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BIOLOGY AND POPULATION DYNAMICS OF *PLACIDULA EURYANASSA*, A RELICT ITHOMIINE BUTTERFLY (NYMPHALIDAE: ITHOMIINAE)

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ABSTRACT. *Placidula euryanassa* is a primitive ithomiine restricted to the Atlantic coast of South America. Females lay eggs in clusters on *Brugmansia suaveolens* (Solanaceae). The larvae are gregarious, passing through five instars. Pupation occurs off the host plant; adults emerge after 8 to 14 days. In the laboratory the sex ratio is statistically equal to unity; in field captures the sex ratio is male biased. Individual mobility is low and the population size varies greatly during the year. Adults show a type II survival curve. Many biological features indicate that *Placidula* is relatively more r-selected than most Ithomiinae.

Additional key words: immatures, r-strategist, mark-recapture, Solanaceae.

Placidula euryanassa (Felder & Felder) is a member of the subfamily Ithomiinae. The systematic position of the species is uncertain (Brown 1987, Motta 1989). The genus *Placidula* is monotypic (Fox & Real 1971), with little or no morphological variation observed throughout its geographic distribution in southeastern Brazil and neighboring countries (D'Almeida 1938, Fox 1940, 1961, Biezanko 1960a, 1960b, Brown & Mielke 1967, Zikán & Zikán 1968, Fox & Real 1971, Brown 1979). Larvae of *Placidula euryanassa* have been found on the solanaceous plants *Brugmansia suaveolens* (Willd.) (= *Datura suaveolens* and *D. arborea*), *B. candida* Pers., *Datura stramonium* L., *D. metel* L., and *Cyphomandra betacea* Sendt. (D'Almeida 1938, Biezanko 1960a, 1960b, D'Araujo e Silva et al. 1968, Brown 1987, Drummond & Brown 1987). The last host plant may be incorrectly recorded (K. S. Brown pers. comm.).

The study of the biology of isolated genera of Ithomiinae is important for understanding relationships between this subfamily and its sister

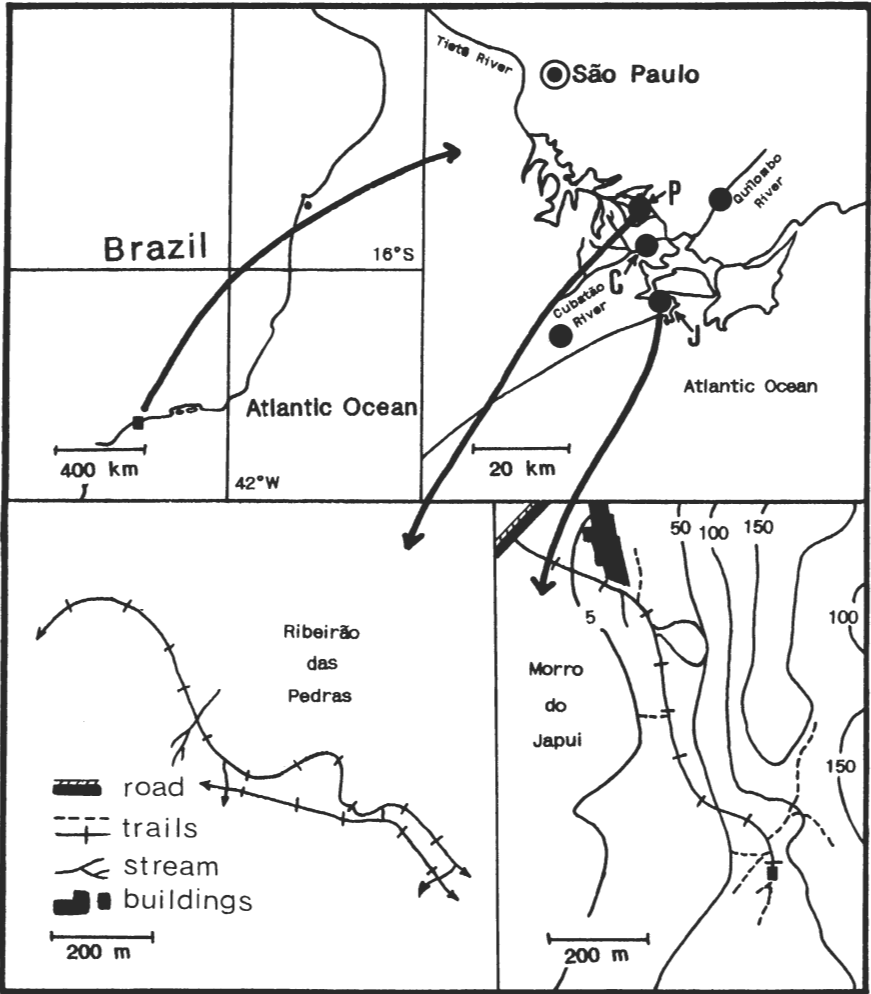


FIG. 1. Study areas in Southeast Brazil. In regional map (upper right), C = Vale do Rio Cubatão, J = Morro do Japui, P = Ribeirão das Pedras. Two additional sampling sites are represented by solid circles.

group Danainae, and the evolution of these two groups (Gilbert & Ehrlich 1970, Young 1978a, Ackery & Vane-Wright 1984, Ackery 1987). Although *P. euryanassa* is considered a primitive ithomiine (Brown et al. 1991), it has many particular features that make it remarkable among the butterflies in this subfamily (the furry aspect of the larvae, the aggregative behavior of larvae, oviposition in large clusters, finely striated pupae). Previous workers have described some of these characteristics (D'Almeida 1938, Fox & Real 1971).

This paper reports on the early stages, larval host plant, habits, and population dynamics of *P. euryanassa*, and relates these features to those of other ithomiines.

