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POPULATION STUDIES OF *AERIA OLENA* AND *TITHOREA HARMONIA* (NYMPHALIDAE, ITHOMIINAE) IN SOUTHEASTERN BRAZIL

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ABSTRACT. Populations of *Aeria olena* and *Tithorea harmonia pseudethra* (Lepidoptera: Nymphalidae: Ithomiinae) showed large variations in abundance along the year in four sites, with peaks at the end of the wet season. The sex ratio of captures in *A. olena* was male biased. In *A. olena*, males showed longer residence times than females. Both species differ from other members of the Ithomiinae community in the region by feeding on Apocynaceae vines as larvae, not congregating in "ithomiine pockets" and having low population numbers in the dry season.

Additional key words: mark-recapture, Ithomiinae pockets.

The Ithomiinae (Nymphalidae) are an exclusively Neotropical butterfly group (Fox 1967, Brown & Freitas 1994) except possibly for the Australian genus *Tellervo* Kirby (Ackery & Vane-Wright 1984). The subfamily is distributed from Mexico to Argentina and is largely restricted to moist forest habitats from sea level up to 3000 m (Fox 1967, DeVries 1987).

Ithomiinae populations are considered difficult to study due to low adult recapture rates, even in dense pockets (Gilbert 1993). Thus there are few published population studies in this subfamily (Drummond 1976, Haber 1978, Young & Moffett 1979, Vasconcellos-Neto 1980, 1991, Trigo 1988, Freitas 1993, 1996, Pinto & Motta 1997). Knowledge of population parameters is important to the understanding of this family and of the whole butterfly community (DeVries 1994, Freitas 1996).

The genera *Tithorea* Doubleday (two species) and *Aeria* Hübner (three species) both belong to basal branches of the Ithomiinae (Brown & Freitas 1994), with aposematic "danaoid" larvae feeding on Apocynaceae (such as *Prestonia acutifolia* (Benth.) K. Schum. and *P. coalita* (Vell.) Woodson) and bearing fleshy tubercles (Brown 1987, Brown & Freitas 1994, Trigo et al. 1996). In Southeastern Brazil, both species are most common in semi-deciduous forests of the interior, being scarce in the humid forests of the Atlantic mountain slopes and coastal plain.

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This paper describes the population parameters of three populations of *Aeria olena olena* Weymer and one of *Tithorea harmonia pseudethra* Butler in semideciduous forest fragments in SE Brazil, comparing them with other populations of Ithomiinae in Brazil.

STUDY SITES AND METHODS

The present study combines four data sets collected by different researchers from 1974 to 1998 in four different sites in São Paulo state, southeastern Brazil. Although the basic method to study all the populations was mark-recapture (see Freitas 1993, 1996), there were some differences among data sets, requiring that methods and results be presented separately. The regional climate in the four sites is markedly seasonal, with a warm wet season from September to April and a cold dry season from May to August.

The most recent study area was in the Santa Genebra Forest Reserve (SG, 22°49′S, 47°07′W), a 250 ha forest fragment in Campinas. The study area is covered by semideciduous forest, with annual rainfall near 1400 mm and an average annual temperature of 20.6°C (Morellato & Leitão-Filho 1995). A large part of the forest is old secondary growth, with a predominance of forest edge plants and lianas.

In this area, a mark-recapture census of *A. olena* extended from January 1997 to June 1998 (AVLF and FV), along an interior trail 1100 m long, with 103 field days of about four hours each at intervals of 2 to 15

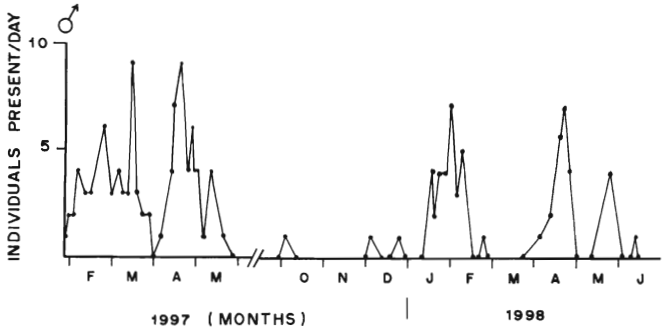

FIG. 1. Number of male *A. olena* present per day (NIPD) from January 1997 to June 1998 in Santa Genebra.

days. Butterflies were captured with an insect net, individually numbered on the underside of both forewings with a felt-tipped pen, and released. Wing wear, forewing length, point of capture, sex and food sources were recorded (as in Freitas 1993, 1996). The age of individual butterflies was estimated based on wing wear, initially using the six categories described by Ehrlich and co-workers (Ehrlich & Davidson 1960, Brussard & Ehrlich 1970, Ehrlich & Gilbert 1973). These six categories were later regrouped into three: fresh, intermediate and old as in Freitas (1993, 1996). Age structure was calculated as the daily proportion of each category, and grouped into monthly means.

