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POPULATION BIOLOGY OF *HETEROSAIS EDESSA* (NYMPHALIDAE) AND ITS ASSOCIATED ATLANTIC FOREST ITHOMIINAE COMMUNITY

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ABSTRACT. The early stages of *Heterosais edessa*, an advanced species of Ithomiinae (Nymphalidae) are described. Adult population size, sex ratio, longevity, food resources and movement are given for this species and compared with those of 17 other members of the local Ithomiinae community.

Additional key words: mark-recapture, Godyridini, *Cestrum*, Solanaceae, K-strategist.

Long term population studies may reveal important features of ecology and adaptation in tropical butterflies (Ehrlich 1984). DeVries (1994) emphasized the importance of such studies as a basis for understanding Neotropical butterfly communities, encouraging studies of life histories. The Ithomiinae, along with the Heliconiini, attracted the attention of early naturalists as central models of mimicry rings in the Neotropics (Bates 1862, Muller 1879), but there are few works concerning population ecology of ithomiine butterflies (Brown & Benson 1974, Drummond 1976, Haber 1978, Vasconcellos-Neto 1980, 1986, 1991, Young & Moffett 1979, Freitas 1993).

Heterosais edessa is a common ithomiine species found in humid primary and secondary forests, mostly in coastal southeastern Brazil, being rare on mountain slopes and nearly absent on the central plateau. Other closely related species or subspecies extend throughout the Amazon and as far northwest as Costa Rica. *Heterosais* is considered one of the most advanced genera within the Ithomiinae (Brown & Freitas 1994), and the study of ecological parameters in this genus may help in the understanding of the evolution of this subfamily.

This paper describes the juvenile biology of *H. edessa* and its adult population ecology in relation to other species of the associated ithomiine community.

STUDY SITE AND METHODS

Observations were made from July 1988 to July 1992, in the locality of "Morro do Japuí" (46°24'W 23°59'S), São Vicente, São Paulo, Brazil. The study area is covered by submontane rain forest (Ururahy et al 1987), with an annual rainfall near 2500 mm and an average annual temperature of 21°C (Setzer 1949, Prodesan 1969, Nimer 1972). A large part of the area is secondary forest, with a predominance of forest edge plants. A detailed map of the locality is given in Freitas (1993).

In order to study the life cycle of *H. edessa*, eggs and larvae were collected on individuals of the host plant species, *Cestrum laevigatum* Schldl. (Solanaceae), in the forest. Larvae were reared on leaves of this host in plastic boxes, cleaned daily. Egg size is presented as length and diameter, and the head capsule size of larvae as the distance between the most external ocelli (as in Freitas 1991, 1993, and Freitas & Oliveira 1992). All measurements were made using a microscope fitted with a calibrated micrometric ocular.

A mark-recapture census for *Heterosais edessa* and 18 other Ithomiinae was conducted from May 1991 to May 1992. Visits were made from 1 to 5 times per week, except from December 1991 to April 1992 (less than once a week). Data on some species were also gathered from 14 January to 11 March 1989. Butterflies were captured with an insect net, individually numbered on the underside of the forewings with a felt-tipped pen, and released at the site of capture. The characteristics of each individual (sex, age, site of capture, source of nectar, and other activities) were recorded for later analysis. The age of individual butterflies was estimated in six categories based on wing wear (Ehrlich & Davidson 1960, Brussard & Ehrlich 1970, Ehrlich & Gilbert 1973, Brown et al. 1981, Freitas 1993). Males and females were analyzed separately. Time of residence (permanence) in the population was estimated following Brussard et al. (1974), as days elapsed between marking and last recapture. This parameter is related to the survivorship of the adults.

Rates of flower visitation were recorded during the 12 months of population studies of *Heterosais edessa*. A plant species was classified as highly visited if 50 or more individuals of *H. edessa* were observed feeding on its flowers, intermediate if 10 to 49 individuals were observed, and low if fewer than 10 individuals were observed on it during the entire study (as in Freitas 1993).

RESULTS

Juvenile Biology of *H. edessa*

Drummond and Brown (1987) recorded *Cestrum amictum* Schldl. (Solanaceae) as the larval host of *H. edessa* in coastal São Paulo. In the

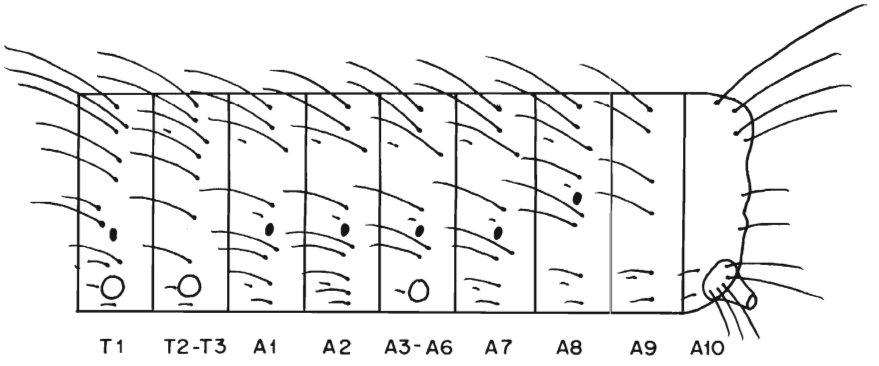

FIG. 1. Distribution of body setae on the first instar larva of *Heterosais edessa*.

