habitat fragments within each data set using the Kruskal–Wallis test (a non-parametric ANOVA; Sokal & Rohlf 1981). In 1996, when both near and far islands were available, pairwise comparisons of abundance were carried out amongst the three categories of study sites, to test the effect of isolation. Tests of significance were assessed using the sequential Bonferroni technique for simultaneous tests as suggested by Rice (1989).

Proportional differences in total butterfly abundances were calculated between each control site and each fragment sampled during the dry season of 1997. As three control sites and three islands were sampled, nine pairs were

Table 2. Details of study sites in Lago Guri, Venezuela. Distance to primary colonizing source (Danto Machado or mainland) is given for each island.

Name	Abbreviations used in text	Distance (km)	Area (ha)
Control sites			
Danto Machado	DM1 to DM7	–	350
Isla Grande	ISGR	–	150
Mainland	ML1 and ML2	–	–
Island sites			
Triangulo	TR1	1.0	1.15
Perimetro	PER	0.5	0.85
Difficil	DIF	0.6	0.10
Bumeran	BME	0.1	0.45
Iguana	IGU	1.2	0.68
Cola	COLA	1.8	0.82
Chiguire	CH1	1.5	0.26
Facil	FAC	2.0	0.31
Reineta	REI	2.2	0.15
Colon	COLO	2.6	0.31
Baya	BAY	2.7	0.23

obtained, each comprising an island and a comparable control site. Proportional differences in butterfly abundance were calculated within each pair as:

$$(\text{island abundance} - \text{control abundance})/(\text{control abundance})$$

This calculation yielded values ranging from −1 to 1, which were negative when an island had fewer butterflies than the comparable control site. Values were positive if an island had more butterflies. Similar proportional differences were calculated for butterfly abundances recorded during the previous wet season. The proportional difference in butterfly abundance between an island and a control site during the dry season was compared with that calculated for the wet season using a Wilcoxon signed-rank test for paired samples (Sokal & Rohlf 1981).

Species richness of fragments was compared with that of control sites using the method of rarefaction (Sanders 1968, Simberloff 1972). Rarefaction is useful for comparing species richness of samples that vary in size, which was true for all three years of sampling. Specifically, the null hypothesis being tested was that the observed species richness on each island was not different from that of unfragmented forest.

Species richness analysis by itself does not reveal changes in the degree of evenness in the abundance of species, an important component of local species diversity (Magurran 1988). To find out whether dominance relationships changed significantly with fragmentation and/or isolation, the Berger–Parker index of evenness (Magurran 1988) was calculated for each site in each year of sampling. The Berger–Parker index (d) expresses the proportional importance of the most abundant species as $d = N_{max}/N$ where N_{max} = number of individuals in the most abundant species and N = total number of individuals in the sample. Kruskal–Wallis tests of means were carried out to find out whether

https://doi.org/10.1017/S0266467499001121 Published online by Cambridge University Press

evenness of species abundance within butterfly communities varied significantly between control sites and islands. In 1996, an additional test was carried out using three categories, i.e. control sites, near islands and far islands to find out whether isolation status of islands affected dominance relationships within butterfly communities.

To further find out whether butterfly species composition varied significantly between control sites and islands, inter-site similarity analyses were undertaken for each year, using the FORTRAN program GDIS (similar to ANOSIM described in Clark 1993). GDIS uses randomization procedures to test whether groups of sites (control sites and islands, in this case) differ significantly in species composition by comparing inter-group similarity to within-group similarity. Community similarity was summarized using the percentage similarity index which is calculated as the percent shared abundances of species occurring in pairs of samples. Relative abundances of species were used for the calculation of similarity indices to avoid undue weighting of abundant species in comparison to rare ones. To test the effects of isolation status, a similar analysis was carried out using classified sites: control sites, near and far islands in 1996.

In most fragmentation studies, species responses are inferred from presence/absence data. However, the degree to which a species' population density decreases or increases in a habitat fragment, is a more powerful indicator of its ability to survive in the changed landscape. For example, the greater the extent of population reduction on fragments as compared to unfragmented habitat, the greater the likelihood of local extinction. Similarly, the extent of population increase on fragments would indicate a species' 'resistance to fragmentation'. A species' response to fragmentation was therefore quantified by calculating the difference in its population densities between control sites and fragments. The mean density (1200 m^{-2}) of every species was calculated for control sites and islands, within each year. Using the mean densities for each year, the percentage difference in density between unfragmented and fragmented sites, was calculated for each species as: [(mean island density – mean control density)/ average (mean control density + mean island density)] * 100. An average value was calculated over 3 y for each species which is henceforth referred to as the 'population response index' (PRI). As it was designed, the PRI ranged from negative (lower population density on fragments as compared to control sites), through zero (no difference in population density between controls and fragments) to positive values (hyperabundance on fragments).

RESULTS

Over the duration of the study, a total of 2602 butterflies belonging to 41 species were trapped from 20 sites in Lago Guri. The trapped butterflies belonged to the subfamilies Charaxinae, Limenitidinae, Morphinae,

https://doi.org/10.1017/S0266467499001121 Published online by Cambridge University Press

Brassolinae and Satyrinae of family Nymphalidae (see Appendix 1 for a classified list of species and Appendix 2 for site- and year-wise listing of species' abundances).