The other three populations were studied by JV and KSB from August 1974 to December 1976 (Sumaré, SP), and by JRT from December 1983 to August 1985 (Campinas—Costa e Silva and Moji-Guaçu, SP), with the same methods for capturing, marking and gathering data (Vasconcellos-Neto 1980, Trigo 1988).

The Horto Florestal de Sumaré (HS, 22°50′S, 47°16′W; Brown & Vasconcellos-Neto 1976), where the population of *A. olena* was censused weekly, had a climate similar to that of Campinas. The population of *A. olena* censused in the "Mata de Costa e Silva" of the Fazenda Santa Elisa, Instituto Agronômico de Campinas (CS, 22°51′S, 47°06′W), occupied a 12-ha fragment of semideciduous forest, with the same climate as Santa Genebra. Most of the area is covered with secondary forest, with a predominance of forest edge plants and lianas. Marking was done along four trails (total of 1000 m), during two consecutive days each month.

A population of *Tithorea harmonia pseudethra* was censused from September 1984 to August 1985 in the "Mata da Pedra" of the Estação Experimental Mogi-Guaçu (Fazenda Campininha) (MP, 22°17′S, 47°12′W), a 30 ha area covered by riparian forest within "Cerrado" vegetation along the Moji-Guaçú river near Martinho Prado. The annual rainfall is about 1500 mm, and the average annual temperature is 21°C. In this area, a mark-recapture census was conducted on a 900 m long trail, for two consecutive days each month. Because the sex ratio was close to 1:1 in this population (see results), the sexes were lumped in some analyses.

The Santa Genebra mark-recapture data were analyzed by the Jolly-Seber method (Southwood 1971) for estimating population parameters. Only males were analyzed because of the low number of females. Daily results were presented as "number of individuals captured per day" (NICD), and "number of individuals present per day" (NIPD), as in Ramos and Freitas (1999). In estimating the NIPD, recaptured individuals were considered to have been present in the population on all previous days since the day of first capture (that is, they were "marked animals at risk").

RESULTS

Population biology of *Aeria olena*. In SG, adults of *A. olena* were captured on 51 of the 103 study days. Males were present on 47 days and females on 23 days. In total, 110 males and 28 females were marked. The NICD (for 51 days with captures) varied from zero to 9 in males (mean = 2.71, SD = 1.99); and from zero to 4 in females (mean = 0.67, SD = 0.93) (Fig. 1). Based on the NIPD, males were most abundant during the end of the wet season (February to May), diminishing in June, and virtually absent along the trail from July to January (Fig. 1). Jolly-Seber analysis for males gave estimated population numbers for only 12 days, varying from one to 19 individuals, with a maximum possible of 80 individuals.

In the HF, 217 males and 145 females were marked on 67 days during the three years of study (Table 1). Males were present on 63 days and females on 54 days. The NICD (for 67 days) varied from zero to 14 in males (mean = 4.82, SD = 3.99) and from zero to 11 in females (mean = 2.85, SD = 2.65). Based on the

TABLE 1. Sex ratio of marked individuals of *Aeria olena* in the three study sites in São Paulo state; rec (%) = percentage of recaptures. An asterisk indicates a male biased sex ratio (chi-square test [X^2], $p < 0.05$).

Study site and dates	Males	Females	Sex ratio	X^2	rec (%)	
					m	f
Sumaré 1974	28	18	1.5:1	2.2	7.0	11.0
Sumaré 1975	131	91	1.4:1	7.2*	27.4	25.9
Sumaré 1976	58	36	1.6:1	5.1*	14.0	17.0
Sumaré (three years)	217	145	1.5:1	14.3*	21.2	22.1
Costa c Silva 1983-84	182	116	1.6:1	14.6*	9.8	12.9
Costa e Silva 1985	180	85	2.1:1	34.1*	14.4	4.7
Costa e Silva (three years)	362	201	1.8:1	46.0*	12.2	9.4
Santa Genebra 1997–1998	110	28	3.9:1	48.7*	20.0	14.3

NIPD, both males and females were rare or absent throughout the early wet season (October to February) and most abundant at the end of the wet season (March to May) (Fig. 2).

