STUDIES ON RESTINGA BUTTERFLIES. II. NOTES ON THE POPULATION STRUCTURE OF *MENANDER FELSINA* (RIODINIDAE)

Curtis J. Callaghan

IBM do Brasil Ltda., P.O. Box 1830, Rio de Janeiro, Brazil

ABSTRACT. The objective of the study was to describe various aspects of the adult behaviour and population dynamics of the riodinid butterfly *Menander felsina* (Hew). The conclusions were based on four years of field observations and a marking-recapture study conducted over a period of 15 weeks.

The population was characterized by low intensive and extensive frequencies (rarity in numbers and space respectively), characteristics shared by many other forest riodinid species. *M. felsina* maintained constant population levels of about 19 individuals over the 15 week marking-recapture period, due to 1) longevity above that of most holarctic lycaenids, 2) low egg laying frequency both in time and space, and 3) male territoriality, which results in older males doing most of the mating. Limited adult and larval food sources were discounted as an explanation.

The population was found to be distributed in small groups or colonies near food plant localities. The reasons for this were the low extensive distribution of foodplants coupled with high female vagility. Depending upon conditions at each foodplant locality, such as predation and exposure to the elements, each colony could become extinct, only to be reestablished by another wandering female.

Studies on the ecology of neotropical butterflies to date have been concerned for the most part with the larger species such as heliconiines (Crane, 1955, 1957; Turner, 1971; Ehrlich & Gilbert, 1973), nymphalines (Benson & Emmel, 1973; Young, 1972), and papilionids (Cook *et al.*, 1971). Smaller butterflies such as riodinids have received only superficial treatment, mainly consisting of scattered notes on observed habits and population density. Early writers such as Bates (1864) and Seitz (1913) made reference to the rarity of individuals and the great numbers of species that characterize neotropical riodinids. This has been confirmed statistically by Ebert (1969), who used the terms low extensive and intensive frequency to denote the rarity of populations and individuals, respectively. However, there has been no attempt to explain the mechanism(s) involved in maintaining populations in spite of such low intensive and extensive frequencies. The opportunity to study this phenomenon was provided to me by the discovery of a reasonably large colony of *Menander felsina* (Hew.) near Rio de Janeiro, Brazil. Whereas the ecology of this butterfly resembles closely that of other forest-dwelling but less common species, it also provides the basis for conclusions of a general nature applicable to other members of this group.

The purpose of this paper is to describe the adult behavior of *M. felsina* in connection with feeding, male patrolling, and mating. The

results of a marking-recapture program are presented with an analysis and discussion of the population parameters.

METHODS

The observations that form the basis of this study were gathered over a period of more than 4 years at Pedra de Itauna, an area near the coast west of Rio de Janeiro, Brazil. The vegetation is typical of the restinga (coastal dune community) described in detail elsewhere (Callaghan, 1977). The area for the mark-recapture study was a trail some 125 m in length just inside the south (seaward) side of the low woods surrounding the Itauna Rock. Because of the density of the brush, little collecting was possible elsewhere in the forest. The mark-recapture project took place over a 14-week period, from 18 July–15 November 1973. Marking was done every weekend except for five near the end, which were lost as a result of inclement weather. An average of ca. 5 h collecting (900–1400 hrs) per day was devoted to the experiment on study days. Individuals, once captured, received a predetermined mark that indicated the day and were immediately released at the same spot. Occasionally, a butterfly would show signs of shock after marking by fluttering to the ground, in which case it was killed and eliminated from the experiment. For analyzing the data, the Fisher and Ford method (Fisher & Ford, 1947) was used because of the relatively small sample sizes.