Butterfly abundance

Comparison between control sites and fragments indicate similar butterfly abundance on islands as compared to control sites in 1995 (Kruskal-Wallis statistic (H) = 2, df = 1, P = 0.16; Figure 2a) and 1996 (H = 3.17, df = 1, P = 0.07; Figure 2b). However, islands had significantly lower butterfly abundance than control sites in 1997 (H = 6.55, df = 1, $P < 0.01$; Figure 2c). Pairwise comparisons of butterfly abundances (using Kruskal-Wallis tests) were carried out amongst the three categories of sites in 1996, when both near and far islands were sampled. Using the sequential Bonferroni technique for simultaneous tests (Rice 1989), none of the pair-wise comparisons were significant, although far islands tended to harbour fewer butterflies than near islands or control sites (near vs. far islands: H = 4.86, df = 1, P = 0.03; control sites vs. near islands: H = 0.0833, df = 1, P = 0.77; control sites vs. far islands: H = 2.16, df = 1, P = 0.14; Figure 2b).

Temporal changes in butterfly abundance

Comparisons in wet and dry seasons indicated that most fragment sites harboured fewer butterflies than control sites in both dry and wet seasons (Table 3a). However, these differences were significantly greater in the dry season than in the wet season (Tables 3b,c; Wilcoxon signed-rank test statistic V = 0, df = 1, P = 0.004).

Species richness and evenness

Figures 3a–c give the species richness of each studied island site in relation to the number of individuals collected in it, for each year. These points are plotted in relation to the rarefaction curve which gives the expected species richness of a subsample and the 95% confidence limits. In 1995, two of the three islands sampled showed significantly lower species richness as compared to control sites. In 1996, five of the nine study islands had fewer species than expected by chance. In 1997, one out of six islands showed significant impoverishment with respect to control sites. When isolation status is considered, near islands showed significant degree of impoverishment in six out of seven cases while far islands showed significant impoverishment in one out of 11 cases.

Kruskal–Wallis tests indicated that Berger–Parker indices of evenness do not differ significantly between fragmented and unfragmented sites (1995: Kruskal–Wallis H = 0.5, P = 0.48; 1996: H = 0.05, P = 0.82; 1997: H = 2.99, P = 0.08; df = 1 all cases). In 1996, Berger–Parker indices of control sites, near islands and far islands do not differ significantly (H = 2.12, df = 2, P = 0.35).

https://doi.org/10.1017/S0266467499001121 Published online by Cambridge University Press

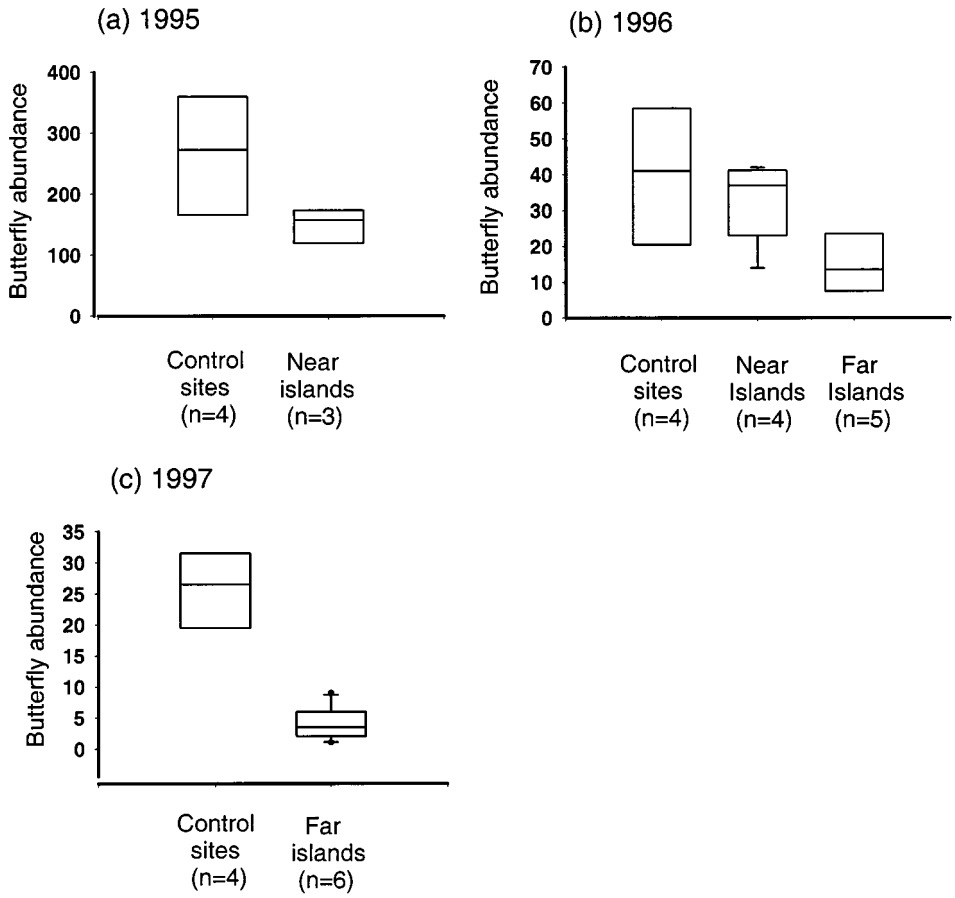

Figure 2. Total numbers of butterflies captured over equal numbers of phenologically-matched sampling days on control sites, near islands and far islands in (a) 1995, (b) 1996, and (c) 1997. Both near and far islands were sampled in 1996. In each box, the line in the centre indicates the median value while the two outer lines together enclose the interquartile range of butterfly abundances. Extreme values are joined to the box by perpendicular lines (Tukey 1977).