Morro do Japuí study site, females followed oviposited only on *Cestrum laevigatum* Schldl. Eggs were laid singly on the underside of old leaves. In general, only one or two eggs were present on each leaf, but as many as six eggs were observed on the same leaf on plants protected from direct sunlight. Although this was not quantified, eggs and larvae were more commonly found on the host plants from April to August.

After hatching, caterpillars ate the entire egg shell. The caterpillars were very sensitive to low humidity and died rapidly in drier environments. Although solitary, larvae were not cannibalistic; several larvae of different instars could be reared together without losses. The caterpillars rested in a J-shaped position on the underside of the leaves. The caterpillars ate all the leaf tissue, even in the first instar. When disturbed, caterpillars could suspend themselves from silk threads, but this behavior was not frequently observed. Pupation usually occurred off the host plant, on neighboring plants but some pupae were found on leaves and stems of *C. laevigatum*.

Egg. White, ovoid (truncated at bottom) with 23 longitudinal ridges and 11 transverse ridges; diameter 0.7 mm, height 0.6 mm. A line drawing of the egg was published by Brown and Freitas (1994).

First instar. Translucent white with transparent head capsule, becoming pale green after feeding; average width of head capsule 0.39 mm (sd=0.02, n=4); distribution of setae as in Fig. 1. Duration 3–4 days.

Second instar. Pale green with a transparent head capsule, dark intestinal contents evident; average width of head capsule 0.58 mm (sd=0.04, n=11). Duration 3–4 days.

Third and fourth instars. Similar to previous instar, with progressively darker green pigmentation; head capsule entirely transparent. Fourth instar larvae with narrow lateral yellow stripe (see also Brown & Freitas 1994). Average width of third instar head capsule 0.9 mm (sd=0.04, n=13); duration 3–4 days. Average width of fourth instar head capsule 1.35 mm (sd=0.05, n=8); duration 3–4 days.

Fifth instar. Green, with narrow lateral yellow stripe (see Brown & Freitas 1994). Head capsule entirely transparent with dark area in ocellar region. Dorsal vessel clearly

TABLE 1. Mark-recapture study of *Heterosais edessa* in Morro do Japuí, Sao Paulo, Brazil. L = maximum longevity, M = maximum movement, m = males, f = females, cap = total, recap = total recaptured.

									Multiple Recaptures				
	CAP		RECAP						males			females	
Month	m	f	m	f	Lm	Lf	Mm	Mf	1	2	3	1	2
May 91	18	2	2	0	3	—	50	—	2	—	—	—	—
Jun 91	11	0	4	0	2	—	100	—	4	—	—	—	—
Jul 91	84	54	17	11	65	21	300	100	14	2	1	11	—
Aug 91	49	33	12	9	23	13	280	100	10	—	2	7	3
Sep 91	7	11	3	6	10	39	100	50	3	—	—	3	3
Oct 91	2	1	0	0	—	—	—	—	—	—	—	—	—
Nov 91	6	1	0	0	—	—	—	—	—	—	—	—	—
Dec 91	1	0	0	0	—	—	—	—	—	—	—	—	—
Jan 92	3	3	0	0	—	—	—	—	—	—	—	—	—
Feb 92	0	0	0	0	—	—	—	—	—	—	—	—	—
Mar 92	0	0	0	0	—	—	—	—	—	—	—	—	—
Apr 92	0	0	0	0	—	—	—	—	—	—	—	—	—
May 92	10	2	1	0	17	—	100	—	1	—	—	—	—
Totals	192	107	37	26	65	39	300	100	32	2	3	21	6

visible. Maximum length 26 mm. Average width of head capsule 2.69 mm (sd=0.21, n=9). Duration 4–6 days.

Pupa. Green, strongly humped (bowed), 0.9 × 1.2 mm; light green first day, acquiring gold stripes after one or two days. A few scattered black dots on wing cases and in ocular area (see Brown & Freitas, 1994). Duration 9 to 11 days.

Adult Ecology of *H. edessa*

In total, 299 adult *H. edessa* were captured during 12 months of study, with 63 later recaptured. Fig. 2 shows individuals present per day; when an individual was recaptured it was considered present in the population on all previous days since the day of first capture. Adults were most abundant from May to September, with abundance decreasing after October and maintaining low population levels during the following months (Table 1). During a short capture period, from January to March 1989, 23 individuals of *H. edessa* were captured on flowers of *Adenostemma viscosum* Forst. (Asteraceae) inside the forest. The population appeared to be breeding continuously, with some peaks (Fig. 2).

The sex ratio of *H. edessa* in the field deviated from 1:1 (197 males and 107 females marked; χ^2=24.2, df=1, p<0.001). Males were the dominant sex throughout the study, except in September 1991 and January 1992 (Fig. 3). The proportions of recapture of males (19.3%) and females (24.3%) can be considered equal (χ^2=0.71, df=1, p>0.20).

For the analysis of age structure, the six initial age categories were grouped into three: new, intermediate, and old (as in Freitas 1993).