STUDY SITES AND METHODS

Observations were made from 1 July 1988 to 30 December 1991, at five sites in São Paulo state, southeastern Brazil. One site is on the coastal plain (0–150 m elevation), three on lower mountain slopes (100–300 m elevation), and one on top of the Serra do Mar (750–800 m elevation), a mountain chain along the Atlantic coast (Fig. 1). Populations in the first and the last places, Morro do Japuí and Ribeirão das Pedras, respectively, were studied most intensively. The Ribeirão das Pedras site (46°31'W 23°49'S) supports montane rain forest (Ururahy et al. 1987) with an annual rainfall of over 4000 mm and an average annual temperature of 18°C (Setzer 1949). A large part of the area is old secondary forest, with a predominance of forest edge plants in the families Solanaceae, Melastomataceae, and Asteraceae. The Morro do Japuí site (46°24'W 23°59'S) supports 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 this area is secondary forest, with a predominance of forest edge plants.

Eggs usually were collected in the field, but some were obtained in the laboratory from females. Three fertile females laid eggs in a glass jar covered with netting, with a leaf of the host plant and a cotton wad soaked in water/honey (3:1). When the jar was heated by a 100 W tungsten bulb at a distance of 20 cm (Freitas 1991), females increased their activity, and after 5–20 minutes began to oviposit. Larvae were reared on leaves of their natural host plant, in plastic boxes covered with netting. The boxes were cleaned daily.

Egg size is presented as height and width. The head capsule size of larvae is the distance between the most external ocelli (as in Freitas 1991). All measurements were made using a microscope with a calibrated micrometric ocular.

A mark-recapture census was conducted during March–December 1990 in Ribeirão das Pedras, and January–December 1991 in Morro do Japuí (Table 1). Visits to Ribeirão das Pedras were 1–3 times per week, and to Morro do Japuí 1–5 times per week. Butterflies were captured with an insect net, individually numbered on the underside of the forewings with a felt-tipped pen, and released at the point of capture. Several characteristics of each individual (sex, age, point of capture, source of nectar, and other activities) were recorded for later analysis.

TABLE 1. Mark-recapture studies of *Placidula euryanassa* in São Paulo, Brazil. Cap = total captured, Recap = total recaptured, L = maximum longevity, M = maximum movement.

Month	Cap		Recap		L	M	Multiple recaptures						
	♂	♀	♂	♀			1	2	3	4	5	6	7
1990: Ribeirão das Pedras													
Jan	0	0	0	0	—	—	—	—	—	—	—	—	—
Feb	0	0	0	0	—	—	—	—	—	—	—	—	—
Mar	2	1	0	0	—	—	—	—	—	—	—	—	—
Apr	24	30	2	1	13	50	3	—	—	—	—	—	—
May	6	12	0	0	—	—	—	—	—	—	—	—	—
Jun	13	10	1	0	6	10	1	—	—	—	—	—	—
Jul	0	2	0	0	—	—	—	—	—	—	—	—	—
Aug	0	1	0	0	—	—	—	—	—	—	—	—	—
Sep	0	0	0	0	—	—	—	—	—	—	—	—	—
Nov	0	0	0	0	—	—	—	—	—	—	—	—	—
Dec	0	2	0	0	—	—	—	—	—	—	—	—	—
Total	45	44	3	1	13	50	4	—	—	—	—	—	—
1991: Morro do Japuí													
Jan	0	0	0	0	—	—	—	—	—	—	—	—	—
Feb	0	0	0	0	—	—	—	—	—	—	—	—	—
Mar	0	0	0	0	—	—	—	—	—	—	—	—	—
Apr	1	1	0	0	—	—	—	—	—	—	—	—	—
May	45	22	10	2	8	50	11	1	—	—	—	—	—
Jun	20	7	7	2	8	100	7	1	1	—	—	—	—
Jul	139	70	33	18	43	270	36	11	3	1	—	—	—
Aug	75	53	26	22	18	200	31	13	3	1	—	—	—
Sep	158	143	90	88	30	100	81	45	27	15	4	3	3
Oct	1	1	0	0	—	—	—	—	—	—	—	—	—
Nov	1	2	0	0	—	—	—	—	—	—	—	—	—
Dec	1	0	0	0	—	—	—	—	—	—	—	—	—
Total	440	299	149	112	43	270	135	68	31	17	4	3	3

The "age" of individual butterflies was estimated by rating them in one of six categories based on wing wear (Ehrlich & Davidson 1960, Brussard & Ehrlich 1970, Ehrlich & Gilbert 1973, Brown et al. 1981). Time of residence in the population was estimated following Brussard et al. (1974), and survival curves follow Ehrlich and Gilbert (1973). The butterflies flew slow enough to be captured easily without damage.

The mark-recapture data were analyzed by the Jolly-Seber method for estimating population parameters (Southwood 1971). Males and females were analyzed separately.

Levels of flower visitation were recorded during the two years of population studies. A plant species was classified as highly visited if 50 individuals or more 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 two years of study.