Species composition and vulnerable species

Similarity analysis indicated that butterfly species composition differs significantly between control sites and islands in each of three years (1995: $P < 0.0001$, 1996, $P < 0.001$; 1997, $P = 0.02$). In 1996, species composition varied significantly amongst control sites, near islands and far islands ($P < 0.001$).

Of the 41 species recorded during the period of study, 21 were not subjected to statistical analysis, as they were recorded three times or less every year. Of the remaining 20 species, while 10 (50%) showed much lower densities on

https://doi.org/10.1017/S0266467499001121 Published online by Cambridge University Press

Table 3. (a) Total butterfly abundance on control sites and island sites during dry and wet seasons and (b) and (c) proportional differences in total butterfly abundances between pairs of control sites and islands during wet and dry seasons. Differences were calculated as $(x - y)/y$ where x = island abundance and y = control abundance. Negative values therefore indicate low densities on islands relative to control sites and positive values indicate an excess of butterflies on islands relative to control sites.

(a) Total butterfly abundance

	Dry	Wet
Control sites		
DM1	12	54
ISGR	8	63
ML2	18	28
Island sites		
TRI	2	42
PER	0	37
BME	0	41

(b) Comparisons in dry season

	TRI	PER	BME
DM1	−0.83	−1	−1
ISGR	−0.75	−1	−1
ML2	−0.88	−1	−1

(c) Comparisons in wet season

	TRI	PER	BME
DM1	−0.22	−0.31	−0.24
ISGR	−0.33	−0.41	−0.35
ML2	0.50	0.32	0.46

fragments compared to control sites (index of −100% or lower), 5 (25%) exhibited slightly lower density on fragments and 5 (25%) showed higher densities on fragments compared to unfragmented sites (Figure 4). Taxa showing much lower densities or absence on fragments include medium-sized satyrines (*Taygetis virgilia*, *T. laches* and *T. echo*), charaxines (*Prepona omphale* and *Archaeoprepona demophon*), *Morpho peleides* and the limenitidine *Myscelia cyaniris*. Small satyrines (such as *T. kerea*, *Pharneuptychia phares* and *Ypthimoides spp*.) and the limenitidine *Historis odius* show only slightly decreased or higher densities on island sites as compared to control sites.

DISCUSSION

The study islands did not vary significantly from control sites in butterfly abundance in 1995 and 1996. However, far islands tended to have fewer butterflies than comparable control sites and near islands in 1996 and 1997, although these differences were not significant in 1996. This indicates that islands located within 1 km of their colonizing sources may not experience

https://doi.org/10.1017/S0266467499001121 Published online by Cambridge University Press