In CS, 362 males and 201 females were captured. In 36 days of study, males were seen on 35 days and females on 33 days. The NICD (in 36 days) varied from zero to 29 in males (mean = 11.2, SD = 8.36) and from zero to 17 in females (mean = 6.25, SD = 5.04). The results of the censuses showed that the population increased in numbers from February to June, decreasing after July and maintaining low numbers from September to January (Fig. 3). In both 1984 and 1985, peak number of individuals were reached from April to June (Fig. 3).

In SG and CS, the maximum number of recaptures was two for both males and females; in HS, males were recaptured from one to three times, and females from one to four times. In the three populations, single recaptures were more than 68% of all recaptures.

Sex ratio. The sex ratio of individuals captured and marked was male biased in all sites (Figs. 4–6, Table 1). In SG, the sex ratio was male biased in all months (Fig. 4), and males were always more than 60% of the total. The recapture rate of males (20.0%) was higher than of females (14.3%), but due to the low number of recaptures of females (n = 4) no statistical comparison could be made.

In HS, the sex ratio was also male biased in all months (Fig. 5), and males were always more than

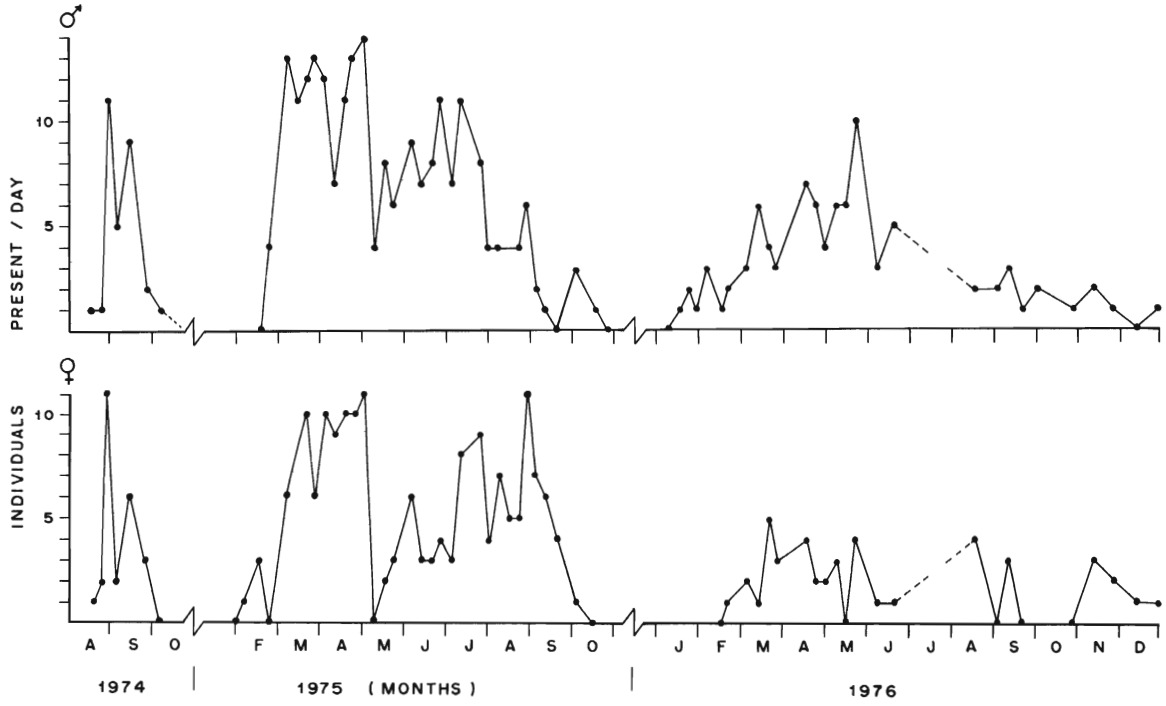

FIG. 2. Number of male and female *A. olena* present per day (NIPD) from August 1974 to December 1976 in the Horto Florestal de Sumaré.