RESULTS

General Behavior: Feeding, Mating, and Patrolling

Menander felsina inhabit exclusively the low woods and nearby flats on the seaward side of the forested areas. They prefer open habitats such as trails and small clearings in the woods, shunning completely the deep shade found in the higher forests. Yet, they are one of the few butterflies that fly on cloudy days, albeit in smaller numbers than on sunny ones. Both sexes can be found sunning in the early morning hours with wings outspread on the upper surfaces of leaves 2–3 m above the ground. When disturbed, they fly off with a rapid, jerky flight, circling a few times before settling, wings outspread on the undersides of leaves not far from where they departed. After a few minutes they sometimes return to the same spot. When resting, they appear to thermoregulate, raising the wings to sharper angles depending on the intensity of the sun's rays.

Group feeding takes place in the morning hours from 800–1100, and to a lesser degree in the late afternoon. The *M. felsina* will visit prac-

tically any plant that happens to be in bloom in the habitat, often becoming so "engrossed" in feeding that they can be removed with forceps. Males and females feed together, the latter being found commonly only at this time.

Starting ca. 1230 hours, males begin taking up positions on the edges of trails and clearings to await females. They sit motionless for long periods on the upper or undersurfaces of leaves from 0.2–2 m above the ground with their abdomens slightly raised. Males seldom leave their perches to investigate other species of butterflies. The only ones investigated were small white pierids (*Eurema* sp.), which to some extent resemble *M. felsina* in flight. Larger butterflies and skippers are completely ignored, which indicates that sight plays a role in the recognition of rivals or mates. This activity continues until ca. 1500. This behavior is in contrast to the habits of lycaenids (Powell, 1968; Scott, 1974) and skippers (MacNeill, 1964). In these cases the males would investigate any object flying past them, including small rocks (MacNeill, 1964).

To determine the extent to which spacing occurs among males, a section of trail some 20 m long was observed on three occasions. In the middle of this area is an opening in the woods that faces outward toward the knee-high vegetation of the flats. Here, an older, slightly worn male took up a station at 1255. From time to time he would take off, flying around in an area some 5 × 3 m and perching for a few minutes on various plants within this area. At 1326, two fresh males moved into the study area, taking up positions to the right and left of the older male. When one of these flew near the older male, the latter rose up, flew around in circles with the other for a few seconds, then returned to his original spot, the fresh male alighting a few yards outside the area of the older male. At 1405, a female alighted on the outward side of the older male's area. He immediately flew over to the female, who took off, and followed her out onto the flats. A half hour later, he had not returned, nor had other females appeared in the areas of the fresh males. The next day at the same time, the same older male was again observed in the same area.

On another occasion only fresh males were observed. They showed less exclusiveness with regard to patrolling areas than the older males. Another male passing nearby would sometimes be engaged in a circular mutual chase, but both individuals would then settle down on leaves sometimes only a meter apart. Once a male left an area, another would often move in. During the observation periods, no females were seen entering the fresh males' areas.

TABLE 1. Basic capture-recapture data on a population of *Menander felsina*. The capture or recapture of each individual butterfly is denoted by 1.

Aug.	Sept.				Oct.			Nov.
18	1	9	17	24	7	14	20	15
1	1							
1	1							
1		1						
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							1	1
Total Released 22	14	15	17	15	19	7	24	22

I conclude that *M. felsina* males do engage in spacing, the older individuals defending their chosen areas more vigorously than the younger, more inexperienced males. That the older male was successful in meeting a female suggests that they may choose and defend the preferred "rendezvous" areas.

TABLE 2. Type A data trellis derived from data in Table 1. Units under "Date of Marking" refer to marks and not animals.

Date	Captured	Released	18	1	9	17	24	7	14	20	15
							Date of Marking				
18 Aug.	22	22									
1 Sept.	14	14	2								
9 Sept.	15	15	2	4							
17 Sept.	17	17	1	4	8						
24 Sept.	15	15		1		1					
7 Oct.	19	19				1	2				
14 Oct.	7[1]	7[1]					1				
20 Oct.	24	24						5	3		
15 Nov.	22	22							2	5	

[1] Low captures due to inclement weather.