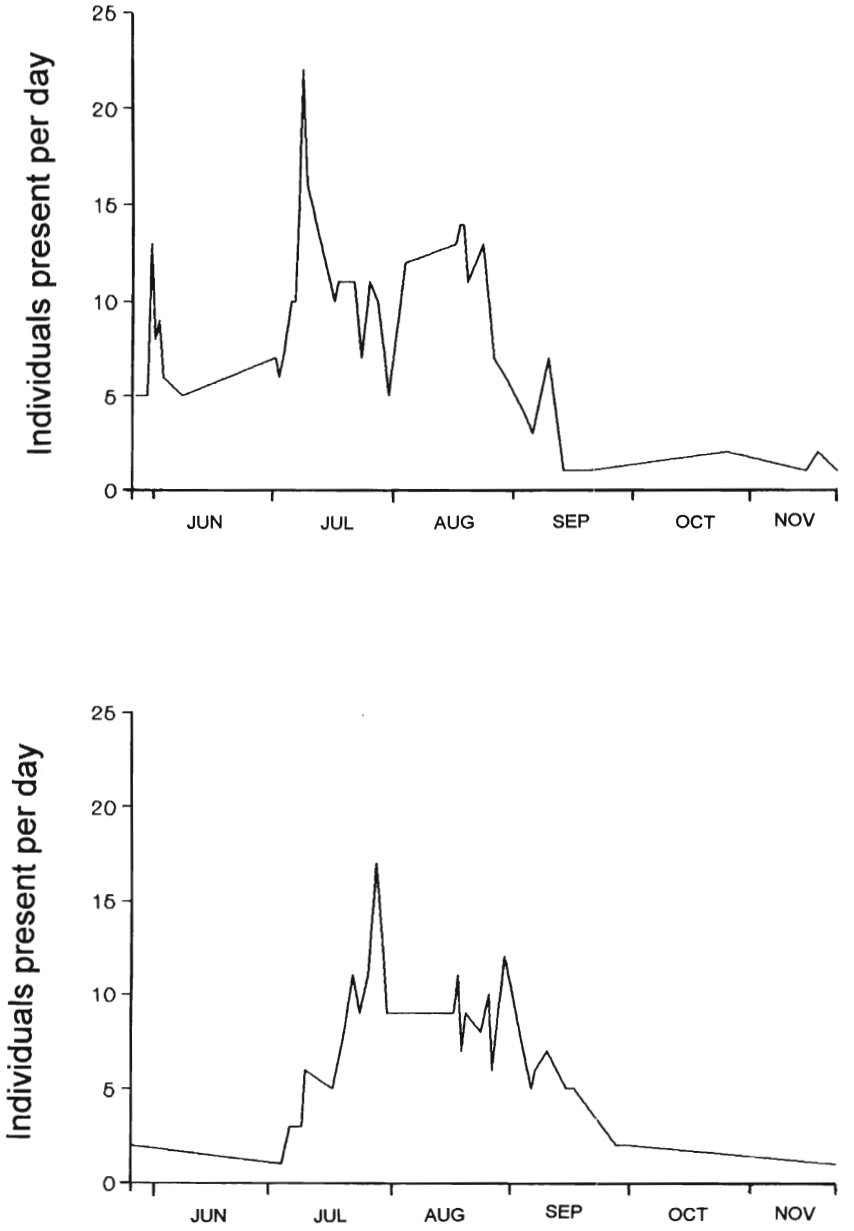

FIG. 2. Individuals of *H. edessa* present per day in Morro do Japuí: males (upper) and females (lower).

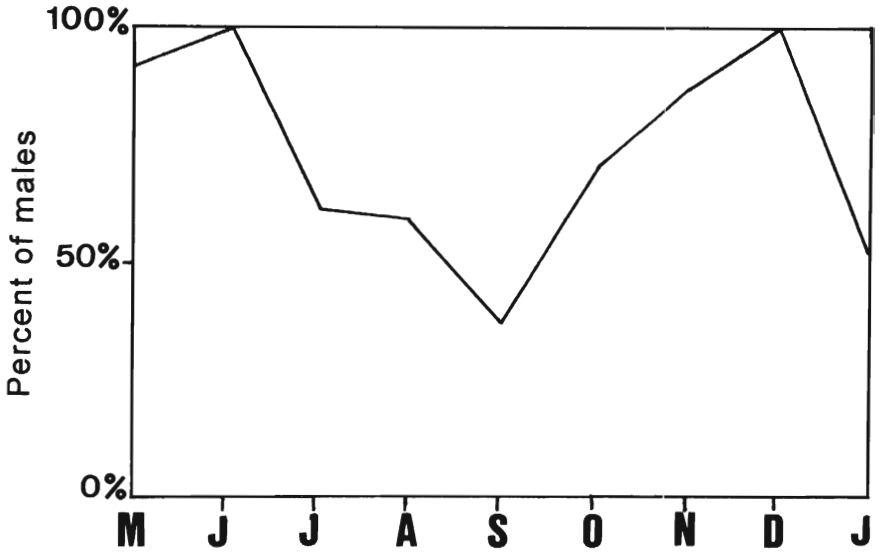

FIG. 3. Sex ratio for *H. edessa* marked in the Morro do Japuí, as percent of males in each day's capture.