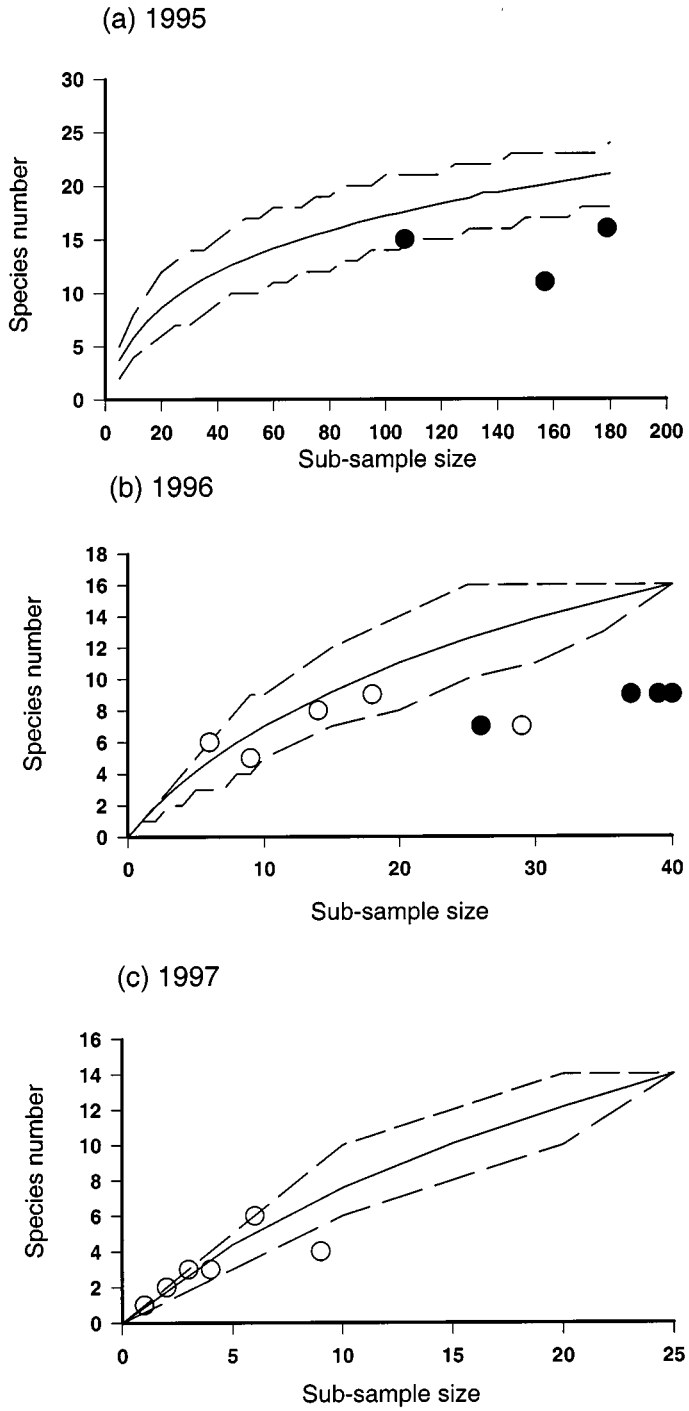

Figure 3. Observed species richness on near islands (filled circles) and far islands (open circles) plotted in relation to rarefaction curves based on relative abundances of species in control sites in (a) 1995, (b) 1996, and (c) 1997. Dashed lines indicate 95% confidence limits.

https://doi.org/10.1017/S0266467499001121 Published online by Cambridge University Press

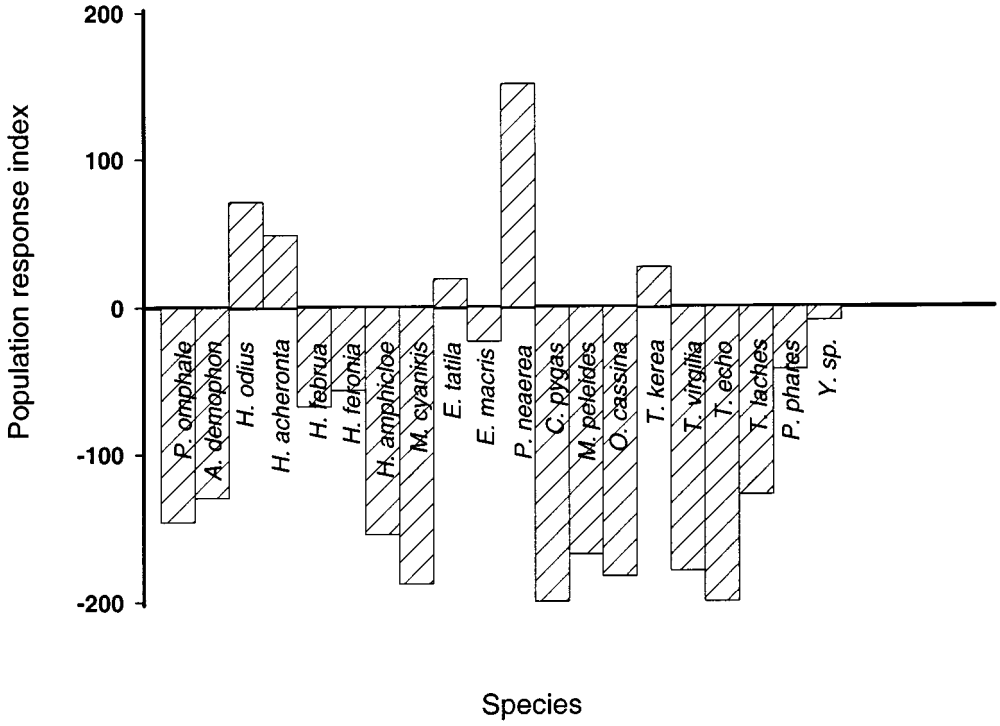

Figure 4. Population response indices for 20 butterfly species indicating differences in densities between islands and control sites averaged over three years. For full species names refer to Appendix 1.

lack of butterfly colonization. However, fragments located more than 1 km from the mainland or large islands may be subject to the effects of reduced colonization.

No clear results were obtained with respect to species impoverishment on study fragments as a whole. However, when isolation status was considered, near islands consistently showed reduced species richness compared to control sites. Contrary to expectation, far islands harboured similar or higher numbers of species as would be expected on control sites.

In general, the islands were found to be impoverished in comparison to unfragmented forest, either in terms of reduced butterfly densities or species richness. Near islands showed a consistent trend of reduced species diversity but normal butterfly abundances. Far islands had as many species as expected by chance but fewer individuals than on comparable control sites. Results from the present study therefore imply that forest fragmentation is likely to have had adverse effects on butterfly communities as found in earlier studies (Baz & Garcia-Boyero 1995, Bierregaard *et al.* 1992, Brown 1991, Daily & Ehrlich 1995, Lovejoy *et al.* 1986, Shreeve & Mason 1980).

It is notable that small fragments harbouring viable populations of generalist insects such as leaf-cutting ants (Terborgh *et al.* 1997; G. Shahabuddin and J.

https://doi.org/10.1017/S0266467499001121 Published online by Cambridge University Press

Terborgh, *pers. obs.*) may be of insufficient size to sustain those of medium-sized to large frugivorous butterflies. Leaf-cutting ants exhibit greatly elevated densities on small Lago Guri fragments in comparison to control sites (Terborgh *et al.* 1997). Our findings thus lend support to the view that specialized insects may be more vulnerable to extinction in habitat fragments than generalist ones, possibly due to their need for integrating resources over a larger area (Gilbert 1980, Thomas 1994).