On one occasion, a complete courting sequence was observed. About 1416, a female alighted on a leaf, wings outspread ca. 1 m from a perched male, who immediately flew around her several times, then alighted and, with wings moving slowly up and down, walked to a face to face position. There they remained for ca. 30 sec. Then, the female walked around to the underside of the leaf, the male followed, and copulation was initiated. This lasted for ca. 22 min. On another occasion, a pair discovered *in copula* under a leaf remained so for 8 min before breaking off. Sexual activity continues until late in life. On 15 November 1973, a male that had been marked three weeks previously was found *in copula* with a freshly emerged female. Finally, mating appears to be done by older territorial males since, of the three cases observed, two involved males that had been previously marked.

POPULATION SIZE AND MORTALITY

Tables 1 and 2 show the basic marking and recapture data gathered during the study, after Sheppard & Bishop (1973). It is instructive to note that few individuals were captured more than once, which indicates that collecting was not very efficient over time. Low captures on 14 October were due to rainy weather. The survival rate (Fisher & Ford, 1947) was 0.45 per week or ca. 0.91 per day. The average life span was 1.82 weeks by the formula $E = \dfrac{1}{1 - \text{survival rate}}$, which assumes that all deaths occur just before sampling. Potential survival is up to 5 weeks in the field, as confirmed by a recaptured female. Observed field survival for males is up to 4 weeks. When the Lincoln index modified by Bailey (1952) is applied to the study data, the weekly

TABLE 3. Population composition over time of new and recaptured butterflies, considering all animals captured and recaptured before and after a determined date to constitute part of the population even though they were not captured on that date.

Date	Total	New	%	Recaptures	%
18 Aug.	22	22	100	–	–
1 Sept.	17	12	71	5	29
9 Sept.	20	9	45	11	55
17 Sept.	19	4	21	15	79
24 Sept.	16	13	81	3	19
7 Oct.	23	19	82	4	18
14 Oct.	11	6	54	5	46
20 Oct.	25	16	64	9	36
15 Nov.	22	15	68	7	31
Average	19.4	10.4	–	7.4	–
Standard Error	±22.6%	±49.2%	–	±42.4%	–

estimates of total population size show great variation as a result of the large differences in recaptures from one sampling to the next.

These fluctuations were felt to be more due to inaccessibility of individuals because of the thick brush on either side of the trail than to changes in the population level. Therefore, to make the capture data more realistic a third table was mounted assuming that those animals captured in week one and recaptured in week three, for example, formed part of the population in week two even though they were not captured at that time. In Table 1 we see that on 18 August, 22 butterflies were marked and released of which five were later recaptured: two on 1 September, two others on the 9th, and one on 19 September. On the 1st, at least three butterflies were not captured.

Therefore, rather than a total of 14 for that date, we have 17 which we know formed part of the population at that time: 12 new plus 2 recaptured plus 3 which were recaptured at later dates. The numbers thus derived were entered in Table 3. The procedure was conducted for each capture period during the study.

This results in considerably smoother total capture figures, which show that if allowance is made for inefficiency in collecting, the estimates of numbers of individuals in the study area was quite stable over the 14–week period (Table 3) with a mean of 19.4 individuals and a standard error of 4.4 or ± 22.6%. More consistent results can be obtained by eliminating data for 14 October. When efforts were made to capture all the M. felsina in the study area—22 July 1973 and 6 June 1974—21 and 22 individuals were recorded, respectively, which again suggests that the number of M. felsina in the study area remains stable over long periods with a low number of individuals.

Sex ratio data gathered during the study were unsatisfactory as a result of the similar appearance and behavior of males and females, except during oviposition and territorial displays. Because of the delicate nature of these butterflies, they had to be kept in the net during marking and afterwards immediately released. This prevented detailed examination. Females, however, were a small minority of all captured. On the two occasions referred to above, 19 males were captured each time with 2 and 3 females, respectively. The reason is that the females entered the study area sporadically only for mating and feeding, thus not being as accessible as the males. The number of females caught under these circumstances is not truly representative of the female population; thus, for the purpose of this study, males and females were considered together.