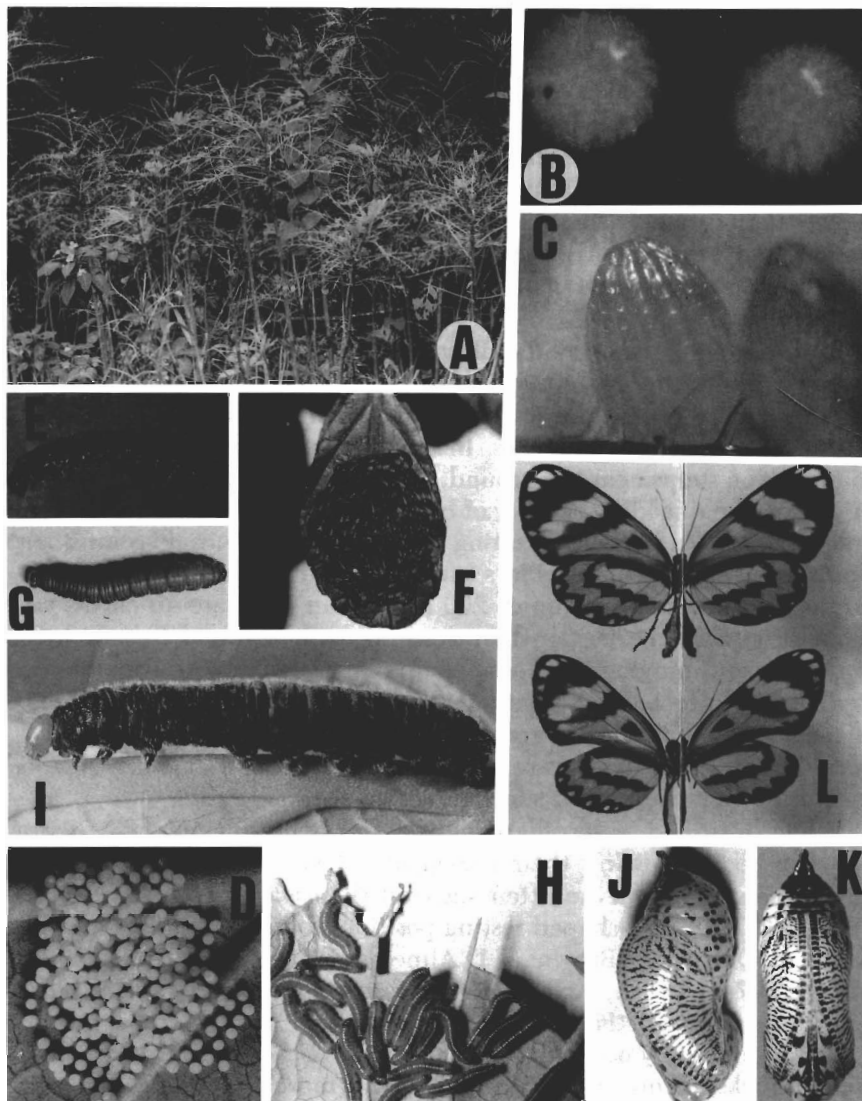


FIG. 2. Natural history of *Placidula euryanassa*. A, defoliated food plants (Ribeirão das Pedras); B, C, 2 eggs (dorsal, lateral); D, egg mass; E, first instar larva; F, group of second instar larvae; G, third instar; H, group of fourth instar larvae; I, fifth instar; J, K, pupa (lateral, ventral); L, adults (female above, undersides on left).

RESULTS

General Biology

Brugmansia suaveolens is the only host plant of *Placidula* in the study areas (Fig. 2A). Before ovipositing, the female usually flies around

the host plant and touches several leaves with its legs and antennae while hovering. After selecting a leaf, the female lands directly on the ventral surface and lays her eggs. Additionally, two egg groups were discovered on boards in contact with the food plant. Eggs were laid in tight clusters (Fig. 2B), generally near water or in very humid sites. On the coastal plain, egg rafts typically were found on leaves 10–100 cm above running water. In Ribeirão das Pedras, all host plants were at least 100 m away from water, but the humidity was very high with mist frequent. Egg rafts contained 107 to 307 eggs (\bar{x} = 212.5; SD = 71.3; n = 9).

After hatching, caterpillars eat part of the egg shell. The caterpillars are very sensitive to low humidity and die rapidly in drier environments. The larvae are gregarious in all stages, resting in compact groups on the lower surface of the leaves. In the fifth instar, however, they rest in groups on stems near the ground, climbing up only to feed on leaves. High nocturnal feeding activity of larvae was observed in the laboratory and on a garden plant, suggesting a pattern of nocturnal feeding and diurnal resting. The caterpillars eat all the leaf tissue, leaving only the larger veins. A single group of 200 larvae can defoliate an entire host plant (Fig. 2A); the larvae then descend to the ground to search for another plant, moving as a loose chain. On 29 July 1990, Ribeirão das Pedras was affected by a strong frost (-1°C), and many of the *B. suaveolens* on which larval groups were being followed, lost their leaves. Some larval clusters later were found in good condition on nearby plants, indicating that they could survive freezing temperatures.

When disturbed, caterpillars rear up and swing the anterior portion of their body, showing their red head. This is different from other Ithomiinae whose larvae often suspend themselves from silk threads (Young 1972). The J-shaped resting position, common in other Ithomiinae and Danainae (Brown & D'Almeida 1970, Young 1972, 1974a, 1974b, 1974c, 1978b, Ackery 1987), was not observed in the tightly gregarious larvae of *Placidula*.

Pupation usually occurs off the host plant in shaded protected places (under rocks, stems and wood boards) no more than 2 m above the ground. Adult eclosion takes place in the early morning with adults generally flying before midday.

Description of Early Stages

Egg (Figs. 2B, C, D): White, oblong, apex tapering to a slightly flattened acute angle, with 17 to 19 longitudinal ridges and 16 to 18 transverse ridges. Average height 1.0 mm (SD = 0.052, n = 21); average width 0.69 mm (SD = 0.076, n = 26), duration 8 to 10 days (for two ovipositions with 200 and 230 eggs obtained in laboratory). Descriptions

and photographs of the egg of *Placidula* have been presented previously by Motta (1989).

First instar larva (Fig. 2E): Translucent white with a dark brown head, becoming pale green after feeding (due to visible intestinal contents); maximum length 3 mm; average width of head capsule 0.44 mm (SD = 0.013, n = 11), duration always 5 days with synchronized molting (n = 30).