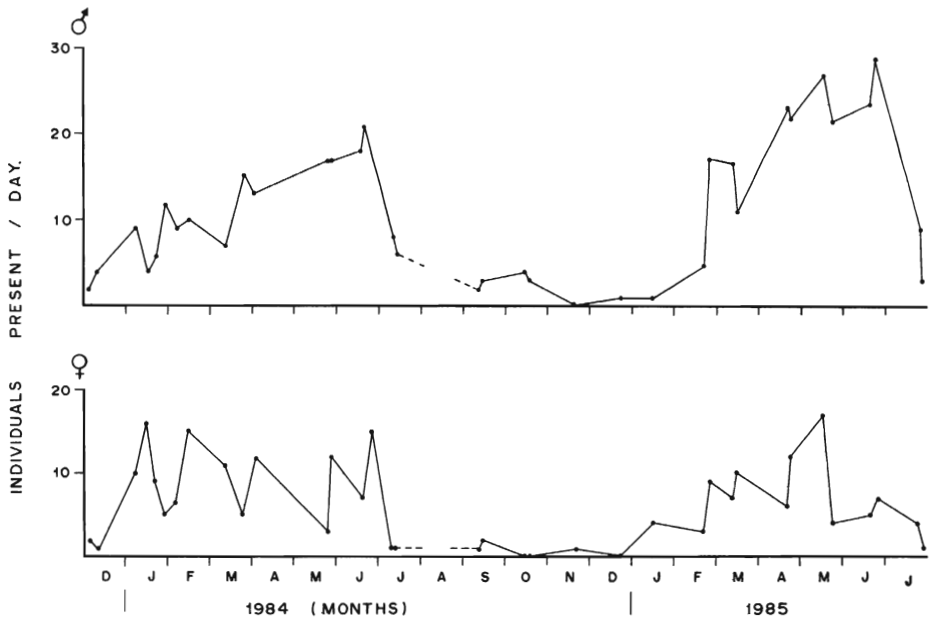

FIG. 3. Number of male and female *A. olena* present per day (NIPD) from December 1983 to July 1985 in Costa e Silva.

60% of the total. The recapture rate of males was higher than that of females in one of the three years (Table 1).

In CS, the sex ratio was male biased from May to July in 1984 and from April to June in 1985 (Fig. 6), and the recapture rate of males was higher in one of the three years (Table 1).

In laboratory rearing, the sex ratio was also male biased, with 29 males and 12 females obtained from larvae from CS ($X^2 = 7.05$, df = 1, $p < 0.01$).

Age structure. Age structure was not stable in the three sites; in general, "fresh" individuals were most common from February to May, replaced by intermediate ones in the dry season.

In SG in 1997, "fresh" individuals were common from February to May, and "old" individuals became more common after April; this pattern was not observed in 1998 (Fig. 7).

In HS (Fig. 8), the variation in age structure was similar in 1975 and 1976, with "fresh" individuals increasing from February to March, decreasing after this to be replaced by the "intermediate" ones in the dry season.

In CS in 1984 (Fig. 9), the age structure was stable in most of the months, with a small decrease of "fresh" and increase of "old" individuals in the dry season months; this pattern was not observed in 1985, when the "fresh" individuals increased in proportion after February, reaching a maximum in July.

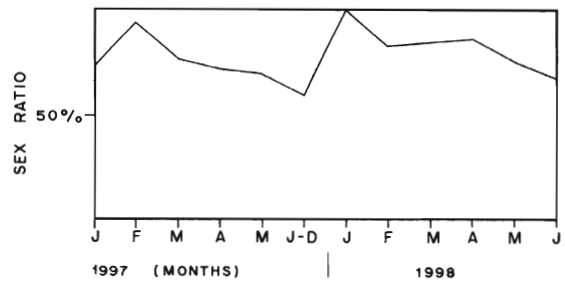

FIG. 4. Sex ratio in *A. olena* in Santa Genebra from January 1997 to June 1998, as percent of males in each day's captures.