Far islands tended to show reduced butterfly abundance but unchanged species diversity. For example, in 1996, the far island Cola recorded only six butterflies, all of which belonged to different species (Appendix 2). The data indicate that far island communities may be dominated by transient butterflies. This speculation is supported by the result of unchanged dominance relationships of species across island categories. Observations indicate that colonization of islands by adult butterflies occurs sporadically on unusually hot days during the wet season. Such irregular colonization by small numbers of butterflies, may result in both reduced reproduction and adult residence times on far islands, due to insufficient total numbers at a given time (Allee effect; see Smith & Peacock 1990). We therefore speculate that most of the butterflies caught on far islands are day-visitors/vagrants, while near island communities possibly consist of a mixture of transients and local populations. This idea requires testing through detailed population-level studies. Reduced species diversity on near islands is more difficult to explain, given that they tended to harbour butterfly densities comparable to those on control sites. It is possible that near islands have more saturated communities because of the constant influx of butterflies from their colonizing sources. Consequently, some butterfly species that are competitively inferior in mainland and near island communities, may experience ecological release on far islands (L. E. Gilbert, *pers. comm.*). This would lead to unchanged species richness in far island communities in comparison to near islands as seen in the present study. Similar dynamics may be operating in Finnish island clusters where weakly flying species were commoner on islands located in clusters while strong-flying species occurred more frequently on scattered islands (Nieminen & Hanski 1998).

The importance of colonization dynamics for maintaining butterfly communities on fragments was confirmed by comparison of butterfly abundances during wet and dry seasons. The results indicate that butterflies are nearly absent on islands during the dry season but harbour many more butterflies after the emergence of imagos and their dispersal to islands during the wet season. This suggests that the small islands in Lago Guri may not be capable of sustaining viable populations until the end of the dry season (November to May), requiring recolonization on an annual basis during the wet season. The study system may be an example of a mainland-island metapopulation in which one or more large sub-populations persist indefinitely while smaller ones frequently undergo extinction and recolonization from the mainland (Harrison

1994). With an increasing number of macro-ecological population studies, there is increasing evidence that such population structures may be far more prevalent than commonly believed, especially of mobile organisms such as lepidopterans and birds (e.g. Brawn & Robinson 1996, Harrison 1994).

The study revealed significant interspecific differences in butterfly responses to fragmentation. While 75% of recorded species showed lower population densities or absence on study islands, others appeared relatively resistant. Differential responses of species were reflected in the significantly changed species composition on islands in comparison to control sites. The patterns of species responses to fragmentation as inferred from the present study are similar to those observed in earlier studies in the neotropics. Population increases or unchanged abundances have been observed in small satyrines after forest disturbance or fragmentation (Daily & Ehrlich 1995, Raguso & Llorente-Bousquets 1990, Singer & Ehrlich 1991). Such effects may be attributed to their dependence on grasses (which grow better in disturbed forest), and small size, allowing them to maintain viable populations even in small forest fragments. Some of the vulnerable species identified in the present study, such as the charaxines, are characteristic of closed canopy forest habitat (DeVries 1987) and may be disproportionately affected by changes in forest quality, such as degree of light penetration, triggered by fragmentation (Brown & Hutchings 1997, Daily & Ehrlich 1995). Low mobility across open habitats, appears important in the case of *Morpho peleides* and *Myscelia cyaniris*, two species that were almost completely absent from habitat fragments and never seen flying over open water (see Appendix 2). Species belonging to the genus *Hamadryas* appear to closely track their host-plant distribution across Lago Guri fragments (authors' unpubl. data). Thus, it appears likely that species-specific constraints related to dispersal, behaviour and host plant distribution may underlie the differential responses of species to fragmentation. Our study implies that an autoecological approach may be necessary to understand the processes underlying community change after fragmentation. A study of the nymphaline *Hamadryas februa* along these lines is in progress, focusing on its dispersal and patch utilization.

The results from the present study should be treated with caution as the number of study sites was low in each year and not all sites could be visited every year. In an effort to equalize sampling effort across sites, the number of butterflies trapped on some far islands was low and may have limited the interpretation of diversity data. Despite its limitations, the study provides indications that fragmentation may have adverse impacts on local abundance and diversity of species and consequently, on population viability and community stability of butterflies on habitat fragments.

ACKNOWLEDGEMENTS

We are grateful to Luis Balbas (Electrificacion del Caroni, Guri) for logistical support in Lago Guri; Cesar Riveros, Maria del Carmen Gomez and Gudrun

Herzner for field assistance; and Dean Urban and Rakesh Barve for help with statistical analysis. We are also grateful to Lee Miller, Jackie Miller, Don Harvey and Jurg de Marmels for their help with the identification of butterflies and to Larry Gilbert and Nigel Asquith for reviewing early drafts of the manuscript. The project was supported by Duke-UNC Program in Latin-American Studies, Duke University's Center for International Studies, an Aga Khan Foundation scholarship to G. Shahabuddin and an NSF grant to J. Terborgh.

