Zeitschrift: Mitteilungen der Schweizerischen Entomologischen Gesellschaft = Bulletin de la Société Entomologique Suisse = Journal of the Swiss Entomological Society

Herausgeber: Schweizerische Entomologische Gesellschaft

Band: 70 (1997)

Heft: 1-2

Artikel: Local movement patterns of three common grassland butterflies in a traditionally managed landscape

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DOI: https://doi.org/10.5169/seals-402655

MITTEILUNGEN DER SCHWEIZERISCHEN ENTOMOLOGISCHEN GESELLSCHAFT
BULLETIN DE LA SOCIÉTÉ ENTOMOLOGIQUE SUISSE
70, 43 – 55, 1997

Local movement patterns of three common grassland butterflies in a traditionally managed landscape

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Local distribution and movement patterns of the three common grassland butterflies *Maniola jurtina* (L.), *Melanargia galathea* (L.), and *Lysandra coridon* (PODA) were studied in a traditionally managed landscape by standard MRR methods. The three species exhibited distinct distribution patterns as well as different movement patterns. *M. jurtina* was moving mainly within managed meadows, *M. galathea* preferred undisturbed grasslands and the pasture, and *L. coridon* short-turfed, warm grassland sites. All three species regularly visited abandoned grassland, in particular females of *L. coridon*, even though considerable obstacles had to be overcome. *L. coridon* males were very mobile, frequently moving between the preferred habitat types. *M. galathea* and *L. coridon* females were more sedentary than males, whereas in *M. jurtina* there was no significant difference between the sexes. *M. galathea* and *M. jurtina* showed clear protandry. Protandry was most pronounced in *M. jurtina*, where the phenologies of the two sexes were almost completely separate.

Keywords: Lepidoptera, *Maniola jurtina, Melanargia galathea, Lysandra coridon*, dispersal, habitat use, MRR-study, grasslands, habitat partitioning.

INTRODUCTION

With the exception of crop pests, knowledge of the natural history and ecology of butterfly species tends to be inversely related to their rarity. Probably the most thorough studies on European butterflies are those concerning the large blue butterfly *Maculinea arion* (L., 1758), during its decline to extinction in England and subsequently after its reintroduction from Sweden (THOMAS, 1991). In contrast, only relatively few detailed studies of common butterflies have been carried out. An exception are the investigations of the Meadow Brown, *Maniola jurtina* (L., 1758) (DOWDESWELL *et al.*, 1949; BRAKEFIELD, 1982a, 1982b; WYNHOFF, 1992). Little attention has been paid to basic ecological knowledge such as life span, movement patterns, or the use of a habitat by resident butterfly species. A previous investigation of the three common grassland butterflies *Maniola jurtina* (L., 1758), *Melanargia galathea* (L., 1758), and *Lysandra coridon* (PODA, 1761) indicated differences in habitat preferences, changes in distribution, and abundance following mowing (LÖRTSCHER, unpubl). The results obtained were based on transect data. Data of this kind can only be used, however, as an indication of local movement patterns. In the present study distribution, local movement patterns, and life span of the three species mentioned above were analyzed, using standard capture-recapture methods.

MATERIALS AND METHODS

Study site

The study site is located on the southern slope of Monte Generoso in the Canton Ticino, southern Switzerland, at an elevation of around 1000m. The area com-

prises a traditionally managed farm (Alpe di Pree) and an abandoned one (Alpe di Poma) (Fig. 1). Alpe di Pree is divided into two pastures and one large hay meadow. The meadow can be further divided into a rather moist and productive zone with deeper soil conditions, exposed to the south-west, and a drier, less productive zone with shallower soil conditions, exposed to the south. The zone exposed to the south-west has a moderate assortment of plant species and is characterized by *Ranunculus bulbosus, Lotus corniculatus, Trifolium pratense, Trisetum flavescens, Bromus erectus*, and *Leontodon hispidus*, whereas the zone exposed to the south has a large variety of species characterized by *Festuca rubra, Festuca tenuifolia, Anthoxanthum odoratum, Scabiosa columbaria*, and *Hippocrepis comosa*. The two pastures are botanically rather similar and characterized by the same plants as the species rich meadow. The only difference between the two pastures is the presence of large, homogenous stands of *Brachypodium pinnatum* in the pasture located above the meadows.

On Alpe di Poma, agricultural use ceased at the beginning of the 1960's. Since then, secondary succession has led to large areas with young birch wood, areas of species-poor grassland dominated by *B. pinnatum*, and areas with a greater variety of species characterized by *Agrostis tenuis, Holcus lanatus, Geranium sylvaticum,* and *Knautia drymeia*. The site is separated from Alpe di Pree by areas of shrubs and trees, with only little grassland vegetation in between.