Second instar (Fig. 2F): Pale gray, head pale brown, dark intestinal contents evident; maximum length 5 mm; average width of head capsule 0.63 mm (SD = 0.023, n = 12); duration 5 days (n = 25).

Third instar (Fig. 2G): Pale gray, head reddish brown; maximum length 12 mm; average width of head capsule 1.0 mm (SD = 0.041, n = 19); duration 4 days (n = 25).

Fourth instar (Fig. 2H): Body black following ecdysis; dark gray with a "furry" aspect owing to many short bristles on the cuticle following feeding and growing; head red with black ocelli; maximum length 21 mm; average width of head capsule 1.5 mm (SD = 0.095, n = 22); duration 5 days, with totally synchronized molting (n = 25).

Fifth instar (Fig. 2I): Body black with a furry aspect; head red, ocelli black; maximum length 32 mm; average width of head capsule 2.30 mm (SD = 0.230, n = 13); mean duration 7.3 days (SD = 1.24, n = 24). When placed in pure methanol, the larva shows a striped color pattern similar to that found in danaines and primitive ithomiine butterflies (Ackery & Vane-Wright 1984, Brown 1987).

Prepupa: Assumes a "J" position, fixed on the substrate by the anal prolegs and abundant silk; body black but with a translucent aspect.

Pupa (Figs. 2J, K): Opaque, sometimes a little reflective, with many small black spots, stripes, and other markings; cremaster black; mean duration in autumn (11–23 May 1989) 10.4 days (SD = 0.50, n = 50), significantly shorter than in winter (1–16 August 1989), i.e., 13.9 days (SD = 0.21, n = 22) (Mann-Whitney test, following Brower & Zar 1984, $t = 6.723$, $P < 0.001$). Average length 1.49 cm (SD = 0.086, n = 25).

Descriptions of the adult (Fig. 2L) have been presented previously by Haensch (1909) (as *Ceratinia euryanassa*), D'Almeida (1938), and Fox and Real (1971). The sex ratio of adults obtained in the laboratory (42 males and 67 females from 3 broods) can be considered 1:1 (chi square test; $\chi^2 = 5.73$; $P > 0.05$; $df = 1$).

Adult Population Biology

Of 101 individuals of *P. euryanassa* marked at Ribeirão das Pedras, only four were recaptured. In contrast, 261 of the 739 individuals marked at Morro do Japuí later were recaptured at least once (Table

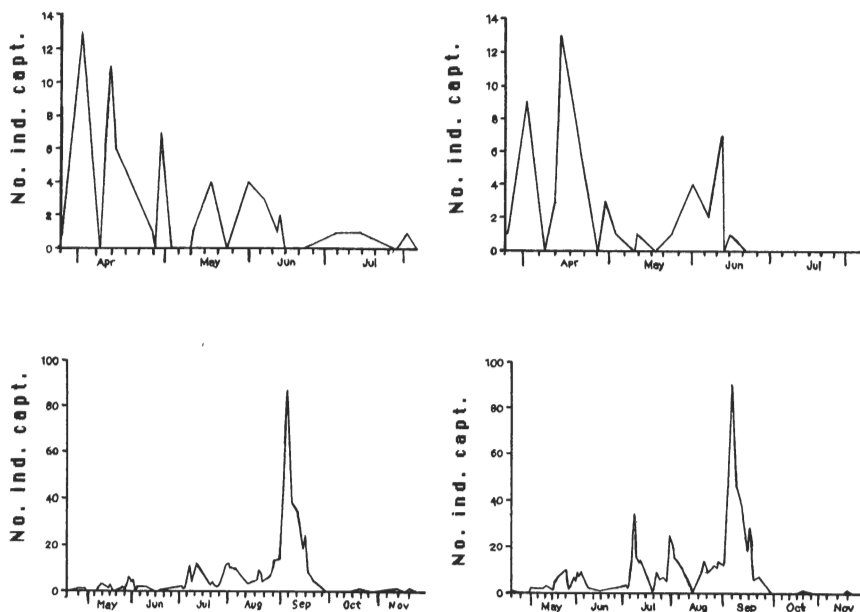


FIG. 3. Daily captures of *P. euryanassa* in Ribeirão das Pedras, 1990 (upper), and in the Morro do Japuí, 1991 (lower), females (left) and males (right). Divisions within months (horizontal axis) represent intervals of 5 days.

1). For this reason, most population parameters were calculated only for the Morro do Japuí population.

At Ribeirão das Pedras, adults were most abundant during April and May, diminishing later in June, and disappearing completely in August. The flight periods of males and females were similar. At Morro do Japuí the population size varied during the year and showed three distinct peaks: small in May, medium in July, and high in August and September. The population of adults diminished abruptly at the end of September, and very few individuals were marked in October, November, and December (Fig. 3). Few individuals of one peak were captured in the following one. The dynamics of the males and females were similar.

Population size was analyzed using the Jolly-Seber method for the three high recapture peaks. The results are presented in Fig. 4. For these three periods, the recaptures were shown to be random by fitting the actual data against a Poisson distribution with the chi-square test.

Sex Ratio

At Ribeirão das Pedras the numbers of males and females were approximately equal (46 males and 55 females marked; $\chi^2 = 1.2$; $P >$

0.20; $df = 1$), except in months with low captures (July and August). However, at Morro do Japu ı the sex ratio could not be considered 1:1 (440 males and 299 females marked; $\chi^2 = 26.9$; $P < 0.001$; $df = 1$). Males were the dominant sex during the study year, except in months with low captures (April, October, and November) (Fig. 5). The proportion of recapture of males (33.9%) and females (37.5%) can be considered equal ($\chi^2 = 1.0$; $P > 0.20$; $df = 1$).