LITERATURE CITED

ALVAREZ, E., BALBAS, L., MASSA, I. & PACHECO, J. 1986. Aspectos ecológicos del embalse Guri. *Intersciencia* 11:325–333.

BAZ, A. & GARCIA-BOYERO, A. 1995. The effects of forest fragmentation on butterfly communities in central Spain. *Journal of Biogeography* 22:129–140.

BIERREGAARD, R. O., LOVEJOY, T. E., KAPOS, V., DOS SANTOS, A. A. & HUTCHINGS, R. W. 1992. The biological dynamics of tropical rainforest fragments. *Bioscience* 42:859–866.

BRABY, M. F. 1995. Reproductive seasonality in tropical satyrine butterflies: strategies for the dry season. *Ecological Entomology* 20:5–17.

BRAWN, J. D. & ROBINSON, S. K. 1996. Source-sink population dynamics may complicate the interpretation of long-term census data. *Ecology* 77:3–12.

BROWN, K. S. 1991. Conservation of neotropical environments: insects as indicators. Pp. 350–401 in Collins, N. M. & Thomas, J. A. (eds). *The conservation of insects and their habitats*. 15th Symposium of the Royal Entomological Society of London. Academic Press, London.

BROWN, K. S. & HUTCHINGS, R. W. 1997. Disturbance, fragmentation and the dynamics of diversity in Amazonian forest butterflies. Pp. 91–110 in Laurance, W. F. & Bierregaard, R. (eds). *Tropical forest remnants: ecology, management and conservation of fragmented communities*. University of Chicago Press, Chicago.

CLARK, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18:117–143.

D'ABRERA, B. 1984. *Butterflies of South America*. Hill House, Victoria. 256 pp.

DAILY, G. C. & EHRLICH, P. R. 1995. Preservation of biodiversity in small rainforest patches: rapid evaluations using butterfly trapping. *Biodiversity Conservation* 4:35–55.

DEVRIES, P. J. 1987. *The butterflies of Costa Rica and their natural history*. Princeton University Press, New Jersey. 327 pp.

DEVRIES, P. J., MURRAY, D. & LANDE, R. 1997. Species diversity in vertical, horizontal, and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest. *Biological Journal of the Linnaean Society* 62:343–364.

DIDHAM, R. K. 1997. An overview of invertebrate responses to forest fragmentation. Pp. 303–320 in Watt, A. D., Stork, N. E. & Hunter, M. D. (eds). *Forests and insects*. Chapman & Hall, London.

GILBERT, L. E. 1980. Food web organization and the conservation of neotropical diversity. Pp. 11–33 in Soulé, M. E. & Wilcox, B. A. (eds). *Conservation biology: an evolutionary-ecological perspective*. Sinauer Associates, Massachusetts.

HANSKI, I., POYRY, J., PAKKALA, T. & KUUSAARI, M. 1995. Multiple equilibria in metapopulation dynamics. *Nature* 377:618–621.

HARRISON, S. 1994. Metapopulations and conservation. Pp. 111–128 in Edwards, P. J., May, R. M. & Webb, N. R. (eds). *Large-scale ecology and conservation biology*. Blackwell Scientific Publications, Oxford.

HILL, J. K., THOMAS, C. D. & LEWIS, O. T. 1996. Effects of patch size and isolation on dispersal by *Hesperia comma* butterflies: implications for metapopulation structure. *Journal of Animal Ecology* 65:725–735.

HUBER, O. 1986. La vegetación de la cuenca del Rio Caroni. *Intersciencia* 11:301–310.

LEWIS, O. T., THOMAS, C. D., HILL, J. K., BROOKES, M. I., CRANE, T. P. R., GRANEAU, Y. A., MALLET, J. B. L. & ROSE, O. C. 1997. Three ways of assessing metapopulation structure in the butterfly *Plebejus argus*. *Ecological Entomology* 22:283–293.

LOVEJOY, T.E, BIERREGAARD, R. O., RYLANDS, A. B., MALCOLM, J. R., QUINTELA, C. E., HARPER, L. H., BROWN, K. S., POWELL, A. H., POWELL, G. V. N., SCHUBART, H. O. R. & HAYS, M. B. 1986. Edge and other effects of isolation on Amazon forest fragments. Pp. 257–285 in Soulé, M. E. (ed.). *Conservation biology: science of scarcity and diversity*. Sinauer Associates, Massachusetts.

MACARTHUR, R. H. & WILSON, E. O. 1967. *The theory of island biogeography*. Princeton University Press, New Jersey. 203 pp.