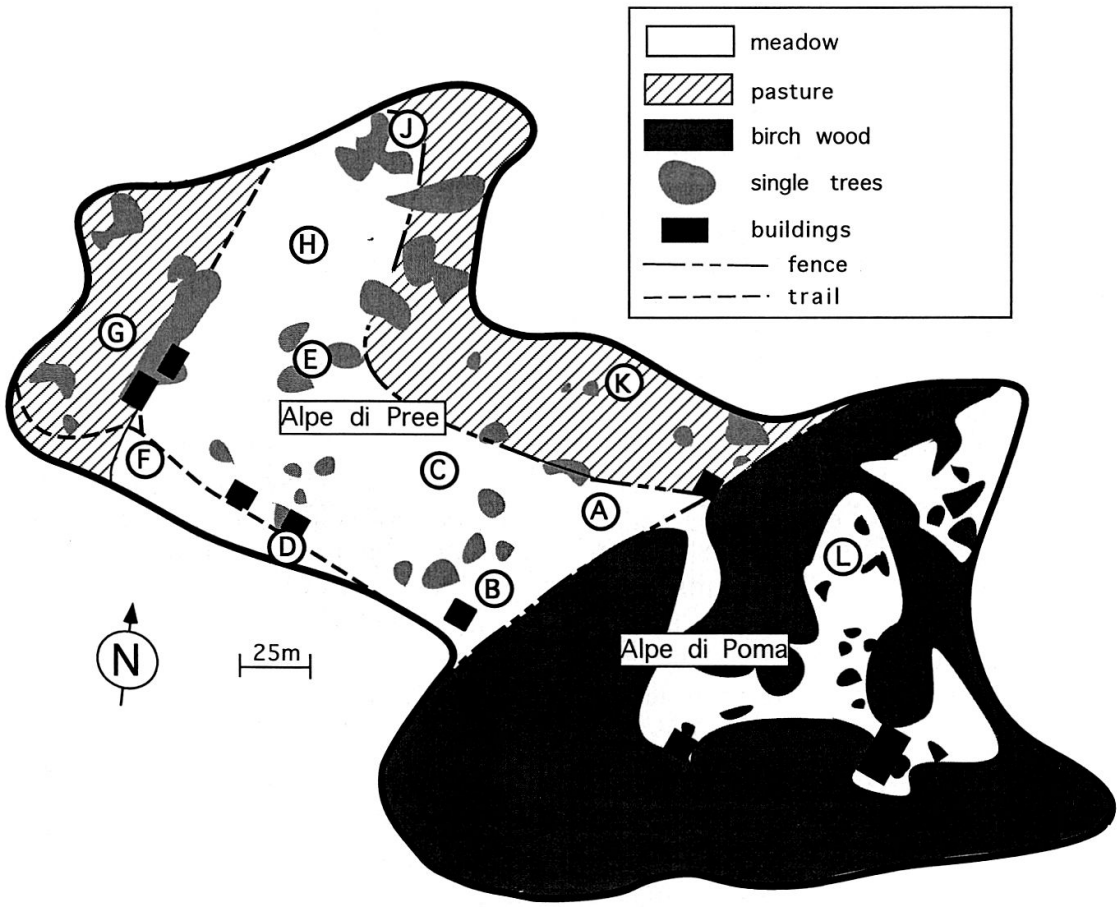

Fig. 1. Study site with the distribution of management types and the location of the marking sectors.

Data collection

Eleven sectors were defined within the study area (Fig. 1). These sectors were surveyed four times between June and August 1990, each survey lasting 4 to 6 days (survey 1, 25.6.–29.6; survey 2, 10.7.–13.7.; survey 3, 28.7.–1.8.; survey 4, 13.8.–18.8.). Every sector was visited two times during each survey, with the exception of site L in survey 1.

The hay meadows are mown once a year. During survey 1 sectors C, D and F were mown, sectors H and J had been mown by the start of survey 2, and sectors B and E were mown during survey 2 (Fig. 2). Sector A was mown between surveys 2 and 3.

Butterflies were marked individually with an accession number on the hindwing underside, using a waterproof felt tipped pen (Stabilo-OHPen96P-S). Location, species, and sex were recorded for every marked butterfly.

Data analysis

During each survey, for every species numbers of marked (M) and recaptured individuals (R), average life span (b), average total distance ($\hat{d}$), and average distance per day ($\hat{d}/t$) were calculated (Tab. 1). Average life span was expressed as the mean time between the marking occasion and the last recapture.