DISCUSSION AND CONCLUSIONS

As noted above, tropical butterfly populations, especially those of theclids and riodinids, are characterized by low intensive and extensive frequencies. The data from the marking-recapture program and other observations on the *M. felsina* population permits a number of suggestions as to why this is so.

Low Intensive Frequency

Low intensive frequency means that an animal is represented by a small number of individuals in a given population. As shown by the recapture data, the number of *M. felsina* frequenting the study area remained low and fairly constant for long periods. Other students have made similar observations on neotropical butterfly populations. Benson & Emmel (1973) observed a roost of *Marpesia berania* (Hewitson) in Costa Rica that maintained constant equilibrium of population size for more than 3 months because of constant rates of recruitment and mortality. Ehrlich & Gilbert (1973) recorded a similar structure for *Heliconius ethilla* Godt in Trinidad over a period of 2 years, as did Young (1972) for *Siproeta epaphus* (Latreille) in Costa Rica. Why do these populations have an equilibrium level and what is the mechanism that enables them to maintain it? Ehrlich & Gilbert (1973) explain the constant population level in *H. ethilla* through the constant recruitment of new adults over time which equals mortality. This was thought to be due to unvarying predator pressure on the immatures and not because of a lack of foodplant, which was quite common in the habitat. The other factor was limited adult nectar resources, which controlled egg production, thereby regulating the production of immatures. Young

(1972) in his study of S. *epaphus* likewise found that egg and adult numbers remained constant throughout the study period. As a mechanism, he suggested low fecundity and low adult vagility as well as the sheltered nature of the forest understory community. Both studies discount outmigration as a factor.

My observations on *M. felsina* allow the following conclusions to be made. First, neither foodplant nor nectar availability appeared to be a limiting factor. The larval damage was always small compared with the amount of foodplant available, showing little pressure on foodplant resources. The adult's preference for nearly anything that is in bloom and its willingness to travel good distances eliminates lack of adult nectar sources as a possibility. The factors that appear to be most significant are low egg–laying frequency, increased longevity, and male spacing.

Low egg–laying frequency was observed on several occasions. The maximum number of eggs seen laid in any one afternoon by the same female was four, these being laid singly and widely dispersed on the foodplant (Callaghan, 1977). The results of this were shown in the low numbers of widely separated larvae in all instars that could be found on the same foodplant. Pupation and emergence were likewise staggered, meaning a fairly even flow of adults over time. Since the larvae were attended and protected by ants (Callaghan, 1977), predation was kept down to a minimum and thus did not appear to be a significant factor as it was in the case of *H. ethilla* (Ehrlich & Gilbert, 1973). For *M. felsina*, then, the low frequency of oviposition assures the low intensive frequency of its populations. Why egg production should be low could not be determined during the course of the present study.

Another factor is longevity. The 1.82 weeks observed for *M. felsina* is high when compared with holarctic butterflies, but low with respect to those tropical nymphalines that have been studied. Scott (1974) reported an average life span of 4.2 days of *Lycaena arota* Bois with a potential of 8 days. Labine (1968), Turner (1971), and Cook *et al.* (1971) reported the life expectancy after marking for 6 holarctic species in the field as from 2.8–12.1 days. Powell (1968) gave a maximum of 16 days for *Incisalia iroides* (Boisduval). On the other hand, Benson & Emmel (1973) demonstrated that the neotropical nymphaline *Marpesia berania* has an average longevity of 43.9 days with a potential of at least 157. Heliconids are especially long lived. Benson (1972) reported *Heliconius erato petiverana* Doubleday in Costa Rica with average observed longevities of 52 days and an individual alive 6 months after

marking. Turner (1971) and Ehrlich & Gilbert (1973) reported similar results. Greater longevity ensures low intensive frequency and is of considerable selective value in the tropics since it enables the widespread dispersal of eggs in both space and time, which may diminish parasitism and ensure a larger number of offspring reaching maturity (Benson & Emmel, 1973). Also, having individuals in all stages of development would permit survival of a natural disaster that might eliminate one stage but not the others. The causes of adult mortality of *M. felsina* are not precisely known, since no actual predation or other forms of natural mortality were observed during the study. However, potential predation exists in the form of lizards, spiders, ants, and birds. Rapid flight and hiding beneath leaves are two methods used by adult *M. felsina* and many other riodinids to avoid predation. On the other hand, its fairly sedentary habits might mean greater predator pressure and lower survival rate for *M. felsina* than for heliconines and nymphalines, which enjoy mimicry, distastefulness, and/or strong flight. Lower survival would be more likely true for males because of their conspicuous behavior.

