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Massimo Masetti, Valerio Scali

Ecological adjustments of the reproductive biology in Maniola jurtina from Tuscany

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Zoologia. — *Ecological adjustments of the reproductive biology in* Maniola jurtina *from Tuscany* (*). Nota di MASSIMO MASETTI e VALERIO SCALI, presentata (**) dal Socio M. BENAZZI.

RIASSUNTO. — Precedenti ricerche sulla biologia riproduttiva del lepidottero satiride *Maniola jurtina* avevano rivelato la presenza di una diapausa estiva nelle femmine delle popolazioni insulari e continentali di pianura in base alla loro attività e maturazione gonadica.

La presenza della diapausa è stata adesso dimostrata direttamente con il metodo di cattura–marcamento–rilascio e ricattura ed anche indirettamente attraverso la stima della vita media dei maschi e delle femmine prima e dopo l'estivazione. Le ricatture di femmine dopo 40–95 giorni dalla prima cattura e senza ricatture intermedie, indicano chiaramente l'esistenza dell'estivazione tenendo conto che la vita media, in popolazioni dove non esiste diapausa, è di circa 13 giorni.

Parimenti la durata della vita media inferiore ai due giorni, stimata alla schiusa, suggerisce la rapida cessazione dell'attività di volo nelle femmine che perciò si nascondono durante il periodo più caldo.

L'attività e l'andamento delle ricatture escludono invece la esistenza di estivazione nelle colonie oltre i 700 metri di altezza. Ad altezze intermedie l'andamento delle raccolte, le ricatture e l'analisi della maturazione gonadica delle femmine hanno messo in evidenza la contemporanea presenza di individui estivanti ed a schiusa tardiva.

La regolazione del periodo e della durata delle schiuse, unitamente alla diapausa, acquista perciò un chiaro significato adattativo di cui viene discussa l'importanza in relazione alla diffusione dell'insetto negli habitats più disparati della regione paleartica.

INTRODUCTION

The meadow brown butterfly (*M. jurtina*) has a palearctic distribution: it is found throughout Europe and extends to Russia, Asia Minor and Persia eastward, while it reaches the Canary Islands and North African countries to the South.

The ability of colonizing extremely diversified habitats is surely linked to a marked physiological adaptability of which the spot-system adjustments are only the best known aspect (Dowdeswell, 1961, 1962; Ford 1971; Scali, 1971 b, 1972).

On extending the spot-distribution analysis to central Italian populations another example of adaptive device at work in this butterfly has been described, namely the occurrence of an imaginal diapause together with a delayed gonadal maturation in the females of insular and plain colonies on the continent (Scali, 1971 a). In such populations, at the time of hatching, males are sexually mature

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(**) Nella seduta dell'11 novembre 1972.

while females are very unripe; their genitalia, however, allow them to copulate and fertilized females store a spermatophore. Males soon die off and during the diapause, coinciding with the hottest season, females ripen their eggs; afterwards by the end of August or the beginning of September when grasses, which had dried off, start to vegetate again, mature females resume their activity and lay eggs. The adaptive value of this reproductive system is clear if one thinks that in this way first instar caterpillars will have the right conditions for feeding.

Mountain populations, because of the much cooler climate they experience, should not present aestivation, but this had not been sufficiently investigated at the time of the first reports so that no conclusive evidence about the aestivation had been collected for mountain colonies. Furthermore for the colonies where the temporary disappearance of flying specimens had been reported, a direct proof that late female populations were due to the reappearance of aestivated females would have been desirable.

This paper deals with the results obtained on these matters by combining field and laboratory techniques over three flying seasons (1970–72).

MATERIAL AND METHODS

To detect the presence of " early " specimens among late captures (post–aestivation) we did extensive collecting and applied the method of capture–marking–release–recapture (Fisher and Ford, 1947) using cellulose paint of different colours at various positions on the hind wings. This technique has given us valuable information for both the direct proof of aestivation and, through the mathematical analysis of the data, the evaluation of average life that the two sexes enjoy during the imaginal stage.

In colonies of intermediate altitudes it was useful to interrelate this kind of information with the actual gonadal maturation of females at a given time of the flying activity.

RESULTS

By arranging the captures of the three flying seasons into a monthly and daily sequence, differences of hatching time and flying activity among the various colonies can be seen (Table I).