Data for males and females were grouped to increase the total data and enhance perception of age patterns along time. The age structure of *H. edessa* was dominated by new and intermediate individuals during most of the study. Old individuals appeared mainly after July, with little increase in number during the following months (Fig. 4). No emergence peaks of new individuals were observed throughout the study, and new individuals reached 100% only on days with only one or two individuals captured.

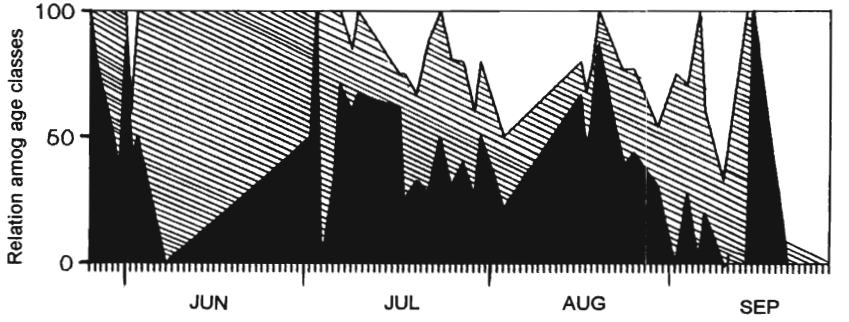

FIG. 4. Age structure of *H. edessa* (males and females grouped) in Morro do Japuí, May to September 1991: black=fresh (new) individuals, hatched=intermediate, white=old, as percent of total for each day.

TABLE 2. Permanance of marked *Heterosais edessa*: days elapsed between marking and last recapture represent the minimum permanance (MP) for each individual.

MP	Males	Females	Total
1–5	16	9	25
6–10	7	5	12
11–15	4	2	6
16–20	3	3	6
21–25	2	5	7
26–30	—	2	2
31–35	1	—	1
36–40	1	1	2
> 40	3	—	3

The movement of adults was limited, and the distance between release site and recapture rarely exceeded 100 m. Of the 63 recaptures, 28 males (75.7%) and 23 females (88.5%) were less than 100 m from the site of first capture, and the other 9 males and 3 females were 100–300 m away. Males had a residence time (12.9 days, sd=15.1, n=37) practically equal to females (13.5 days, sd=10.3, n=26) (Table 2).

Nectar sources utilized by *H. edessa* are available during the entire year, as shown in Table 3. Some individuals were also observed on bird droppings and broken stems of several *Eupatorium* species. Adults were often encountered near a nectar source, but sometimes they were observed flying low inside the forest or near streams and valleys many times away from any nectar source. Adults were frequently found on flowers of Asteraceae, flying erratically near the ground (rarely over 1 m), like other transparent species of Ithomiinae found in the study area (such as *Pseudoscada erruca* (Hew.), *Oleria aquata* (Weymer), *Pteronymia carlia* Schaus, *Hypoleria adasa* (Hew.), *Ithomia drymo* Hübner, *I. agnosia zikani* D'Almeida and *I. lichyi* D'Almeida).

The Ithomiinae Community in Morro do Japuí

Besides *H. edessa* and the seven species mentioned above, another 12 ithomiine species were present in the study area, including: *Melinaea ludovica paraiya* Reakirt, *M. ethra* (Godart), *Placidula euryanassa* (Feld. & Feld.), *Methona themisto* (Hübner), *Mechanitis l. lysimnia* (Fabricius), *M. polymnia casabranca* Haensch, *Epityches eupompe* (Geyer), *Hypothyris ninonia daeta* (Boisduval), *Dircenna dero celtina* (Burmeister), *Prittwitzia hymenaea* (Prittwitz) (one individual in six years), and *Episcada clausina striposis* Haensch. All 12 of these species were also marked and recaptured at the same time as *H. edessa*, but some species were not abundant enough to permit continuous graphs of population dynamics (Fig. 5). Other Ithomiinae found in hills up to 5 km around

TABLE 3. Nectar sources visited by adult *Heterosais edessa* during 1989–1992 in Morro do Japuí, S. Vicente, Brazil. Continuous lines are periods of intense flowering, broken lines indicate few flowers available (1–5 individuals with flowers). Level of visitation of nectar sources: *** = high, ** = intermediate, * = low. *Vernonia condensata* and *Persea americana* are introduced plants in the study area.

Nectar source	J	F	M	A	M	J	J	A	S	O	N	D
ASTERACEAE												
Eupatorium vitalbae D.C. *						..	———	———	———	..		
E. laevigatum Lam. ***				..	———	———	...					
E. punctulatum D.C. *										..	———	..
E. inulaefolium H.B.K. *		..	———	———	...							
Mikania lundiana D.C. *		..	———	...								
M. micrantha H.B.K. *			..	———	.....							
M. cordifolia (L.F.) Willd *			..	———	.....							
Trixis antimenorrhoea Mart. ex Baker **					...	———	...			....		
Vernonia condensata Baker ***					..	———	.....					
V. beyrichii (Less.) *				..	———	...						
V. scorpioides (Lam.) *					...	———	———	———	———	———	...	
Adenostemma viscosum Forst. ***		———	.....							..	———	
Ageratum conyzoides Linn. *	———	———	———	———	———	———	———	———	———	———	———	———
Bidens pilosa Linn. *	———	———	———	———	———	———	———	———	———	———	———	———
Emilia sonchifolia D.C. *	———	———	———	———	———	———	———	———	———	———	———	———
ROSACEAE												
Rubus rosaefolius Smith. ***				...	———	———	———	———	———	———	.....	
LAURACEAE												
Persea americana Mill **								.	———	....		
BORAGINACEAE												
Cordia verbenacea D.C. *	.....	———	.....	———	.....	———	.....	———	.....	———	.....	———