Finally, male spacing seems to select for longevity, since older males have been observed to be more aggressive and fixed to their habitual areas and thus are easily able to drive off younger, more inexperienced newcomers. The result is that females appearing at the rendezvous area will be more likely to mate with strong, long-lived males. This is turn assures longer-lived offspring, which can effectively distribute their eggs widely in space and time. These three factors combined, then, might provide for the perpetuation of the low intensive frequencies observed in the *M. felsina* population. Although to date other forest riodinids have not been studied in such detail, I suspect that their low intensive frequencies may be explained on much the same basis.

Low Extensive Frequencies

Low extensive frequency means that populations are found rarely within a given faunistic region. This is the case with *M. felsina* as well as other forest riodinids. The key factor here in the case of *M. felsina* is foodplant distribution. Individuals of *Norantea brasiliensis* Choisy (Marcgraviaceae), the *M. felsina* foodplant, are widely and sparingly distributed on the restinga, but this does not prevent their being visited by ovipositing females.

There is a tendency on the part of the newly emerging butterflies to establish a colony at a suitable locality near the site of their foodplant. This was observed on several occasions, the most notable of which was

when two males were seen engaging in patrolling behavior on a small clump of bushes near a foodplant some 500 m from the main colony. These same two individuals were there one week later, a little bit worn but still recognizable. Before the next visit, they had disappeared and no others had taken their place. On the nearby foodplant, larvae were discovered in various instars. I did not observe any other case of actual colonization occurring on that particular clump of bushes. Undoubtedly, this attempt failed as a result of the rather harsh, unsheltered conditions in that particular section of the restinga. Females, then, are the colonizers for *M. felsina*, traveling considerable distances many times in search of foodplants on which to lay their eggs.

This phenomenon has been recorded indirectly with other riodinid butterflies. On numerous occasions a single butterfly will be encountered at a particular place and time, whereas subsequent visits under comparable conditions will fail to turn up additional specimens. In the same woods as the *M. felsina* habitat, a single male *Calydna lusca* (Geyer) was captured on 18 July 1973. On 7 July 1972, a male and female *Nymphidium lisimon attenuatum* Stichel were taken and a single female *Leucochimona philemon* (Cramer) was taken on 7 July 1973. Before and since, 46 collecting days over 4 years have failed to reveal additional examples from this small wood. The best explanation is that the females are very vagile, always on the move searching for new foodplant localities. Similar conclusions have been reached by other students of tropical riodinids. Ebert (1969) mentions that little species such as riodinids "migrate continuously within a great area of favorable biotypes. . . ."

Finally, the question arises concerning the barriers that female riodinids will cross in their movement. In the case of *M. felsina*, open flat areas do not appear to provide a serious obstacle, although this might be expected because of their preference for a low forest habitat. Observations on deep forest riodinids are few but significant. On 19 January 1975, a lone female *Nymphidium mantus* (Cramer) was observed passing through dry secondary shrub near Linhares, Espirito Santo, Brazil, an area very different from its normal habitat in the deep forest near the edges of swamps. Water does not appear to be a significant barrier since many riodinid populations on either side of large rivers such as the Amazon are virtually indistinguishable (Callaghan, in prep.).