For places such as Il Boschetto, Torre Riccardi and S. Maria del Giudice (see map, fig. 1) we can say that on the coastal plains the hatching mainly occurs during June even if minor differences for both the beginning and the duration of it are found for different years. After this spell, flying specimens greatly decrease and later on completely disappear; odd specimens only are now and then found during the second half of July and most of August. By the beginning of September numbers rise again and the new populations are then mainly made up of females.

TABLE I

Daily and monthly sequence of captures of Maniola jurtina *at various localities in Tuscan Mainland (Central Italy) for 1970–72.*

TORRE RICCARDI (1 m a.s.l.)			IL BOSCHETTO (1 m a.s.l.)		
DATE	sex		DATE	sex	
	♂♂	♀♀		♂♂	♀♀
17 June 71	73	5	26 May 72	37	3
19–21 June 72	284	29	19–21 June 72	228	147
22 June 71	52	7	22–24 June 72	196	77
22–24 June 72	230	13	30 June 71	52	40
30 June 71	60	2	4 July 72	58	16
2 July 71	51	4	5 July 71	47	31
4 July 72	64	8	7 July 71	60	20
14 July 71	4	5	9 July 71	35	18
14 July 72	11	3	11 July 72	25	17
20 July 71	6	0	12 July 71	44	17
22 July 71	0	2	14 July 72	12	19
26 July 71	0	0	15 July 71	20	12
28 July 71	0	2	17 July 72	15	13
16 Aug 72	0	2	19 July 71	9	14
18 Aug 71	0	1	22 July 71	9	2
24 Aug 72	0	7	26 July 71	0	2
28 Aug 71	0	7	28 July 71	0	1
8 Sept 71	0	3	16 Aug 72	0	2
11 Sept 72	0	75	18 Aug 71	0	0
12–13 Sept 72	5	64	24 Aug 72	0	1
14 Sept 71	0	40	28 Aug 71	0	6
17 Sept 71	1	19	8 Sept 71	0	2
17 Sept 72	2	19	11 Sept 72	0	60
21 Sept 71	0	35	12–14 Sept 72	4	128
24 Sept 71	1	41	15 Sept 71	1	42
28 Sept 71	0	40	17 Sept 72	2	36
4–6 Oct 71	0	89	20 Sept 71	2	25
8 Oct 71	0	26	23 Sept 71	3	28
12 Oct 71	0	29	27 Sept 71	0	14
16 Oct 71	0	3	1 Oct 71	0	17
21 Oct 71	0	6	5–7 Oct 71	0	22
			11 Oct 71	0	6
			16 Oct 71	0	2
			21 Oct 71	0	0

Continued: TABLE I.

S. MARIA DEL GIUDICE (120 m a.s.l.)		
DATE	sex	
	♂♂	♀♀
13–16 June 72	180	14
17 June 71	32	2
21 June 70	57	14
21 June 71	15	7
24 June 70	75	7
25–26 June 70	149	20
28 June 71	25	4
3 July 71	33	3
13 July 71	41	16
16 July 71	15	10
17 July 70	8	13
21 July 71	20	6
25 July 70	1	9
28 July 71	4	6
30 July 71	4	8
6 Aug 70	0	0 (*)
20 Aug 71	0	3
27 Aug 71	0	14
30 Aug 70	2	63
2 Sept 71	6	31
3 Sept 72	5	49
8 Sept 71	0	37
18 Sept 71	1	17
22 Sept 70	0	18
22 Sept 71	0	18
25 Sept 71	0	10
30 Sept 71	0	0

PRUNETTA (1000 m a.s.l.)		
DATE	sex	
	♂♂	♀♀
3 July 71	0	0
4 July 70	5	0
8 July 72	87	11
8 July 72 (**)	99	64
11 July 70	39	7
14 July 71	53	6
21 July 70	31	7
24 July 71	43	4
25 July 72 (**)	48	27
1 Aug 70	20	15
4 Aug 70	16	18
22 Aug 71	0	26
22 Aug 72 (**)	4	60
27 Aug 70	0	33
1 Sept 71	0	13
17 Sept 71	0	0

S. MARCELLO (700 m a.s.l.)		
DATE	sex	
	♂♂	♀♀
2 July 72	88	35
4 July 70	17	10
11 July 70	30	26
14 July 71	30	13
15 July 70	71	22
21 July 70	54	13
24 July 71	66	20
1 Aug 70	19	16
4 Aug 70	25	30
22 Aug 71	7	19
22 Aug 72	8	51
27 Aug 70	3	13
1 Sept 71	0	98
17 Sept 71	0	1