the study area were *Aeria olena* Weymer, *Callithomia lenea* (Cramer), *Thyridia psidii cetoides* (Rosenberg & Talbot), *Pteronymia euritea* (Cramer) and an as yet undescribed subspecies of *Pseudoscada quadrifasciata* Talbot. These five species are probably present erratically in the study site, perhaps even as established colonies, since the foodplants are available and the characteristics of the vegetation are the same as in the adjacent forests. As the São Paulo coast receives rainfall all year round, no Ithomiinae "pockets" were observed during the six years of constant visits to the study area, but some small aggregations were found near streams on hot summer days.

Sex ratios. The sex ratios of all species in the study site were male-biased, except in those species with very few individuals marked (Table 4). The sex ratios showed few changes from month to month, and only *I. drymo* showed a tendency for increase in the number of females during the study (Table 5). The two species of *Melinaea* (studied in 1989), showed an extreme case of male-biased sex ratio (Table 6). During the

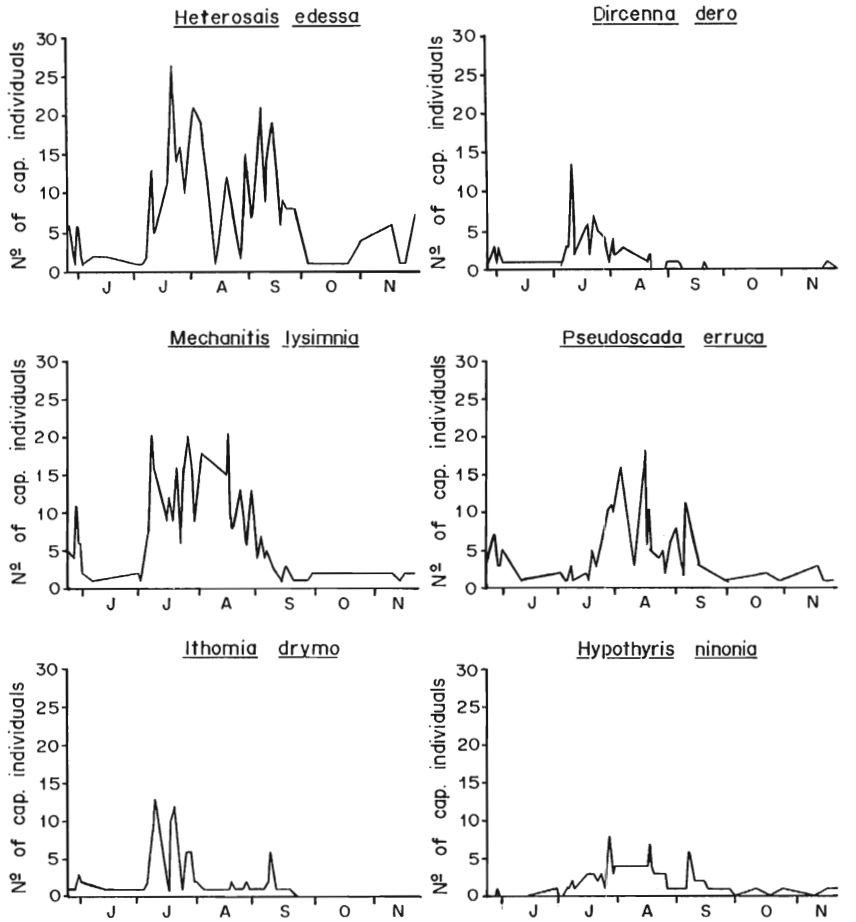

FIG. 5. Individuals of six Ithomiinae species (males and females combined) captured per day in Morro do Japui.

study no females of *Melinaea ethra* and only two of *M. ludovica* were recorded, both flying inside the forest.

Longevity. Permanence in the population (an indirect predictor of life span) was measured only for a few species, due to the low rates of recapture for most. In three species studied in 1991–1992 (*M. lysimnia*, *D. dero* and *H. edessa*) and in the two *Melinaea* studied in 1989, average permanence was typically more than 10 days (though near this in females of *D. dero*), except in *P. euryanassa*, (average less than 10 days; Freitas 1993). In all species studied, maximum permanence was over one month, exceeding two months in some species (Table 7).

TABLE 4. Sex ratios of 18 Ithomiinae species captured in Morro do Japuí, S. Vicente, Brazil, from 26 May 1991 to 26 May 1992. Asterisks indicate sex ratios significantly different ($p<0.05$) from 1:1 using chi-square. Percent total = percentage of all captures represented by that species. Days present = number of days a given species was present during the entire study.