Vagility

At Ribeir o das Pedras the few individuals recaptured were at the same location as marked, and little information could be obtained (although two individuals were recaptured 15 days after marking). At Morro do Japu ı the movement of adults was limited; the distance between point of release and recapture rarely exceeded 100 m. Of 261 recaptures, 125 males (83.9%) and 93 females (83.0%) were recaptured less than 100 m from the site of first capture, and 24 males (16.1%) and 19 females (16.9%) were recaptured 100–300 m away. The greatest distance was 300 m, although some individuals were followed for more than 100 m before being captured. The host plants at Morro do Japu ı are concentrated in a single area 450 m from the most distant point of capture and 100 m from the nearest source of nectar. From 1988 to 1992, some individuals of *P. euryanassa* were collected in the city at least 1000 m away from any place considered suitable for maintenance of a colony. Seven of these were females and two were males. These data provide limited support for the hypothesis that females disperse widely while searching for places to lay eggs. A female transferred from the city to Morro do Japu ı was captured in the same place as released, 20 days later.

Age Structure

The 6 initial age categories were grouped into 3: 1) new, including freshly emerged and new; 2) intermediate (the same); and 3) old, including old, very old, and tattered.

At Ribeir o das Pedras, the age structure of the *P. euryanassa* population was dominated by new individuals (only seven intermediate and one old were marked during the entire year). At Morro do Japu ı, the age structure of *P. euryanassa* was unclear during the initial months of the study owing to the low number of individuals captured per day. Data from different days were not combined, however, because the age structure was easily observed in population peaks.

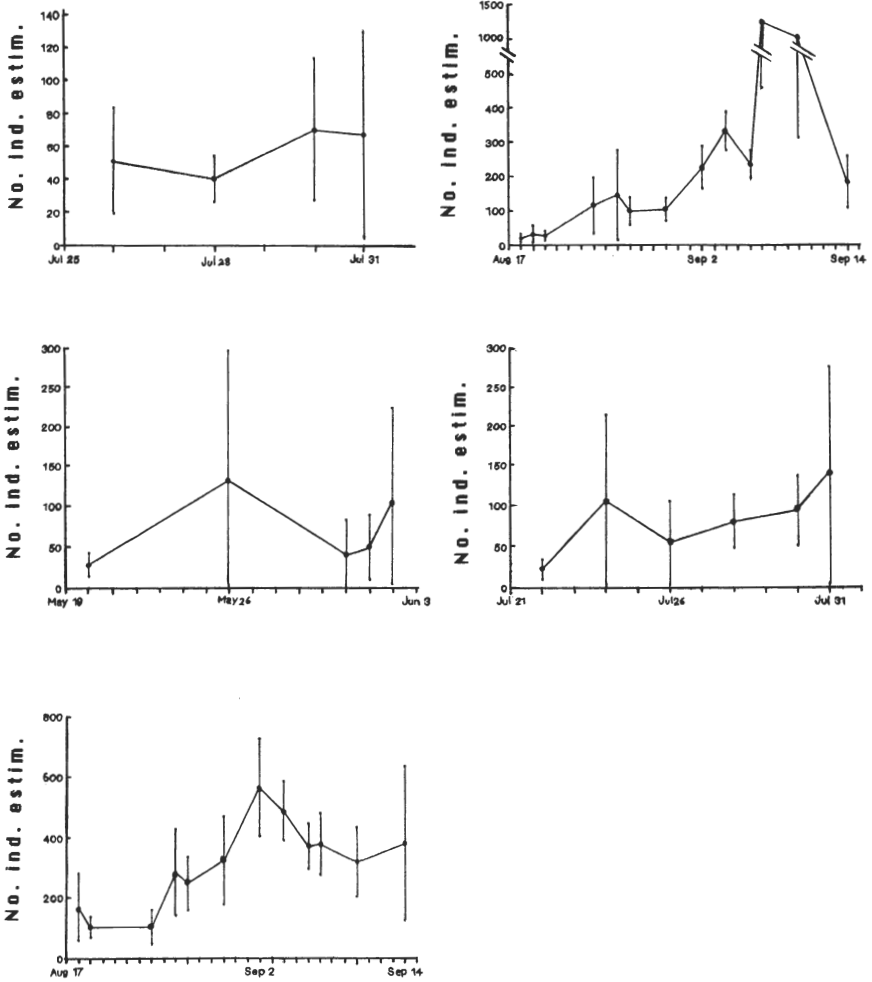


FIG. 4. Estimated population size (Jolly-Seber) for *P. eurynassa*, Morro do Japu, 1991. Females (top row, two peaks) and males (middle and bottom rows, three peaks).

In general, each population peak started with many new individuals. Later in the peak, intermediate individuals predominated, and at the end of the population peak, most individuals were scored as old, both males and females, especially in the August/September period (Fig. 6).

Time of Residence

Males have a residence time ($\bar{x} = 8.38$; $SD = 8.34$; $n = 149$) longer than females ($\bar{x} = 7.23$; $SD = 5.69$; $n = 112$) (Table 2). The survival curves of *P. eurynassa* are similar in males and females (type II), but