(*) By vigorous shaking of bushes 2 males and 3 females have been roused.
(**) From the Vivaio Demaniale

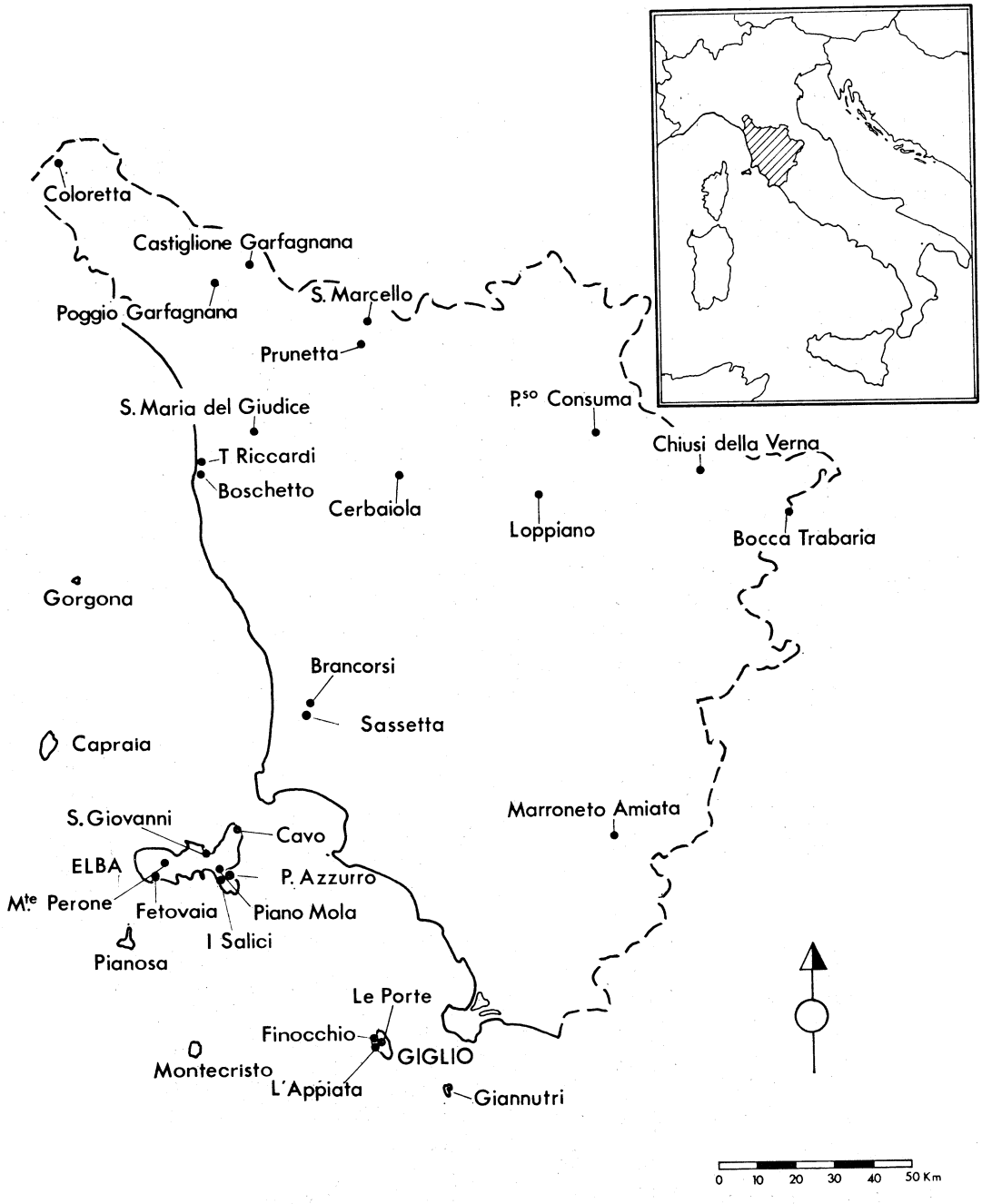

Fig. 1. – Map of Tuscany showing the collecting sites. The inset shows the position of Tuscany.