Species	Males	Females	Total	Percent Total	Days present
P. euryanassa *	414	301	715	38.6	50
H. edessa *	192	107	299	16.1	49
M. lysimnia *	182	88	270	14.6	47
D. dero *	90	61	151	8.1	46
I. drymo	64	45	109	5.9	34
M. polymnia *	68	30	98	5.3	33
P. erruca *	48	20	68	3.7	29
H. ninonia *	32	16	48	2.6	20
P. carlia	13	10	23	1.2	19
H. adasa	12	9	21	1.1	15
O. aquata	11	4	15	0.8	12
M. ludovica *	10	2	12	0.6	6
M. themisto	3	6	9	0.5	5
M. ethra *	5	1	6	0.3	4
E. eupompe	1	2	3	0.2	2
E. clausina	1	1	2	0.1	2
I. lichyi	1	1	2	0.1	1
I. agnosia	1	0	1	0.1	1

TABLE 5. Sex ratios for four Ithomiinae species marked in Morro do Japuí, given as percent (boldface) of males in the total (T) for each month.

Species	May T/%	Jun T/%	Jul T/%	Aug T/%	Sep T/%	Oct T/%	Nov T/%
D. dero	14/**71**	6/**83**	40/**57**	35/**51**	23/**52**	3/**67**	5/**60**
M. lysimnia	15/**80**	7/**86**	119/**68**	43/**62**	46/**54**	5/**80**	15/**67**
I. drymo	2/**100**	7/**86**	73/**62**	10/**50**	10/**30**	0/**0**	0/**0**
P. erruca	4/**75**	4/**100**	48/**62**	8/**87**	2/**100**	1/**100**	1/**100**

TABLE 6. Populational parameters for *Melinaea ludovica* and *M. ethra*, 14 January 1989 to 11 March 1989. TM = total marked, TC = total captured, MOV = maximum movement (meters), PER = maximum permanance (days), x = average permanance (with standard deviation), m = males, f = females. All males collected were feeding on *Adenostemma viscosum*.

	TM		TR	MOV	PER		Multiple recaptures			
	m	f	m	m	m	x	1	2	3	4
M. ludovica	113	2	32	300	55	14.1 ± 14.1	25	5	2	0
M. ethra	115	0	33	300	47	13.7 ± 12.9	25	4	2	2

TABLE 7. Permanence in the population for four species of Ithomiinae studied in Morro do Japuí, 1991–1992. x = average permanance (days, with standard deviation).

Species/sex	x	range	SD	N
P. euryanassa males	8.4	1–45	8.3	149
P. euryanassa females	7.2	1–23	5.7	112
M. lysimnia males	15.5	1–67	15.4	72
M. lysimnia females	18.3	1–72	16.2	31
D. dero males	9.4	3–23	6.9	21
D. dero females	10.9	3–49	10.5	23
H. edessa males	12.9	1–65	15.1	37
H. edessa females	13.5	2–39	10.3	26

All species studied showed a peak of abundance between July and August (Figs. 2, 5; see also Freitas 1993 for abundance graphs of *P. euryanassa*), except the two *Melinaea* species, which were most abundant from November to March (summer months); in 1991–1992 they were not as abundant as in 1989 and 1990.

Food sources. Adult Ithomiinae were usually observed on flowers, especially of Asteraceae (Table 8). Nectar sources in the study site were available all year round (Table 3). All species showed a preference for flowers in the Asteraceae, except the transparent blue Ithomiinae species (*H. edessa, I. drymo, I. lichyi, I. agnosia, P. erruca, P. carlia* and *O. aquata*), that prefered flowers of *Rubus rosaefolius* (Rosaceae), all year (Table 8; other transparent blue species not present in the Table were also captured mostly on these flowers: *H. adasa*, 17 of 22 feeding records; *P. carlia*, 12 of 23; *O. aquata*, 6 of 7). The apparent strong pref-

TABLE 8. Frequency of flower visitation for 8 species of Ithomiinae studied in Morro do Japuí, 26 May 1991 to 16 May 1992. Plants with an asterisk are known PA sources. Bold numbers indicate that visitation is male biased. Results presented as males/females. See Table 3 and text for full names of plants and butterflies (*A.cura.* = *Asclepias curassavica*).

	Pla. eur.	*Mec. lys.*	*Mec. pol.*	*Dir. der.*	*Het. ede.*	*Ith. dry.*	*Hyp. ada.*	*Pse.* err.
E.laev. *	**81/34**	**27/4**	30/19	**34/11**	**24/4**	2/0	4/0	0/1
E.punc. *	2/0	—	1/0	1/0	1/0	—	—	—
M.lund.	4/2	0/1	—	3/1	1/3	2/2	—	—
T.anti.	24/13	3/4	—	2/0	6/3	8/9	—	3/4
V.cond.	**167/111**	**61/33**	2/1	45/56	31/30	6/2	11/10	4/2
R.rosa.	23/15	36/29	0/1	8/9	**106/74**	32/26	15/16	**34/14**
P.amer.	274/265	27/28	—	16/16	6/12	3/2	4/3	—
C.verb.	13/7	4/4	—	3/0	0/1	2/0	—	—
A.cony. *	0/1	1/0	—	—	—	—	—	—
V.scor.	0/1	1/0	—	—	—	—	—	—
A.visc. *	—	3/0	6/0	—	1/1	—	—	—
A.cura.	—	—	1/0	0/1	—	—	—	—

erence of *P. euryanassa* for flowers of *Persea* (Table 3) may have been due to chance, since this seemed to be the most abundant flower during the population peak of this species (Freitas, 1993). In general, the records of males and females were near 1:1 on all nectar sources. On *E. laevigatum* males were more abundant for most of the species. In 1989, *Adenostemma viscosum* also attracted mainly males of *Melinaea* (Table 6), as well as *H. edessa* (25 males and no females) and *O. aquata* (21 males and 1 female). Adult Ithomiinae individuals of both sexes were also observed puddling on mud, and feeding on bird droppings, rotting fruits, and broken stems of several *Eupatorium* species.