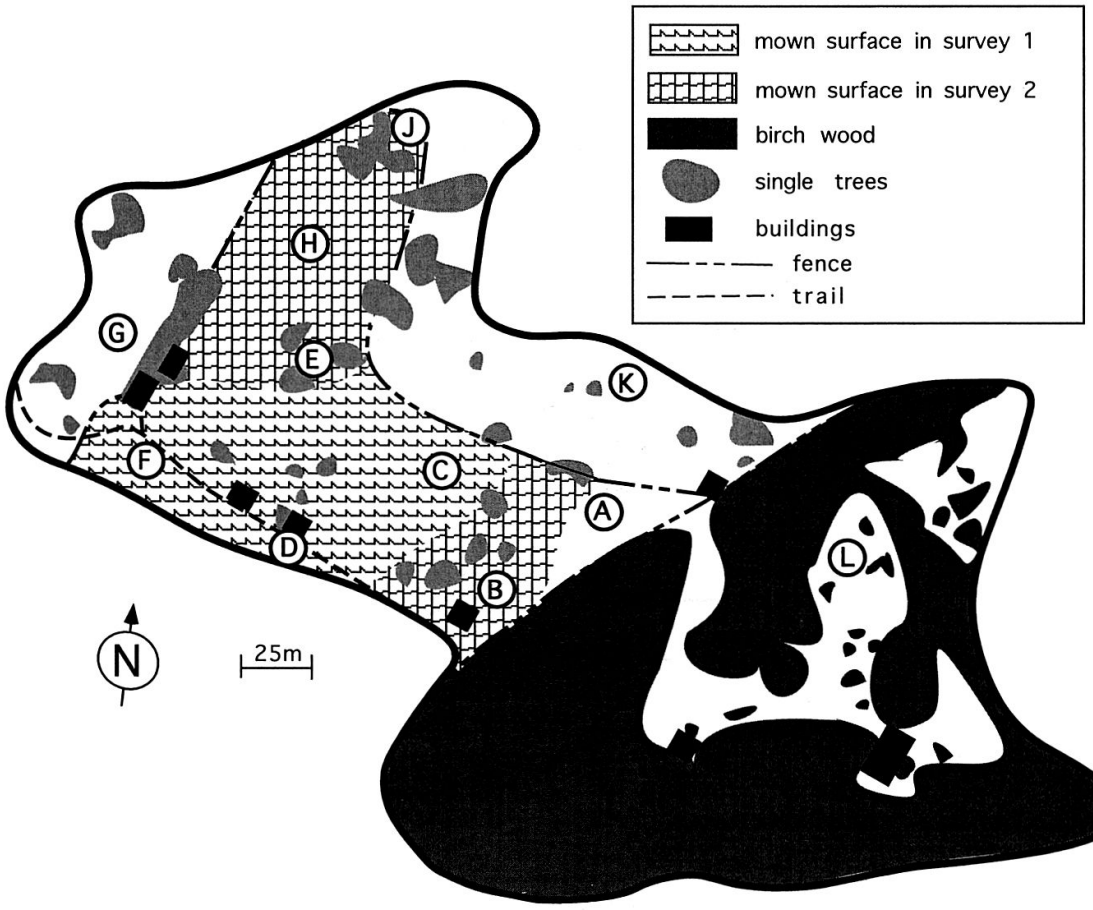

Fig. 2. Study site with the traditional course of the mowing of the meadows.

Tab. 1. MRR-data of the three butterfly species. Values for each species, sex, and survey are given separately. M = number of marked individuals, R = number of recaptured individuals, b = mean life span, max b = maximal observed life span, $\hat{d}$ = mean total distance, $\hat{d}/t$ = mean distance per day, max d = maximal observed distance.

		Period	M	R	%	b	max b	$\hat{d}$	$\hat{d}/t$	Max d
M. jurtina	Males	P0	331	51	15%	-	-	83.1	33.77	298
		P1	190	23	12%	-	-	78.61	36.12	197
		P2	29	1	3%	-	-	0	0	0
		P3	5	-	-	-	-	-	-	-
		Total	555	93	17%	6.01	18	88.5	27.91	376
	Females	P0	10	-	-	-	-	-	-	-
		P1	16	-	-	-	-	-	-	-
		P2	13	-	-	-	-	-	-	-
		P3	177	12	7%	-	-	134.5	59.5	377
		Total	216	15	7%	7	40	126.63	45.7	377
	Total		771	108	14%	6.21	40	94.2	30.54	377
M. galathea	Males	P0	33	7	21%	-	-	117.71	34.4	252
		P1	66	25	38%	-	-	110.76	41.59	433
		P2	36	6	17%	-	-	51.83	15.53	126
		P3	3	-	-	-	-	-	-	-
		Total	138	39	28%	5.51	36	112.72	30.53	433
	Females	P0	2	2	100%	-	-	120	40	240
		P1	0	-	-	-	-	-	-	-
		P2	3	3	100%	-	-	27	6.75	81
		P3	3	3	100%	-	-	66.67	50.22	126
		Total	52	8	15%	2.75	4	65.13	31.37	240
	Total		190	47	25%	5.04	36	104.62	30.67	433
L. coridon	Males	P1	40	18	45%	-	-	129.72	57.03	393
		P2	361	80	22%	-	-	131.41	59.38	712
		P3	66	28	42%	-	-	117.04	52.27	500
		Total	467	140	30%	5.06	22	134.66	50.51	712
	Females	P1	1	-	-	-	-	-	-	-
		P2	56	5	9%	-	-	96.8	75.8	274
		P3	73	11	15%	-	-	52.55	33.8	135
		Total	130	16	12%	4.12	18	88.77	45.84	274
	Total		597	156	26%	4.96	22	129.66	50	712

Average total distance was calculated by averaging the total of distances between recaptures; average distance per day was expressed as the mean of the total distances divided by the life span (b). In addition, the observed maximum moved distance (max d) and the observed maximum life span (max b) are also indicated (Tab. 1).