SUMMARY

The results of the marking-recapture and observations of adult behavior allow a number of conclusions to be drawn with respect to the

population structure of the neotropical riodinid butterfly *M. felsina*. It was found that this butterfly exhibits the structure common to most forest butterflies, that of low intensive and extensive frequencies. The reasons for the former are low egg-laying frequency, longevity, and male spacing. The latter was explained by a combination of high female vagility and low intensive and extensive foodplant distribution, which lead to the establishment of new colonies by females at widely dispersed foodplant localities. Depending on conditions at these localities, such as parasitism and exposure to the weather, the colony may become extinct only later to be reestablished by another wandering female. It is suggested that similar population structures for other neotropical forest butterflies, particularly riodinids, may be explained on this same basis.

ACKNOWLEDGMENTS

LITERATURE CITED

BAILEY, N. T. J. 1952. Improvements in the interpretation of recapture data. J. Animal Ecol. 21: 120–127.

BATES, H. W. 1864. The naturalist on the River Amazons. University of California Press (1962 reprint of the second edition, John Murray, London). 465 p.

BENSON, W. W. 1972. Natural selection for Müllerian mimicry in the Heliconius erato in Costa Rica. Science 176: 936–939.

BENSON, W. W. & T. C. EMMEL. 1973. Demography of gregariously roosting populations of the nymphaline butterfly *Marpesia berania* in Costa Rica. Ecology 54: 326–335.

CALLAGHAN, C. J. 1977. Studies on restinga butterflies. I. The life cycle and immature biology of *Meander felsina* (Riodinidae). J. Lepid. Soc. 31: 173–182.

COOK, L. M., K. FRANK, & L. P. BROWER. 1971. Experiments on the demography of tropical butterflies. I. Survival rate and density in two species of *Parides*. Biotropica 3: 17–20.

CRANE, J. 1955. Imaginal behavior of a Trinidad butterfly *Heliconius erato hydara* Hewitson, with special reference to the social use of color. Zoologica 40: 167–196.

————. 1957. Imaginal behavior in butterflies of the family Heliconiidae: Changing social patterns and irrelevant actions. Zoologica 42: 135–146.

EBERT, H. 1969. On the frequency of butterflies in eastern Brazil, with a list of the butterfly fauna of Pocos de Caldas, Minas Gerais. J. Lepid. Soc. 23: Suppl. 3, 48 p.

EHRLICH, P. R. & L. E. GILBERT. 1973. Population structure and dynamics of the tropical butterfly *Heliconius ethilla*. Biotropica 5: 69–82.

FISHER, R. A. & E. B. FORD. 1947. The spread of a gene in natural conditions in a colony of the moth *Panaxia dominula* (L.). Heredity 1: 143–174.

LABINE, P. A. 1968. The population biology of *Euphydryas editha*. VIII. Oviposition and its relation to patterns of oviposition in other butterflies. Evolution 22: 799–805.

MACNEILL, C. D. 1964. The skippers of the genus Hesperia in western North America with special reference to California (Lepidoptera: Hesperiidae). Univ. California Publ. Ent. 35: 230 p.

POWELL, J. A. 1968. A study of area occupation and mating behavior in *Incisalia iroides* (Lepidoptera: Lycaenidae). J. N. Y. Ent. Soc. 76: 47–57.

SCOTT, J. A. 1974. Population biology and adult behavior of *Lycaena arota* (Lycaenidae). J. Lepid. Soc. 28: 64–72.

SEITZ, A. 1913. Macrolepidoptera of the World. Vol. 5. The American Rhopalocera. Alfred Kernen Verlag, Stuttgart. 1143 p.

SHEPPARD, P. M. & J. A. BISHOP. 1973 (1974). The study of populations of Lepidoptera by capture-recapture methods. J. Res. Lepid. 12: 135–144.

TURNER, J. R. G. 1971. Experiments on the demography of tropical butterflies. II. Longevity and home-range behaviour in *Heliconius erato*. Biotropica 3: 21–31.

YOUNG, A. M. 1972. The ecology and ethology of the tropical nymphaline butterfly, *Victorina ephaphus*. I. Life cycle and natural history. J. Lepid. Soc. 26: 155–170.

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