This sequence of events is very similar to that already described for insular and coastal continental colonies (Scali, 1971 a); however, the extensive collecting has more precisely defined the duration of emergence, which on the mainland lasts about 4–5 weeks, that is to say 1 or 2 weeks longer than on islands.

A very different picture of the imaginal activity has been obtained from Prunetta (1.000 m a.s.l.): hatching begins more than one month later and no complete disappearance or even temporary decrease in numbers is detectable throughout the Summer, so that from the number of flying specimens no aestivation seems to occur here.

Due to fir-tree planting in 1968 (see Scali, 1971 b) the ecology of this site has changed and during 1972 apparently reached a critical point being increasingly less suitable for *M. jurtina* as the season proceeded; we therefore started collecting in another place, the Vivaio Demaniale, located at the same altitude and not far away from the original collecting area. In this new area *M. jurtina* seems to have the same pattern of activity judging from the 3 available samples.

At S. Marcello (700 m a.s.l.) no gap of activity or reduction in numbers is found during the hottest season and therefore this population is very similar to that of Prunetta; hatching, however, here starts earlier (at the very beginning of July numbers are already high) and on the whole it lasts longer.

The situation found on Tuscan mountain colonies is in very good agreement with that found in the populations of Great Britain where no diapause seems to exist (Scali, 1971 b); the only difference one can notice is the remarkably shorter spell of hatching for highest sites: at Prunetta it only lasts about 4 weeks compared with the 8–9 of the British populations.

Fig. 2 shows the results of the marking-recapture method for the above mentioned colonies: recaptures fully support the real existence of an imaginal diapause for Il Boschetto, Torre Riccardi and S. Maria del Giudice, while indicating its absence from S. Marcello and Prunetta. Section A reports the recaptures of pre-aestivation females for the first group of colonies: it can easily be seen that the bulk of recaptures falls within 5 days while no specimens are recaptured between the 17 th and the 41 st days, and that a few are recaptured after 41 to 97 days. The average life of the insect, in populations where no diapause occurs, is about 13 days (Dowdeswell *et al.*, 1949); therefore the only explanation consistent with these recapture data is that the imaginal life of females is greatly prolonged because of the diapause. These results, therefore, directly prove the aestivation in the female sex for these three colonies.

On the other hand this pattern of recapture scattering is not found in mountain colonies (fig. 2, C) and, even allowing for small numbers, this difference very likely reflects a condition of continuous activity. The graph obtained for Prunetta and S. Marcello is actually very similar to that obtained for recaptures in post-aestivation populations of Il Boschetto, Torre Riccardi and S. Maria del Giudice (fig. 2, B).