Patterns of emergence were analyzed for an eventual earlier emergence of males in all three species, using the Wald-Wolfowitz runs test. To compare life spans and distances covered between the sexes, a non-parametric two-sample rank test (Mann-Whitney) was applied to the data. When comparing the values between species or between surveys within species, a non-parametric analysis of variance (Kruskall-Wallis) was made. For multiple comparisons the method proposed by ZAR (1984) was applied. To analyze the movement rates of sexes and species, the number of individuals recaptured at the site of marking was compared with the

number of individuals recaptured at another site, using a contingency table analysis. The distributions of marked individuals over the eleven sectors were compared between and within species using a two (species or sexes) by eleven (sectors) contingency table analysis. To analyze the effect of mowing on the number of marked individuals per sector, numbers from mown sectors were compared with numbers from unmown sectors, using a nonparametric two-sample test (Mann-Whitney).

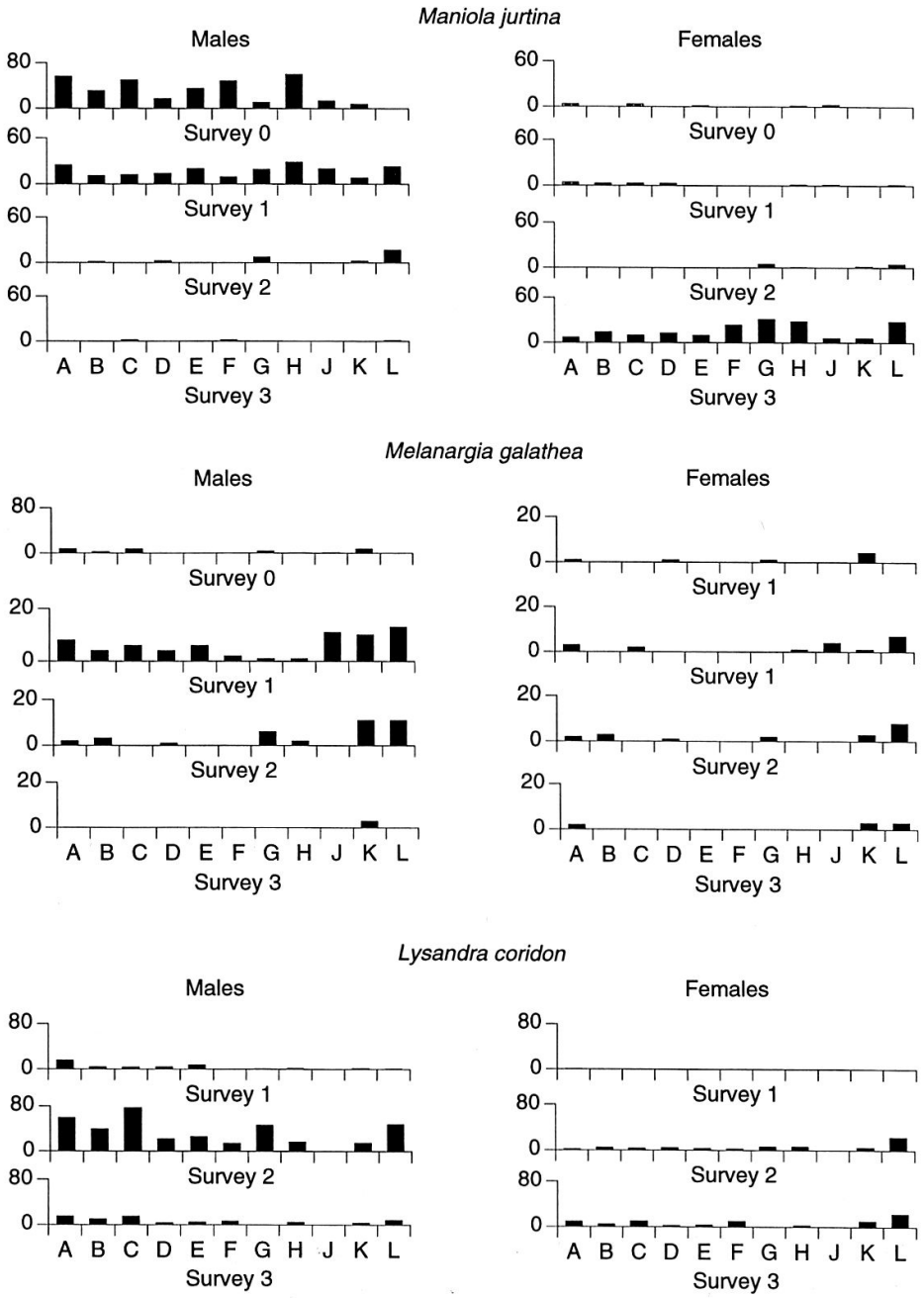

Fig. 3. Number of marked individuals at the eleven marking sectors for each species, both sexes and all surveys.