MAGURRAN, A. E. 1988. *Ecological diversity and its measurement*. Princeton University Press, New Jersey. 179 pp.
MORALES, L. C. & GORZULA, S. 1986. The interrelations of the Caroni River Basin ecosystems and hydroelectric power projects. *Intersciencia* 11:272–277.
NIEMINEN, M. & I. HANSKI. 1998. Metapopulations of moths on islands: a test of two contrasting models. *Journal of Animal Ecology* 67:149–160.
RAGUSO, R. A. & LLORENTE-BOUSQUETS, J. 1990. The butterflies (Lepidoptera) of the Tuxtlas Mts., Veracruz, Mexico, revisited: species richness and habitat disturbance. *Journal of Research on the Lepidoptera* 29:105–133.
RICE, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43:223–225.
RODRIGUES, J. J. S., BROWN, K. S. & RUSZCZYK, A. 1993. Resources and conservation of neotropical butterflies in urban forest fragments. *Biological Conservation* 64:3–9.
SANDERS, H. L. 1968. Marine benthic diversity: a comparative study. *American Naturalist* 102:243–282.
SHREEVE, T. G. & MASON, C. F. 1980. The number of butterfly species in woodlands. *Oecologia* 45:414–418.
SIMBERLOFF, D. F. 1972. Properties of the rarefaction diversity measurement. *American Naturalist* 106:414–418.
SINGER, M. C. & EHRLICH, P. R. 1991. Host specialisation of satyrine butterflies and their responses to habitat fragmentation in Trinidad. *Journal of Research on the Lepidoptera* 30:248–256.
SMITH, A. T. & PEACOCK, M. M. 1990. Conspecific attraction and the determination of metapopulation colonization rates. *Conservation Biology* 4:320–323.
SOKAL, R. R. & ROHLF, F. J. 1981. *Biometry*. W. H. Freeman & Company, New York. 859 pp.
TERBORGH, J., LOPEZ, L., TELLO, J., YU, D. & BRUNI, A. R. 1997. Transitory states in relaxing ecosystems of land-bridge islands. Pp. 256–274 in Laurance, W. F. & Bierregaard, R. (eds). *Tropical forest remnants: ecology, management and conservation of fragmented communities*. University of Chicago Press, Chicago.
THOMAS, J. A. 1994. Why small cold-blooded insects pose different conservation problems to birds in modern landscapes. *Ibis* 137:S112–S119.
TUKEY, J. W. 1977. *Exploratory data analysis*. Addison-Wesley, Massachusetts. 688 pp.

Appendix 1. List of frugivorous butterfly species of Lago Guri area. Species marked with an asterisk were caught outside of sampling sessions.

Latin Name	Authority	Latin Name	Authority
Family Nymphalidae; Subfamily Charaxinae		Family Nymphalidae; Subfamily Brassolinae	
Prepona omphale	Fruhstorfer	*Opsiphanes cassina*	Boisduval
Archaeoprepona demophon	Fruhstorfer	*Catoblepia berecynthia* *	Cramer
Siderone marthesia	Cramer	*Caligo illioneus* *	Butler
Zaretis itys	Cramer	*Eryphanis polyxena* *	Felder
Memphis morvus	Fabricius		
Hypna clytemnestra	Cramer	Family Nymphalidae; Subfamily Satyrinae	
		Pierella hyalinus	Gmelin
Family Nymphalidae; Subfamily Limenitidinae		*Manataria maculata*	Hopffer
Colobura dirce	Linnaeus	*Taygetis kerea*	Butler
Historis odius	Fabricius	*Taygetis virgilia*	Staudinger
Historis acheronta	Fabricius	*Taygetis penelea*	Cramer
Biblis hyperia *	Cramer	*Taygetis mermeria*	Butler
Hamadryas februa	Hübner	*Taygetis echo*	Cramer
Hamadryas feronia	Fruhstorfer	*Taygetis laches*	Fabricius
Hamadryas amphicloe	Staudinger	*Magneuptychia ocypete*	Fabricius
Hamadryas amphinome	Lucas	*Cissia terrestris*	Butler
Myscelia cyaniris	Doubleday	*Pareuptychia ocirrhoe*	Fabricius
Eunica tatila	Herrich-Schäffer	*Amphidecta callioma*	Felder
Eunica macris	Godart	*Pharneuptychia phares*	Godart
Temenis laothoe	Fabricius	*Ypthmoides* sp.	–
Pyrrhogyra neaerea	Godman and Salvin	*Cissia penelope*	Fabricius
Nessaea aglaura	Doubleday	*Magneuptychia libye*	Linnaeus
Callicore maimura	Hewitson	*Hermeuptychia hermes*	Fabricius
Adelpha iphiclus	Linnaeus	*Amphidecta* sp.	–
Family Nymphalidae; Subfamily Morphinae			
Morpho peleides	Butler		
Morpho theseus *	Butler		

Appendix 2. Numbers of butterflies of each species caught during 1995, 1996 and 1997 in Lago Guri. Details of sample size and methods are given in Table 1 and in the text. For site names see Table 2 and for full species names, refer to Appendix 1.