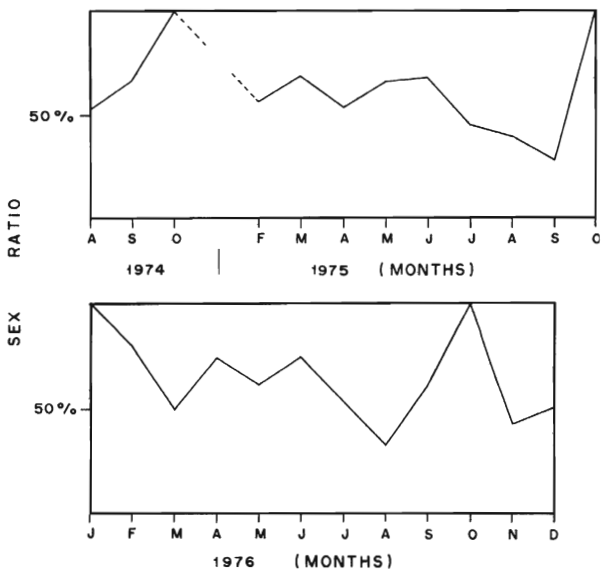

FIG. 5. Sex ratio in *A. olena* in the Horto Florestal de Sumaré from August 1974 to December 1976, as percent of males in each day's captures.

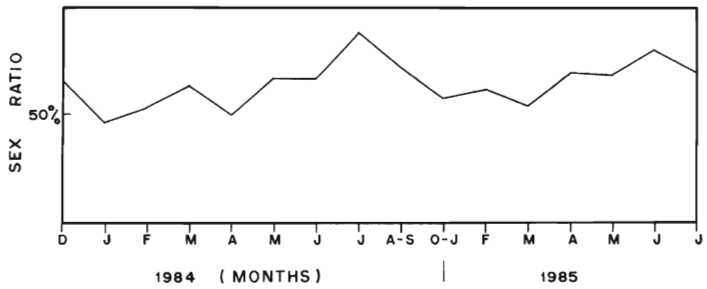

FIG. 6. Sex ratio in *A. olena* in Costa e Silva from December 1983 to July 1985, as percent of males in each day's captures.

Residence time. In SG, females had a residence time (mean = 9.5 days, SD = 4.04, n = 4) almost equal to that of males (mean = 9.14 days, SD = 5.34, n = 22); the significance could not be calculated due to low numbers of females. Estimated residence time for males ("life expectancy" of Cook et al. 1967) was 6.8 days. The maximum individual permanence (survival) was at least 24 days for a male and 13 days for a female.

In HS, females had a residence time (mean = 23.2 days, SD = 14.38, n = 32) statistically the same as that of males (mean = 20.7 days, SD = 19.24, n = 46) (t = 0.615, df = 76, p = 0.54). The maximum individual permanence was at least 120 days for a male and 56 days for a female.

In CS the residence time for males (mean = 6.79 days, SD = 7.36, n = 44) was considered equal to that for the females (mean = 11.1 days, SD = 10.38, n = 19) (t = 1.898, df = 62, p = 0.06). The maximum individual permanence was at least 24 days for a male and 27 days for a female.

Vagility. In SG, most males were recaptured away from the point of first capture (59.1%), with the maximum distance recorded being 800 m (male number 6, seven days after first capture), but in general ranging from 50 to 250 m (mean = 84.1 m, SD = 172.78, n = 22). All females recaptured were at the same place as the first capture.

In CS, 54% of the individuals were recaptured away from the point of first capture; the average distance traveled by an individual *A. olena* was 107.4 m (SD = 82.69, n = 34), with the maximum distance recorded being 300 m (for three males and one female).

In HS numerous recaptures showed individuals moving 100–400 m in a single day.

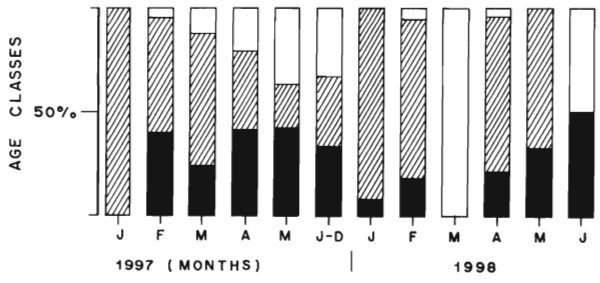

FIG. 7. Age structure of *A. olena* males (black = fresh individuals, hatched = intermediate, white = worn individuals) from January 1997 to June 1998 in Santa Genebra.