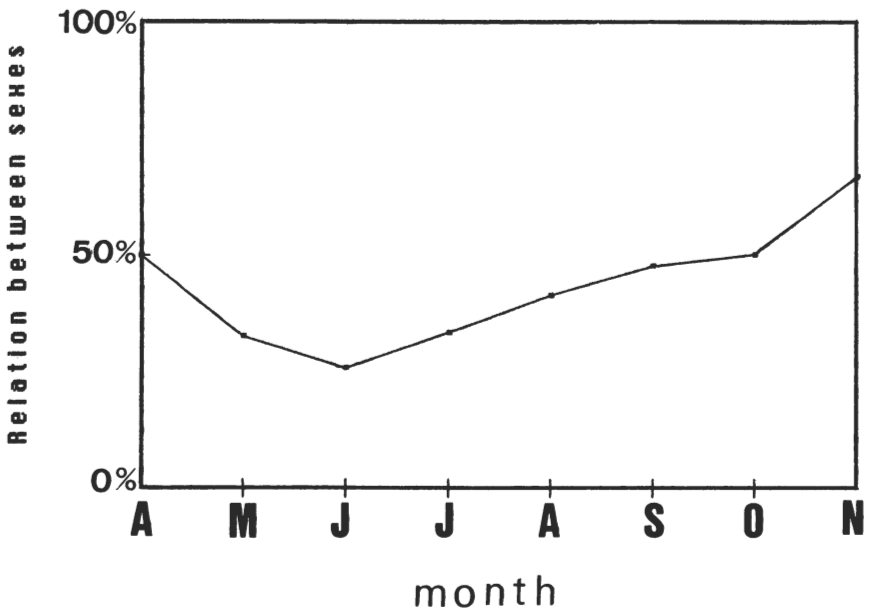
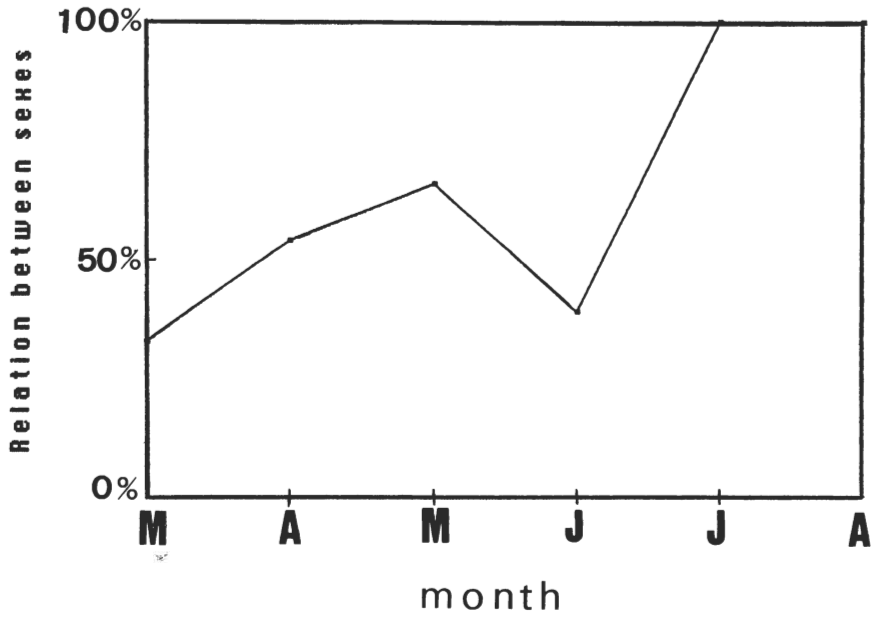


FIG. 5. Sex ratio for *P. euryanassa* marked in the Ribeirão das Pedras (1990, upper) and Morro do Japuí (1991, lower), as percent of ♀♀ in each day's captures.

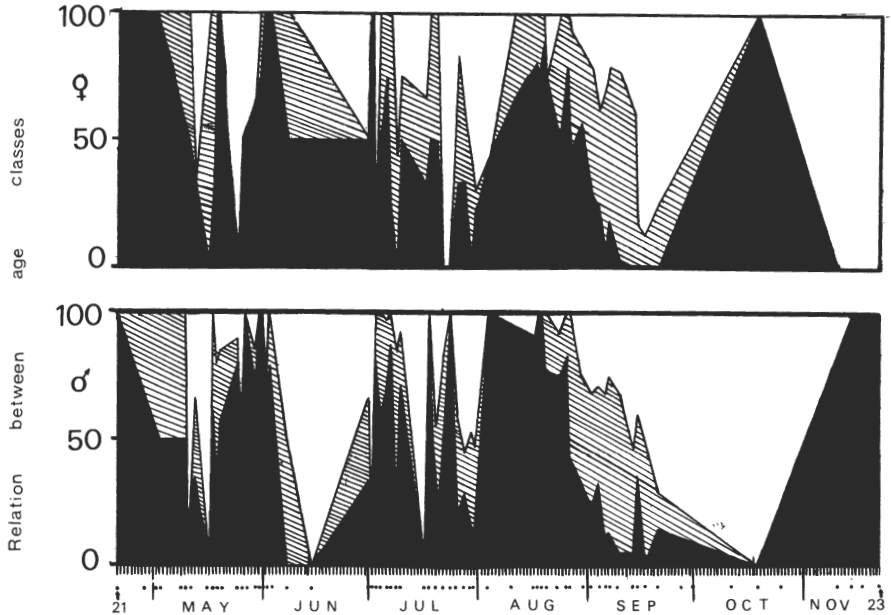


FIG. 6. Age structure of females (above) and males (below) of *P. euryanassa* in Morro do Japuí, April to November 1991: black = Fresh individuals, hatched = intermediate, white = old, as % of total on each day. Actual sampling days are indicated by points along the horizontal axes.

the survivorship of the latter is higher in individuals from 6 to 20 days of age (Fig. 7).

Adult Food Sources

Adults always were encountered near a nectar source. A few individuals were observed sucking broken stems of *Eupatorium punctu-*

TABLE 2. Permanence of marked *P. euryanassa*. Days elapsed between marking and last recapture represent the minimum permanence (MP) for each individual.