Species	(a) 1995							(b) 1996							
Sites:	DM1	DM2	DM3	DM4	TRI	PER	BME	DM1	ISGR	ML1	ML2	TRI	PER	DIF	BME
P. omphale	1	3	1	2	–	1	1	2	3	1	–	1	1	–	–
A. demophon	1	5	2	2	–	–	–	1	2	–	–	1	–	–	–
S. marthesia	–	–	1	–	1	1	–	–	–	–	–	–	–	–	1
Z. itys	–	1	–	–	–	–	1	–	–	–	1	–	–	–	–
Memphis spp.	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
H. rufescens	–	1	1	–	–	–	1	–	–	–	–	–	–	–	–
C. dirce	–	3	–	–	1	–	–	–	–	–	–	–	–	–	–
H. odius	15	8	19	11	24	17	16	–	4	–	1	–	2	1	1
H. acheronta	9	7	38	59	53	11	38	1	8	–	–	2	12	10	3
B. hyperia	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
H. februa	64	12	76	104	32	5	20	8	1	3	5	25	2	2	15
H. feronia	4	2	12	13	7	3	4	4	–	–	1	2	–	–	8
H. amphicloe	–	–	–	4	1	–	–	3	1	–	11	5	–	2	1
H. amphinome	1	–	–	1	–	–	–	–	–	–	–	–	–	–	–
M. cyaniris	55	41	97	98	9	7	6	2	9	2	–	–	–	–	–
E. tatila	2	–	49	16	15	3	43	–	–	–	–	–	–	–	–
E. macris	2	4	31	5	14	4	25	–	1	–	–	–	–	–	–
T. laothoe	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
P. neaerea	–	–	3	–	3	2	2	–	–	–	–	–	3	–	–
N. aglaura	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–
C. maimura	4	2	2	1	–	–	–	–	–	–	–	–	–	–	–
A. iphiclus	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–
M. peleides	3	10	–	4	–	–	–	8	28	3	4	–	1	–	1
M. theseus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
O. cassina	9	7	–	2	1	1	–	4	–	–	–	–	–	–	–
C. berecynthia	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
P. hyalinus	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–
M. maculata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
T. kerea	11	25	10	3	8	47	–	5	1	–	–	2	14	7	–
T. virgilia	2	5	2	8	1	–	–	3	–	–	2	–	–	–	–
T. penlea	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
T. mermeria	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
T. echo	–	1	–	2	–	–	–	7	3	4	3	–	–	–	–
T. laches	1	–	1	3	–	–	–	2	1	–	–	–	1	1	–
M. ocypete	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
C. terrestris	–	1	–	–	–	–	–	1	–	–	–	–	–	–	–
P. ocirrhoe	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
A. callioma	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–
P. phares	6	2	9	19	5	1	–	–	–	–	–	1	–	3	3
Ypthmoides spp.	–	–	6	1	4	–	–	–	–	–	–	1	1	–	8
C. penelope	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
M. libye	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
H. hermes	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Amphidecta spp.	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–

Appendix 2. (*cont.*)

Species	(b) 1996 cont'd							(c) 1997							
Sites:	DM1	DM2	DM3	DM4	TRI	PER	BME	DM1	ISGR	ML1	ML2	TRI	PER	DIF	BME
P. omphale	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–
A. demophon	–	–	–	–	–	–	–	1	–	–	–	–	1	–	–
S. marthesia	–	–	–	–	–	0	–	–	–	–	–	–	–	–	–
Z. itys	–	–	–	–	–	4	2	1	1	–	–	–	–	–	–
Memphis spp.	–	–	–	–	–	0	1	–	–	–	–	–	–	2	1
H. rufescens	–	–	–	1	–	0	–	–	–	–	–	–	–	–	–
C. dirce	1	–	–	–	–	–	–	–	1	–	–	–	–	–	1
H. odius	1	2	1	1	–	–	–	–	–	1	–	–	–	–	–
H. acheronta	3	10	5	1	1	0	–	–	–	–	–	–	–	–	–
B. hyperia	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
H. februa	2	2	–	1	–	1	4	5	3	–	3	–	1	–	1
H. feronia	–	4	3	–	1	1	3	2	1	–	–	–	–	–	1
H. amphicloe	–	–	2	–	–	4	1	2	1	–	–	–	–	–	–
H. amphinome	–	–	–	–	–	0	–	1	–	–	–	–	1	1	1
M. cyaniris	–	–	–	–	–	1	8	8	1	–	–	–	–	–	–
E. tatila	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
E. macris	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
T. laothoe	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–
P. neaerea	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
N. aglaura	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
C. maimura	–	–	–	–	–	0	–	–	1	–	–	–	–	–	–
A. iphiclus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
M. peleides	2	–	2	–	–	–	–	1	2	–	–	–	–	–	1
M. theseus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
O. cassina	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–
C. berecynthia	–	–	–	–	–	0	–	–	–	–	–	–	–	–	–
P. hyalinus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
M. maculata	–	–	–	–	–	0	–	–	–	–	–	–	–	–	–
T. kerea	–	7	1	1	–	–	1	1	1	–	3	–	–	–	–
T. virgilia	–	1	–	–	–	1	8	4	2	–	–	–	–	–	–
T. penlea	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
T. mermeria	–	–	1	–	–	0	–	–	–	–	1	–	–	–	–
T. echo	–	–	–	–	–	2	–	2	1	–	–	–	–	–	–
T. laches	2	–	2	–	2	2	–	–	3	–	–	–	–	–	–
M. ocypete	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–
C. terrestris	–	–	–	–	1	–	1	1	–	–	–	–	–	–	–
P. ocirrhoe	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
A. callioma	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–
P. phares	–	–	1	–	–	–	–	–	1	–	–	–	–	–	–
Ypthmoides spp.	2	3	–	–	4	0	2	–	1	–	–	–	–	–	–
C. penelope	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–
M. libye	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–
H. hermes	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
Amphidecta spp.	–	–	–	–	–	0	–	–	–	–	–	–	–	–	–