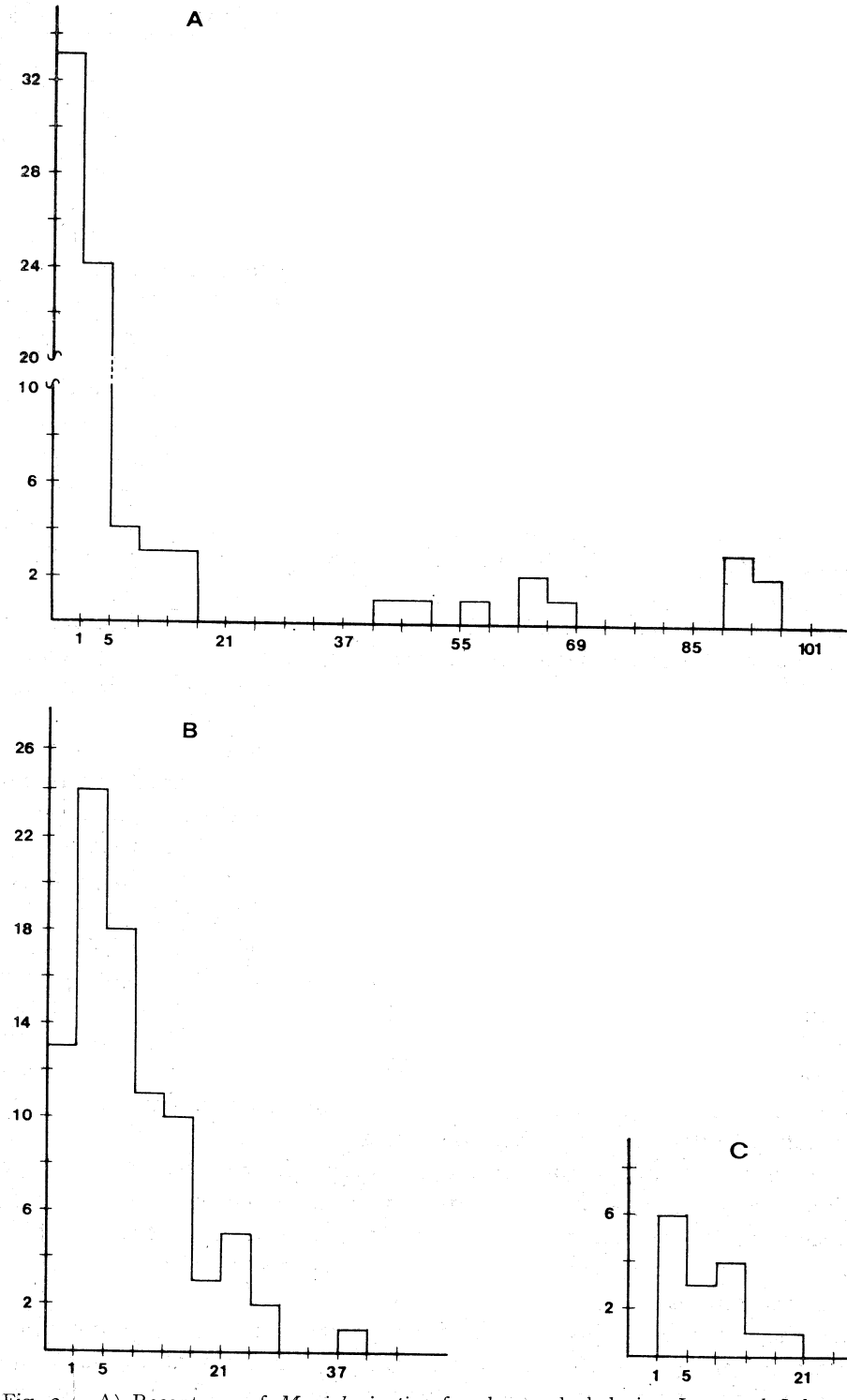

Fig. 2. – A) Recaptures of *Maniola jurtina* females marked during June and July 1970-72 at Torre Riccardi, Il Boschetto and S. Maria del Giudice. B) Recaptures of *Maniola jurtina* females marked during August and September 1970-72 at Torre Riccardi, il Boschetto and S. Maria del Giudice. C) Recaptures of *Maniola jurtina* females marked during July, August and September 1970-71 at Prunetta and S. Marcello. In each graph the ordinates represent the number of specimens, the abscissae the days from the marking.

The colony of Poggio deserves a separate description. For its intermediate altitude (430 m a.s.l.), the activity pattern of *M. jurtina* is very variable and intricate. Table II A reports the usual monthly and daily arrangement of captures: it is quite clear that no gap of flying specimens has been noticed, but only a temporary reduction in numbers particularly marked at the end of July. This would seem at variance with previous reports which indicated the existence of a summer diapause in the Poggio colony (Scali, 1971); but this is not quite so, because among the females flying during late August some recaptures of 47–64 days have been found indicating that, even for those years when no complete interruption of flying specimens is realized, an aestivation occurs just the same. What the new data indicate is that in some years the hatching is not completed during July and that when the hatching is very prolonged there is an overlapping of late emergers with early aestivated females.

TABLE II

A) *Daily and monthly sequence of captures of* Maniola jurtina *at Poggio (Central Italy) for 1970–72.*

DATE	Sex	
	♂♂	♀♀
17 June 1972	130	17
24 June 1971	106	24
27 June 1970	99	69
28 June 1970	111	46
29 June 1970	103	38
29 June 1972	96	23
12 July 1970	46	22
16 July 1971	75	16
29 July 1972	33	9
13 Aug 1970	15	73
29 Aug 1971	7	95
31 Aug 1970	1	89
4 Sept 1972	3	78
25 Sept 1970	0	32

B) *The reproductive condition of female* Maniola jurtina *collected from Poggio on the 13th August 1970.*

♀♀ examined	unfertilized	fertilized	ripe	unripe
73	0	73	27	46

The analysis of gonadal maturation has shown (Table II B) that for 1970 in this colony on the 13th of August only 27 out of 73 dissected females were ripe; furthermore among the mature specimens 10 had not yet started egg-laying: this situation indicates the existence of late emergers, and the copulating pairs observed throughout this month support this view as well.