Species composition. Data on relative species abundance were analyzed only for the period from 26 May to 23 November 1991, when individuals were most abundant and the censuses were more frequent. Throughout this period, four species (*P. euryanassa*, *H. edessa*, *M. lysimnia* and *D. dero*) accounted for at least 70% of the captured Ithomiinae on any day (see also Table 4 and Fig. 6A). The number of species captured per day varied from 2 to 13 (mean 6.96, sd=2.6, n=54), with at least 6 species present on most days (Fig. 6B). The most abundant species were also the ones that were seen on most days (Table 4), showing that they were well distributed throughout the year (see also Fig. 5, and Freitas 1993). The days with more than six species captured were mostly in July and August, also the period when the largest number of individuals were seen per day (Fig. 6B). The abundance of some species varied from year to year: *Ithomia lichyi* was very abundant in 1989 and 1990, but *I. agnosia* and *E. clausina* were always sparse from 1988 to 1993. Some abundant species may be rare in other years: *Pseudoscada erruca*, a moderately common species from 1988 to 1993, was practically absent in the first part of 1994 in Morro do Japuí, although it continued to be common in other forests near the study area.

DISCUSSION

Biology of *H. edessa*

Heterosais edessa has immatures typical for its tribe (Godyridini), with solitary larvae, little pigment in the larval cuticle including cephalic capsule, and a bent, green pupae; all these are considered derived traits in the Ithomiinae (Brown & Freitas 1994). Although larvae are solitary, they do not exhibit cannibalistic habits, common in solitary larvae of Heliconiini (Brown 1981 and pers. obs.). Several other Ithomiinae with solitary larvae were also not aggressive towards other smaller larvae (pers. obs.); this trait may have allowed the development of gregarious behaviour in Ithomiinae larvae. In fact, gregarious larvae are considered to be a polyphyletic trait in Ithomiinae, appearing erratically in many Ithomiinae radiations (see Brown & Freitas 1994).

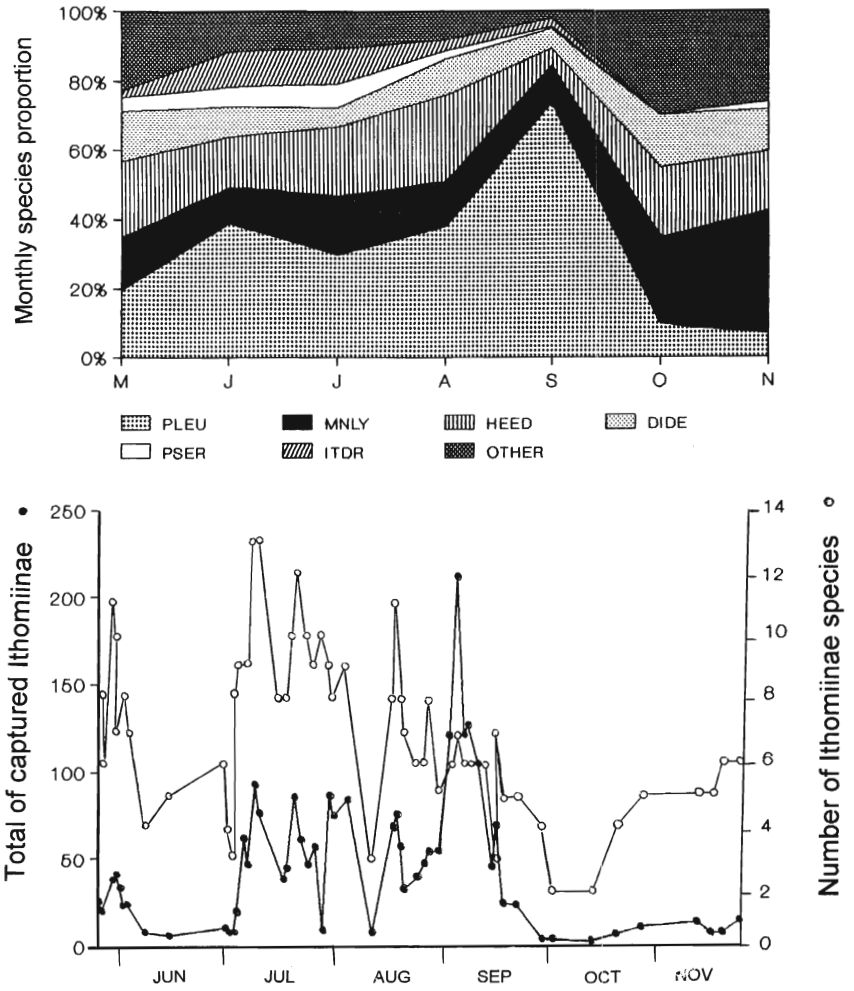

FIG. 6. Upper: species ratio of Ithomiinae captured in Morro do Japuí from May to November 1991. Bottom: total of individuals of all Ithomiinae captured in Morro do Japui from May to November 1991 (filled circles) and number of Ithomiinae species captured per day in the same period (open circles).