Population biology of *Tithorea harmonia pseudethra*. The number of individuals was highest from March to May 1984, and decreased after June 1985 (Fig. 10). The sex ratio was statistically equal to 1:1 in all months except August 1985 (Fig. 11). The sex ratio in the laboratory was also 1:1, with 10 males and 9 females obtained from larvae from this region (X^2 = 0.05, df = 1, p > 0.2). The proportion of recaptures of males (3.9%) was almost equal to that for females (3.6%). Except for September 1984, the age structure (with both sexes lumped) was stable, with "fresh" and "intermediate" individuals equivalent in proportions and more abundant than the "old" individuals (Fig. 12). The maximum residence time was 34 days, recorded for three males. The average distance traveled by an individual *T. harmonia pseudethra* was 83 m (SD = 58, n = 6).

DISCUSSION

The general pattern observed in the three populations of *A. olena* indicates that population numbers decrease in the dry season, the same time that all other Ithomiinae reach maximum numbers in Ithomiinae "pockets" (Brown & Benson 1974, Brown & Vasconcellos-Neto 1976, Vasconcellos-Neto 1980, 1991, AVLF unpubl. data). This discrepancy may be related to the low availability of the leaves of the larval host plant *Prestonia coalita* (Trigo 1988) during the dry season. The low numbers continue until the next wet season, when populations start to increase and reach maximum size at the end of the wet season, possibly due to high recruitment of new individuals during the periods of maximum availability of new and mature leaves. In *Heliconius* butterflies, periods of dry climate were also observed to cause a decrease in popu-

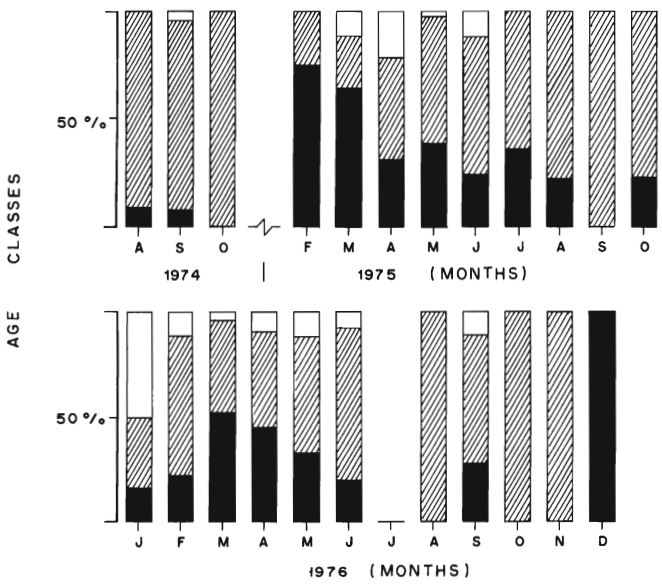

FIG. 8. Age structure of *A. olena* males (black = fresh individuals, hatched = intermediate, white = worn individuals) from August 1974 to December 1976 in the Horto Florestal de Sumaré.

lation numbers (Benson 1978, Ramos & Freitas 1999), probably as a result of low availability of meristems of Passifloraceae, eaten by the larvae of most species in this genus.

Some population parameters of *A. olena* are similar and others dissimilar to those observed in other Ithomiinae species. The male biased sex ratio in the field, low recapture rates of adults and a moderate adult survival rate are often observed in Ithomiinae (Brown & Benson 1974, Drummond 1976, Haber 1978, Young & Moffett 1979, Vasconcellos-Neto 1980, Trigo 1988, Freitas 1993, 1996, Pinto & Motta 1997), and considered as typical for species of this subfamily (even if more studies are needed to confirm these tendencies). The absence of adults in Ithomiinae pockets and low numbers in the dry season are clearly distinct from patterns recorded in other species of Ithomiinae.

The results indicate that *A. olena* occurs in areas where other Ithomiinae species are scarce or appear mostly as individuals moving between humid areas. Males are often found visiting flowers that have PAs (pyrrolizidine alkaloids) at the end of the wet season, showing a marked sex-bias for these sources (Trigo et al. 1996). Early observations suggested that *A. olena* usually flew outside the perimeters of the Ithomiinae pockets, being more tolerant of dry areas of the forests even during the early dry season, when the remaining species concentrate in the wettest spots. However, in the very strong dry season of 1997, even *A. olena* became scarce along the main trail of SG, probably as a result of both decrease in recruitment and migration away from the bright, hot trail.