MP	Males	Females	Total
1-5	75	55	130
6-10	34	21	55
11-15	17	23	40
16-20	9	12	21
21-25	5	1	6
26-30	5	0	5
31-35	2	0	2
36-40	1	0	1
41-45	1	0	1
Total	149	112	261

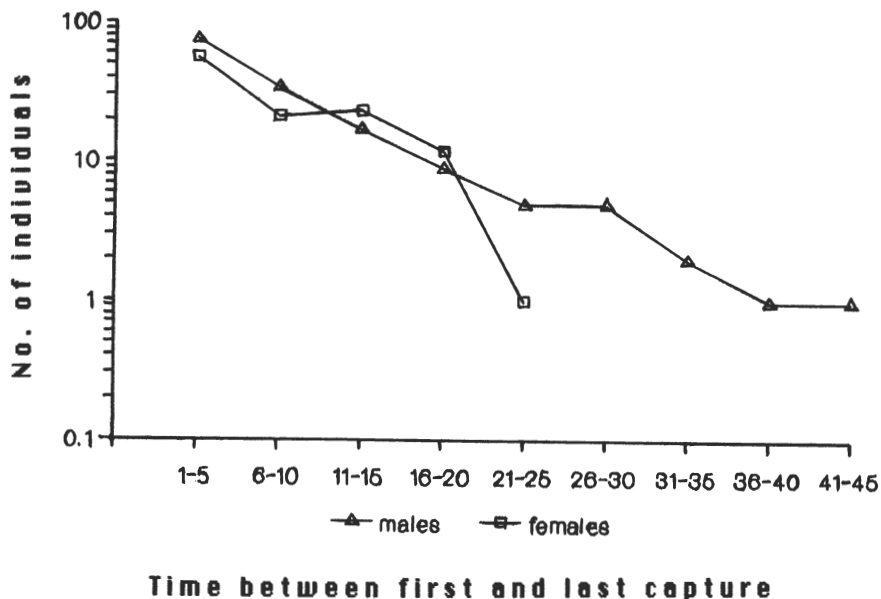


FIG. 7. Survivorship curves for *P. euryanassa*, Morro do Japuí, 1991 (following Ehrlich & Gilbert, 1973).

latum D.C. (Asteraceae) (three males), and leaves of *E. inulaefolium* H.B.K. (Asteraceae) (one male), perhaps attracted by the pyrrolizidine alkaloids contained in these plants (Brown 1985, 1987). Most flowers visited by *P. euryanassa* are in the Asteraceae, but the use of many other families was observed (Table 3).

Adult Behavior

Placidula euryanassa is a common species found in secondary forests. Adults frequently are found on Asteraceae flowers or near their host plants, flying slowly 1–5 m above the ground.

Where flowers were not present, adults were captured in flight; they typically flew below 3.5 m (reach of the net). Adults of *P. euryanassa* flew higher than other Ithomiinae present in the study areas [such as *Heterosais edessa* (Hewitson), *Pseudoscada erruca* (Hewitson), *Hypoleria adasa* (Hewitson) and *Hypothyris ninonia daeta* (Boisduval), that fly less than 2 m above the ground], being comparable only to *Dircenna dero celtina* Burmeister, *Melinaea ludovica paraiya* Reakirt, and *M. ethra ethra* (Godart) (species that fly above 5 m when not feeding).

Adults of *P. euryanassa* were observed resting in sunlight on cold days (14–16°C) during early morning (0800 h). These individuals generally were so sluggish that they could easily be captured by hand.

TABLE 3. Level of visitation of nectar sources by adults of *Placidula euryanassa*. *** = high, ** = intermediate, * = low.

Nectar source	Level
Asteraceae	
<i>Eupatorium gaudichaudianum</i> D.C.	***
<i>E. laevigatum</i> Lam.	***
<i>E. betonicaeforme</i> (D.C.) Baker	***
<i>E. inulaefolium</i> H.B.K.	**
<i>E. maximiliani</i> Schraeder	**
<i>E. punctulatum</i> D.C.	*
<i>Mikania lundiana</i> D.C.	**
<i>M. micrantha</i> H.B.K.	**
<i>M. lanuginosa</i> D.C.	**
<i>M. cordifolia</i> (L.F.) Willd	*
<i>M. hatschbachii</i> G. M. Barroso	*
<i>Mikania</i> sp.	**
<i>Vernonia scorpioides</i> (Lam.)	**
<i>V. lindbergii</i> Baker	***
<i>V. beyrichii</i> (Less.)	***
<i>V. condensata</i> Baker ¹	***
<i>Trixis antimenorrhoea</i> Mart. ex. Baker	***
<i>Senecio</i> sp.	***
<i>Alomia fastigiata</i> Benth.	***
<i>Adenostemma viscosum</i> Forst.	*
<i>Ageratum conyzoides</i> Linn.	*
<i>Emilia sonchifolia</i> D.C.	*
Rubiaceae	
<i>Mitracarpus hirtus</i> D.C.	**
<i>Borreria</i> sp.	**
Rosaceae	
<i>Rubus rosaefolius</i> Smith	**
Verbenaceae	
<i>Lantana camara</i> L.	*
Boraginaceae	
<i>Cordia verbenacea</i> D.C.	*
Lauraceae	
<i>Persea americana</i> Mill. ¹	***

¹ Introduced plants.

The few females observed ovipositing were always evaluated as intermediate (n = 2) or old (n = 1) in age class, and ovipositions in the laboratory were obtained only with females in these categories (i.e., 1 intermediate and 2 old; 4 new females did not oviposit).