Tab. 2 Number and percentages of individuals beeing recaptured at the site of marking (stat) or at another site (move). Values for each species, sex, and survey are given separately.

		Period	N	stat	% stat	move	% move
M. jurtina	males	P0	80	21	0.26	59	0.74
		P1	26	7	0.27	19	0.73
		P2	1	1	1.00	0	0.00
		P3	-	-	-	-	-
		Total	107	29	0.27	78	0.73
	females	P0	-	-	-	-	-
		P1	-	-	-	-	-
		P2	-	-	-	-	-
		P3	18	3	0.17	15	0.83
		Total	18	3	0.17	15	0.83
M. galathea	males	P0	9	2	0.22	7	0.78
		P1	35	8	0.23	27	0.77
		P2	7	4	0.57	3	0.43
		P3	-	-	-	-	-
		Total	51	14	0.27	37	0.73
	females	P0	2	1	0.50	1	0.50
		P1	-	-	-		-
		P2	3	2	0.67	1	0.33
		P3	3	1	0.33	2	0.67
		Total	8	4	0.50	4	0.50
L. coridon	males	P0	-	-	-	-	-
		P1	23	6	0.26	17	0.74
		P2	95	16	0.17	79	0.83
		P3	36	6	0.17	30	0.83
		Total	154	28	0.18	126	0.82
	females	P0	-	-	-	-	-
		P1	-	-	-	-	-
		P2	12	3	0.25	2	0.17
		P3	10	4	0.40	5	0.50
		Total	15	7	0.47	7	0.47

RESULTS

MRR data

A total of 771 individuals of *M. jurtina*, 190 of *M. galathea*, and 597 of *L. coridon* were marked. *M. jurtina* exhibited lower recapture rates (14%) than *M. galathea* (25%) and *L. coridon* (26%). In all three species females were recaptured less often than males. Sex ratios were strongly biased with approximately 3:1 towards males