The general behavior of *H. edessa* larvae, like the J-shaped resting position and the suspension by silken threads when disturbed, is very similar to that of other known Ithomiinae (Brown & D'Almeida 1970, Young 1972, 1974a, 1974b, 1974c, 1978a, 1978b, Ackery 1987). Larvae of *H. edessa* are basically cryptic in color pattern and behavior.

The Ithomiinae Community of Morro do Japuí

Although more abundant in the winter months, *H. edessa* is found in Japuí all year round; the low numbers in some months may be due mostly to the low number of plants in bloom. This pattern of fluctuation seems to be present in varying degrees in most Ithomiinae (Vasconcellos-Neto 1980, Freitas 1993). The vagility of *H. edessa* is low, with individuals usually tracking their nectar sources. Because the larval food plants are present throughout the area, females do not need to search widely to find them, so both male and female movement is more related to nectar sources.

Sex ratio was male biased in *H. edessa* and seven other ithomiine species. Male biased sex ratios in the field have been reported for many species of butterflies, even when sex ratio in the laboratory was 1:1 (Brussard & Ehrlich 1970, Brussard et al. 1974, Brown & Ehrlich 1980, Matsumoto 1984, 1985, Freitas 1993). In the Ithomiinae, the predominance of males in field collections has been attributed to their appearance at sources of pyrrolizidine alkaloids (PAs) (Brown 1985, Trigo 1988, Freitas 1993), as seen with *E. laevigatum* in this study. The fact that male biased sex ratios were also detected on other plants (e.g., *R. rosaefolius*) may be explained by the existence of behavioral differences between males and females (Ehrlich 1984), resulting in males generally flying in the same places as the collectors, with females more dispersed throughout the habitat.

The residence times of *H. edessa* and the other Ithomiinae in the study area were relatively high compared to species in other butterfly families, but were lower than those for species of *Heliconius* in the same area (Rogner & Freitas, unpubl. data). Some individuals may survive for more than two months, and two females older than 30 days were observed ovipositing and with apparently distended abdomens, indicating continual egg production as in *Heliconius* species (Dunlap-Pianka et al. 1977). The relatively short lifespan of Ithomiinae in this study site in relation to that in other regions (Vasconcellos-Neto 1980, Brown 1985) may be due to the continuously humid climate, and concomitant lack of reproductive diapause in this region. The age structure of adult *H. edessa* shows that the population has continuous recruitment of new individuals throughout the year, though probably diminished from July to December. These data suggest that *H. edessa*, like most other Ithomiinae in the study site, is more K-selected (Pianka 1970) than *Placidula euryanassa* (Freitas 1993).

The Ithomiinae community in Morro do Japuí is typical for the São Paulo coastal region. The absence of montane species results in a low richness in relation to the interior (28 species in the "Serra do Japi," in-

terior of São Paulo; Brown 1992), although some species like *H. edessa* are absent in the interior, or occur only as migrants from the coast (the two *Melinaea* and *O. aquata*). Also, several species in the coastal Atlantic transparent yellow complex (Brown & Benson 1974) are absent in the region (like *Scada karschina*), appearing only 100 km east of São Vicente in São Paulo state (São Sebastião municipality).

The number of species captured per day throughout the year was almost always more than six, reaching 13 on some days, with high numbers of individuals, reflecting a relatively high diversity. Eleven species are common enough to be captured on almost any day in the study site. A relatively complete list of Ithomiinae of a given coastal São Paulo site may be obtained in four to five days of intense work from June to September, especially with the use of *Heliotropium indicum* baits to attract males of rarer species, or by searching for the right flowers (habitat "pockets" that concentrate adult Ithomiinae in winter are virtually absent in most of the São Paulo coastal region; see also Brown 1972). A survey of the 26 Ithomiinae species of São Sebastião was made in only seven collecting trips from May to September 1992.

The data presented here provide valuable information for two kinds of community studies. Firstly, the study of plant-based food webs is of great importance in the understanding of tropical ecosystems. For example, the data obtained for a given taxonomic group of herbivorous insects can be useful in studies of diversity and health of a given plant assemblage. This is especially true for groups like Ithomiinae which are rapidly sampled and depend on a diverse set of plants for larval and adult hosts (Gilbert 1980). Ithomiinae have been suggested as especially good indicator organisms for this kind of study (Brown 1991, Beccaloni & Gaston 1995). Secondly, an understanding of the seasonal patterns of each species, as well as their behavior, habits and preferences can lead to greater efficiency in collecting data in a given area, especially if many areas must be surveyed in little time. Some sites are difficult to reach, so that the knowledge of which months are better to census butterflies is valuable to those who intend to carry out inventory and monitoring.

The present paper attempts to define some of these patterns for the São Paulo coastal forests, to help future work in this region. Similar work is needed in other areas to reveal the different patterns, especially in places with marked seasonality or with different climatic regimes.

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