DISCUSSION AND CONCLUSIONS

Biology of Immatures

Eggs laid in clusters and gregarious larvae are characteristic features of the biology of *P. euryanassa*. The habit of not eating the egg shell (or eating only a part) may be related to the proximity of the eggs of

siblings that could be eaten by mistake. Many Ithomiinae that lay eggs in clusters do not eat the egg shell, including members of the genus *Mechanitis* and *Hypothyris euclea laphria* (Doubleday) (pers. obs.). On the other hand, Ithomiinae that lay eggs singly usually eat the entire egg shell (Brown & D'Almeida 1970, Young 1974a, 1974b, 1974c, 1978a, 1978b, Muysshondt et al. 1976). The genus *Tellervo*, however, lays eggs singly and larvae eat only part of the egg shell (Ackery 1987).

The choice of oviposition sites can be related to climatic factors, especially weather and humidity, with eggs always near water except when atmospheric humidity is always at the saturation point (100%).

A "J" shaped resting position is observed in many larvae of Ithomiinae and Danainae, including *Tellervo* (Young 1972, 1974a, 1974b, 1974c, 1978b, Ackery 1987), but not in *Placidula*. The proximity of larvae when feeding or at rest can explain the inconvenience of this behavior. The "J" shape position is rare or absent in other gregarious Ithomiinae and also in young larvae of *Dircenna dero*, that rest along leaf veins (pers. obs.).

Among the Ithomiinae, the behavior of larvae resting in groups near the ground (or water) is known only in *Placidula*. The striped pattern of *P. euryanassa* larvae illuminated when placed in methanol and the corrugated cuticle, typical of late instars, are very similar to those of *Danaus*, *Lycorea*, *Ituna*, and primitive Ithomiinae, such as *Tithorea*, *Aeria*, *Elzunia*, and *Melinaea* (Gilbert & Ehrlich 1970, Muysshondt et al. 1976, Young 1978a, Brown 1987). These two features are considered as important indications of phylogenetic relationships between Ithomiinae and Danainae butterflies (Young 1978a, Gilbert & Ehrlich 1970). The furry aspect of late instar larvae occurs only in *Dircenna* and *Hyalenna* among other Ithomiinae (Young 1973, pers. obs.).

Larvae of *P. euryanassa* have been considered aposematic in color pattern and behavior (Brown 1985), but no focused studies have tested this hypothesis. The close association of *Placidula* and *Brugmansia* suggests a dependence on some compounds from these plants, with chemical protection derived from this relationship.

Adult Biology

The differences in the seasonal changes of population size of *P. euryanassa* between Ribeirão das Pedras and Morro do Japuí probably are due to climatic differences in these two places. In March, *P. euryanassa* is rather common in Ribeirão das Pedras (where the temperature is colder than in Morro do Japuí) and the population begins to increase, while in Morro do Japuí this increase happens only in May. The severity of the winter in Ribeirão das Pedras (June–July) could determine the low number of adults after June. It is possible that adults migrate to warmer places on the coastal plain or die due to low tem-

peratures (K. Brown pers. comm.). However, the population increases during this period in Morro do Japuí, where the winter has milder temperatures (never less than 8°C). Ribeirão das Pedras may be colonized each year in the early autumn (March–April), until the population decreases abruptly in late winter (July–August). In Morro do Japuí, the population appears to be maintained at low densities during the summer (November–March), increasing by reproduction and migration in late autumn (May–June). Although tropical butterflies may have constant populations with little variation throughout the year (Benson & Emmel 1972, Ehrlich & Gilbert 1973), *Placidula euryanassa* shows a considerable fluctuation in size throughout the year, a pattern also reported in other Ithomiinae (Vasconcellos-Neto 1980). This picture of fluctuation in size is more common in temperate species (Ehrlich 1984) and reinforces the idea that *Placidula* is a subtropical genus (Brown 1979).

Male-biased sex ratios in the field have been observed many times in butterflies, even when the sex ratio in the laboratory is 1:1 (Brussard & Ehrlich 1970, Brussard et al. 1974, Brown & Ehrlich 1980, Matsumoto 1984, 1985). Behavioral differences between males and females probably account for this “catchability difference” between sexes (Ehrlich 1984). In *Placidula euryanassa*, the same situation was observed. The difference in catchability can be related to the frequent visitation to sources of pyrrolizidine alkaloids by males (Brown 1985).

The age structure of *P. euryanassa* through time, from a predominance of new individuals in the beginning of each population peak to old individuals at the end of the peak, suggests that each population peak can be considered as an eclosion period (i.e., one generation of *P. euryanassa*).

Vagility data indicate that all capture sites in Morro do Japuí represent a single population of *P. euryanassa*; the population may be even larger than estimated (Fig. 4). Capture points were closely related to nectar sources, and dispersal between sites occurred whenever a new nectar source became available.

The time of residence indirectly reflects survivorship of the adults (Ehrlich 1961, Ehrlich & Gilbert 1973); *Placidula* shows a low survivorship compared with other Ithomiinae butterflies (Brown pers. comm., Freitas unpubl.). According to Brown and Ehrlich (1980), data obtained as time of residence are distributed as a truncated Poisson curve, as in the present study (Table 3). Thus it is not possible to test significance of difference of residence times calculated from these data against previously published residence times. Low permanence of females in a population can be explained by high dispersal, as happens with *Acinote pellenea pellenea* (Hübner) (Nymphalidae: Acraeinae) (Francini 1989). The survivorship curves of adult males and females are of type

II. Although type II curves are most common in K-strategists (Pianka 1970), other features suggest that *P. euryanassa* is an r-strategist. Among these are low survivorship of the adult, great number of eggs, easy colonization of secondary environments, rapid decrease of the populations ("catastrophic" mortality), short time of larval development and instability of the populations of this species. All these factors contrast with those of long-lived K-strategist butterflies such as *Heliconius* (Ehrlich & Gilbert 1973, Gilbert 1991) and many other Ithomiinae (Vasconcellos-Neto 1980, 1986, 1991).

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