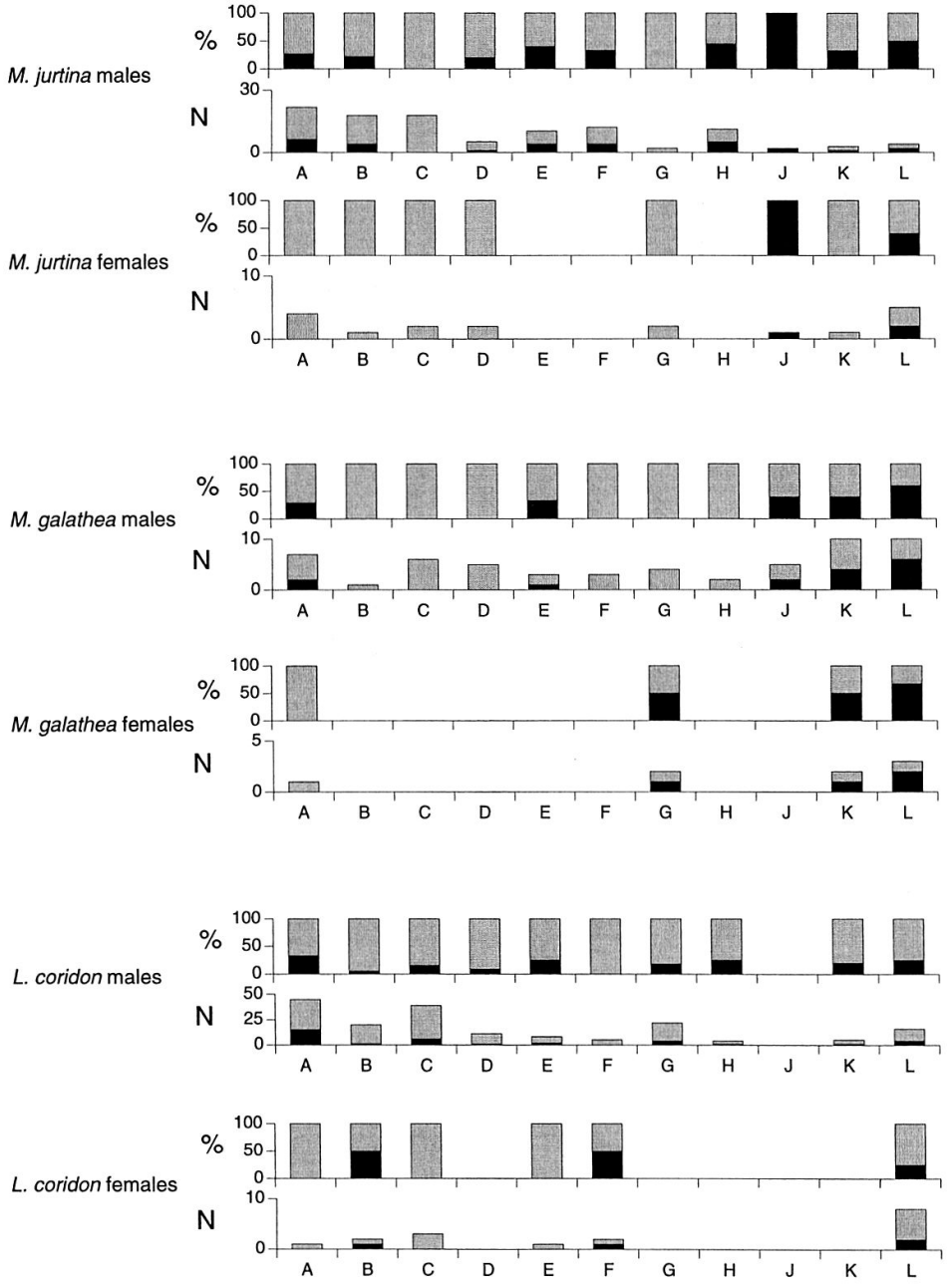

Fig. 4. Number (N) and proportion (%) of marked individuals in all eleven marking sectors that were recaptured at least once. The proportion of individuals that were recaptured at the site of marking is indicated in black.

in all three species (Tab.1). Males emerged before females did in *M. jurtina* ($Z = 20.14$; $p < 0.001$) and *L. coridon* ($Z = 5.33$; $p < 0.001$). Males of *M. jurtina* predominated during surveys 1 and 2, while the large majority of females was caught in surveys 3 and 4, showing that their phenologies were almost entirely separate (Fig. 3). *L. coridon* males were predominant during survey 3, whereas greater numbers of females were marked during surveys 3 and 4. Both sexes of *M. galathea* were marked during all four surveys (Fig. 3). Neither did average life span differ significantly between species nor between the sexes of a given species.

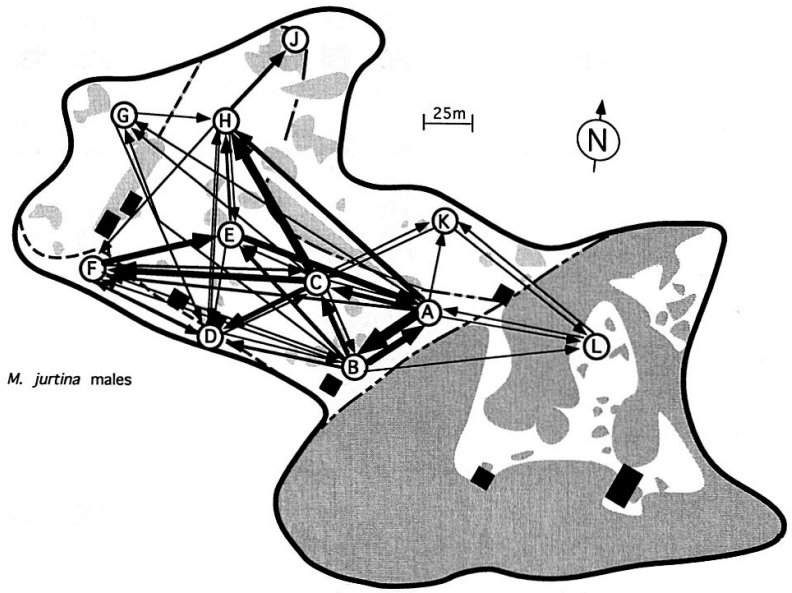

Fig. 5. Movement patterns of males of *M. jurtina* in the study area. The breadth of the arrows is proportional to the number of individuals moving in that particular direction.

Distribution in the habitat

The numbers of marked individuals at the eleven sectors are shown in Fig. 3. The distributions of males and females of *M. jurtina* differed significantly ($X^2 = 44.51$; $p < 0.001$). Males were most often marked in sectors located within meadows, whereas females were most often marked in the area around sectors F, G and H, which are situated in the more productive zone of the farm as well as on the abandoned farm on site L. In *M. galathea,* the distribution of the sexes did not differ significantly ($X^2 = 10.64$; $p = 0.36$). When most of the meadow area was mown in survey 3, the majority of individuals was marked on sites K, L and G, while before a considerable number was also marked on the meadow sites. *L. coridon* males were mainly marked on sites of the less productive zone exposed to the south-west, the pasture land of sector G and the abandoned farm L, while females of *L. coridon* exhibited a preference for sector L ($X^2 = 66.6$; $p < 0.001$).