Another kind of approach to the demonstration of the peculiar female reproductive behaviour in " diapause populations " is provided by the mathematical evaluation of the average life according to the Fisher and Ford method. Fig. 3 reports the recaptures in the colony of Il Boschetto 1972, arranged in the usual triangular disposition. From these data it follows that the elimination rate of males greatly differs from that of the pre-aestivation females, while it is similar for the post-aestivation ones; the actual values are 0.19, 0,55 and 0.23 respectively. The figure obtained for the elimination rate of the pre-aestivation females is extremely high and corresponds to an average life of less than 2 days. This paradoxical result, according to which the pre-aestivation females should live less than males and aestivated females, is simply explained by assuming that the high elimination rate is not due to death but to the hiding for aestivation.

Finally we would like to draw attention to the fact that during September in continental colonies, together with aestivated females a few males are consistently captured. We can now believe that these late males represent newly emerged specimens because not a single case of recapture has occurred in 5 years marking with thousands of marked early males involved. Another reason for believing so is provided by the fact that a copulating pair was observed at Il Boschetto on the 17th September 1972. Females are fertilized soon after hatching and this therefore indicates that even in the " diapause colonies " very few females with a very delayed emergence exist and that a similar proportion of males could hatch at the same time assuring the fertilization of those late females. It would seem quite likely that very late hatching specimens experience a pupal diapause though no direct proof of it is available.

Conclusions

Among the various means of adaptation developed by the meadow brown butterfly the diversified and precise regulation of its reproductive biology is of outstanding importance. This adjustment is achieved by the development of a summer diapause of adult females in those colonies which have a dry and hot climate. This characteristic feature of the female reproductive biology obviously makes *M. jurtina* able to colonize hot and dry places and therefore to spread into the most southern parts of the palearctic area (Dowdeswell and McWhirter, 1967; Brockie, 1972). The occurrence of aestivation previously reported on the basis of flying activity and late population structure (Scali, 1971 a, b, 1972) has now been demonstrated in two more ways: the first is the recapturing of specimens marked at the time of