The population structure of *T. harmonia pseudethra* appears to follow the same tendencies as that of *A. olena*, including the fluctuation in numbers throughout the year, the low recapture rates, and a moderate

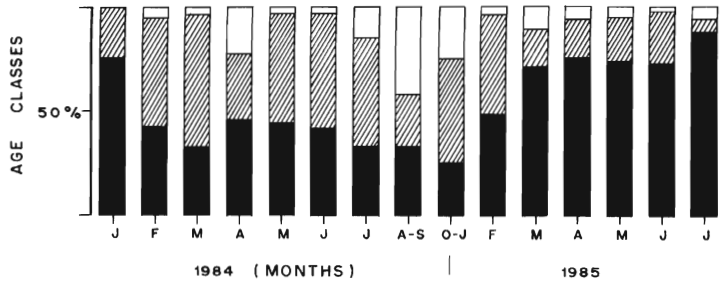

FIG. 9. Age structure of *A. olena* males (black = fresh individuals, hatched = intermediate, white = worn individuals) from January 1984 to July 1985 in Costa e Silva.

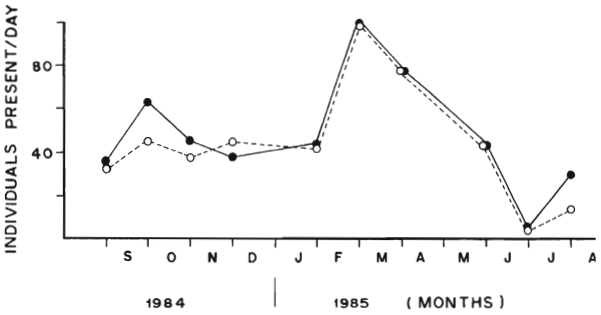

FIG. 10. Number of *T. harmonia pseudethra* individuals present per day (NIPD), males (solid line), females (hatched line), from August 1994 to August 1985 in the Mata da Pedra.

adult rate of survival. However, the sex ratio was equal in most months, differing from the pattern observed in most other Ithomiinae (Freitas, 1993, 1996). As in *A. olena*, the fluctuations appear to be related to seasonal changes in climate, with a marked decrease after the beginning of the dry season. Again, the effects of climate on the availability of fresh leaves and seedlings of their larval host plant *Prestonia acutifolia* during the dry season could be the main factor in the population decrease in the dry months (Trigo 1988). Adults of *T. harmonia pseudethra* do not occur frequently in Ithomiinae pockets, and are more common in forests near rivers. Both sexes were little attracted to PA sources, but frequently visited flowers without PAs (Brown 1985, 1987, Trigo et al. 1996).

Tithorea harmonia pseudethra and *A. olena* belong to the most basal branches of the Ithomiinae (Brown & Freitas 1994 and unpubl. data), with larvae feeding on Apocynaceae vines and immatures probably sequestering PAs (Brown 1985, 1987, Brown & Freitas 1994, Trigo et al. 1996). They also represent unique syndromes in behavior and population variation (not concentrating in Ithomiinae pockets, low numbers during the dry season). This suggests that population studies of other Ithomiinae genera are needed for a better understanding of the evolutionary biology of this butterfly subfamily.

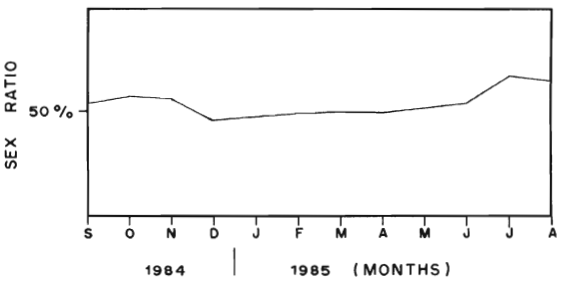

FIG. 11. Sex ratio in *T. harmonia pseudethra* in the Mata da Pedra from September 1984 to August 1985, as percent of males in each day's captures.

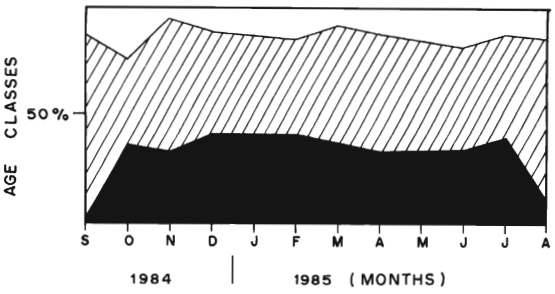

FIG. 12. Age structure of *T. harmonia pseudethra* males (black = fresh individuals, hatched = intermediate, white = worn individuals) from September 1984 to August 1985 in the Mata da Pedra.

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