Movement patterns

In *L. coridon* and *M. galathea*, no differences of dispersal measurements between the sexes could be detected. In *M. jurtina*, however, males moved over significantly longer total distances and distances per day ($Z = -2.3$, $p = 0.02$; $Z = -2.58$, $p = 0.01$, respectively).

When comparing all three species, differences in total distance and distance per day were present only in males. Males of *L. coridon* were the most mobile, covering on average longer total distances than males of *M. jurtina* ($p < 0.01$) and longer distances per day than males of *M. jurtina* ($p < 0.001$) and *M. galathea* ($p < 0.05$).

Movement rates of the sexes between sites were similar for *M. jurtina* ($X^2 = 0.88$; $p = 0.35$), but different for *M. galathea* ($X^2 = 6.3$; $p < 0.01$) and *L. coridon* ($X^2 = 7.88$; $p < 0.01$). In both cases, males changed sites more often than females

(Tab. 2). Males of *M. jurtina* remained most frequently at the marking site in sectors E, F, and H (Fig. 4). Based on only a few observations, the high percentage of stationary individuals in sectors K and L must be regarded with caution. Females of *M. jurtina* were mainly stationary in sector L on Alpe di Poma (Fig. 4). Males of *M. galathea* were most often recaptured on the marking site in sectors L, K, J, and A. In the other sectors no individual was recaptured at the same site. The same trend is shown by the females of this species (Fig.4). In *L. coridon*, generally only few individuals were recaptured in the marking sector. Only in sector A more males were recaptured than in the other sectors. Due to the few recapture data, dispersion patterns of females are difficult to interpret (Fig. 4).

During survey 3, when the majority of the meadow had been mown, in various sectors a negative effect on the abundance of both males and females of *M. jurtina,* and males of *M. galathea* could be detected.

Actual movement patterns of males of the three species are shown in Figs 5–7. Males of *M. jurtina* restricted their movements to the sites situated in the mown meadows. Only occasionally butterflies moving between the pastures and the abandoned farm and vice-versa could be found (Fig. 5), though this may be due to the lack of marking in sector L during survey 1, when the males of this species were most abundant. Males of *M. galathea* moved over the whole study area with a preference for movements between the pasture site K and the site L on the abandoned farm (Fig. 6). Males of *L. coridon* moved rather freely across the whole study area with a preference along the axis G, E, C, A, and L. A particularly strong movement was noted between sites A and L (Fig. 7). Females of *M. jurtina* often moved from meadow sites to the abandoned farm site L (Fig. 8). The movement of individual females between the managed surface and the adjacent abandoned grasslands was observed in the two other species as well, even though less frequently.

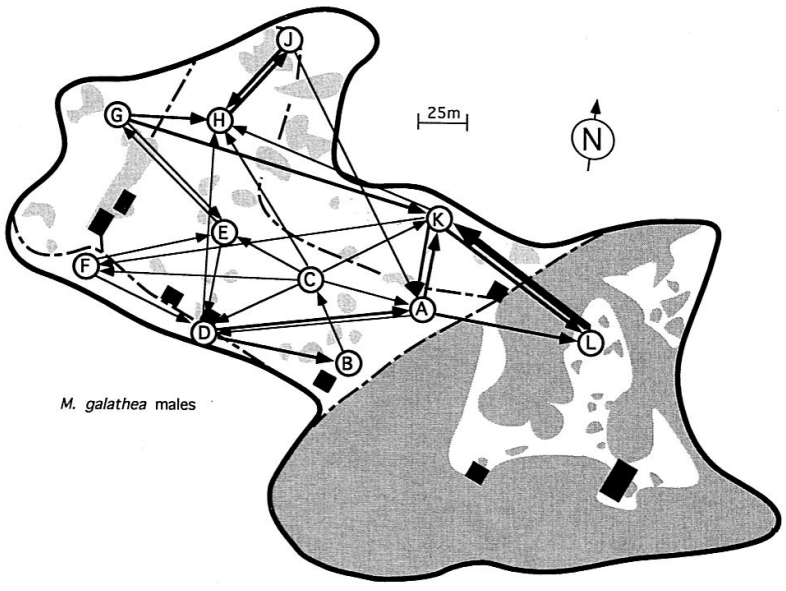

Fig. 6. Movement patterns of males of *M. galathea* in the study area. The breadth of the arrows is proportional to the number of individuals moving in that particular direction.