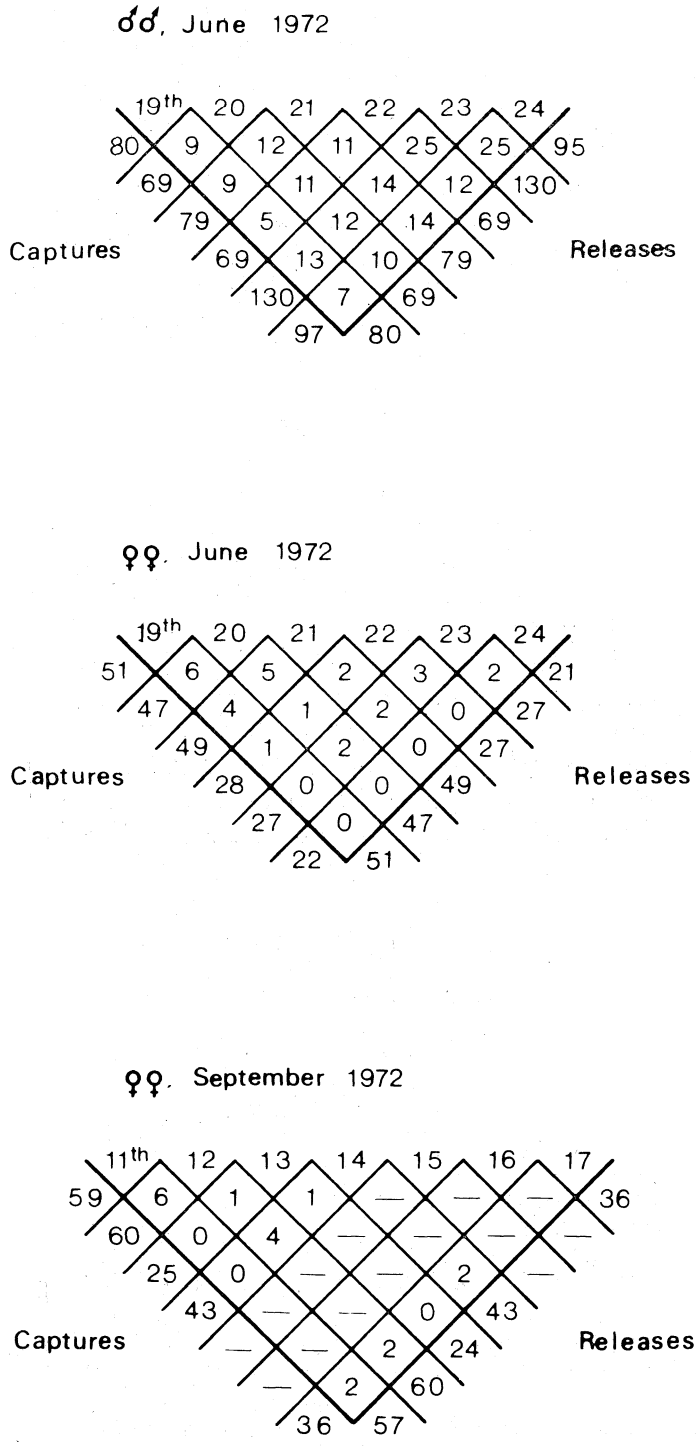

Fig. 3. – Captures, releases and recaptures of *Maniola jurtina* at Il Boschetto, in 1972. In each table the total captures are entered in the left-hand diagonal column; the total releases are entered in the right-hand diagonal column. Recaptures are entered in the body of the tables.

their hatching among egg-laying females (direct proof), and the second is the evaluation of average female life in both pre- and post-aestivating populations. The same methods have proved consistent in excluding the diapause from mountain colonies (above 700 metres). The new data about the presence or absence of the aestivation are also relevant to the interpretation of the intraseasonal changes noticed in the spot-distribution of the females in the different colonies (Scali, 1971 b, 1972).

From extensive capturing over the last three flying seasons a better picture of the hatching timing has been obtained even for those medium high colonies where the hatching pattern is rather complicated. From the available evidence it is clear that the hatching as well acts as an adaptive device for micro-ecological adjustments.

On the whole we can say that *M. jurtina* has, besides others, two variables to play with for a convenient answer to varied ecological demands: one is the duration of larval and pupal development affecting the time and the scattering of emergers; the other is the ovary maturation delay. In places such as Prunetta and S. Marcello only the first is used while in insular and continental plain colonies mainly the second is active; at intermediate altitudes such as in the Poggio colony both are at work.

The insular habitats seem more extreme than those of continental plains because the hatching is shorter there and no late emergers at all are present judging from the complete absence of males in post-aestivation collections; continental colonies which have been selected for a delayed gonadal maturation of the females, owing to the presence of a few late emergers still maintain the possibility of a balance of the kind encountered at Poggio.

References

BROCKIE R. E., *Evolutionary studies on* Maniola jurtina *in Sicily*, « Heredity » (Lond.), *28*, 337–345 (1972).

DOWDESWELL W. H., *Experimental studies on natural selection in the butterfly* Maniola jurtina, « Heredity » (Lond.), *16*, 39–52 (1961).

DOWDESWELL W. H., *A further study of the butterfly* Maniola jurtina *in relation to natural selection by* Apanteles tetricus, « Heredity » (Lond.), *17*, 513–523 (1962).

DOWDESWELL W. H., FISHER R. A. and FORD E. B., *The quantitative study of populations in the Lepidoptera*, « Heredity » (Lond.), *3*, 67–84 (1949).

DOWDESWELL W. H. and MCWHIRTER K. G., *Stability of spot-distribution in* Maniola jurtina *throughout its range*, « Heredity » (Lond.), *22*, 187–210 (1967).

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

FORD E. B., « Ecological Genetics », 3 ed. (Lond.), Chapman & Hall XX+410 pp. (1971).

SCALI V., *Imaginal diapause and gonadal maturation of* Maniola jurtina (*Lepidoptera: Satyridae*) *from Tuscany*, « Jour. Animal Ecology », *40*, 467–472 (1971 a).

SCALI V., *Spot-distribution in* Maniola jurtina (L.) (*Lepidoptera Satyridae*): *Tuscan Mainland 1967-69*, « Monitore Zool. Ital. » (n.s.), *5*, 147–163 (1971 b).

SCALI V., *Spot-distribution in* Maniola jurtina: *Tuscan Archipelago, 1968-1970*, « Heredity » (Lond.), *29*, 25–36 (1972).