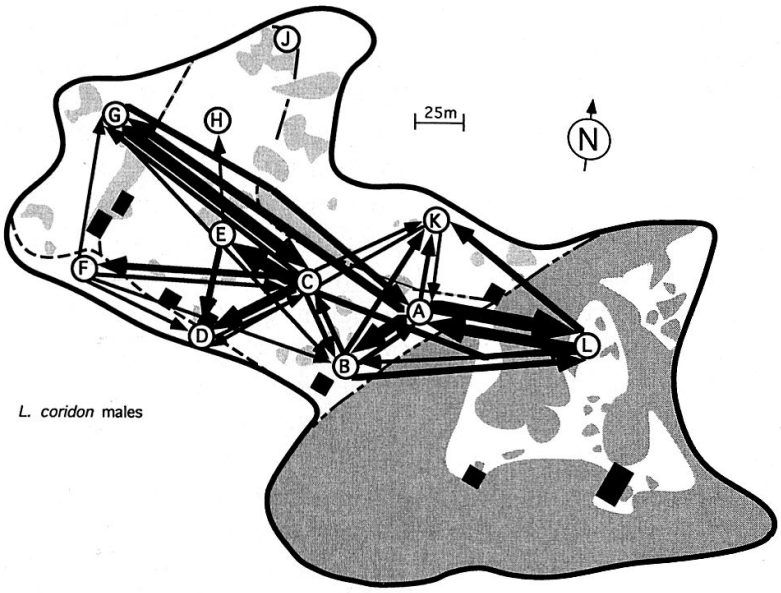

Fig. 7. Movement patterns of males of *L. coridon* in the study area. The breadth of the arrows is proportional to the number of individuals moving in that particular direction. Only movements involving more than one exchange are included.

DISCUSSION

In most butterflies with non-overlapping generations where females mate only once, males tend to exhibit a behaviour called protandry, in which males emerge before females do (THORNHILL & ALCOCK, 1983; WARREN, 1992). To varying degrees, protandry was observed in *M. jurtina* and *L. coridon*. The almost complete separation of phenology of the two sexes in *M. jurtina* deserves further comments. From an evolutionary point of view the earlier emergence of males only makes sense if they have a higher chance of encountering a virgin female (THORNHILL & ALCOCK, 1983). However, the very pronounced protandry in *M. jurtina*, in combination with the relatively short life span of males, would prevent the majority of them from ever encountering a female. Reasons for this puzzling data may be as follows: The average life spans obtained from MRR studies tend to be an underestimation of the real life spans (SHREEVE, 1992b). Females might not have been easily detected at the beginning of the survey when the meadow vegetation was rather dense, because in fact one female was marked already on the first day of the study. Males may have needed a precopulatory time span, for example for establishing a territory (THORNHILL & ALCOCK, 1983). However, it is considered that this species displays a patrolling mate locating strategy (SHREEVE, 1992a). Finally, the observed discrepancy may represent an exceptional event, occurring only in the year the study was conducted.

The average life span, calculated as the average time an individual was known to be alive, is certainly underestimated. In the present study marking efforts were restricted to specific surveys, interrupted by several days without marking. This may have led to underestimating the average life span even more. Nevertheless, the values observed are largely in accordance with data on temperate butterflies (SCOTT, 1973; WARREN, 1992). WARREN (1992) attributed longer average life spans to females of *M. jurtina* than to males, however, this was not confirmed in the present

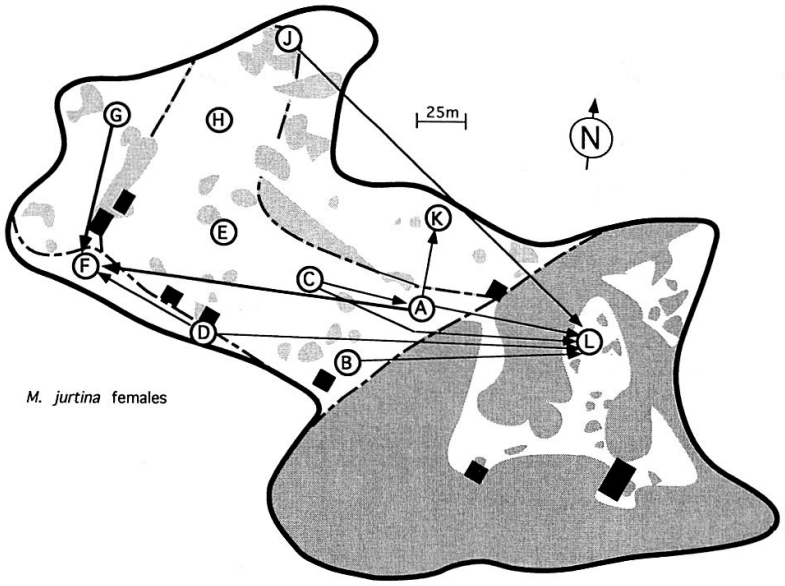

Fig. 8. Movement patterns of females of *M. jurtina* in the study area. The breadth of the arrows is proportional to the number of individuals moving in that particular direction.

study. Previously determined maximum life spans for the two sexes of *M. jurtina* (POLLARD, 1981; WARREN, 1992) and *L. coridon* (DAVIES *et al.*, 1958) largely correspond with the present findings, except for the extreme value of 40 days observed in one female of *M. jurtina*. This indicates that MRR studies of the average life spans might grossly underestimate real life spans.

Local movements of butterflies are often correlated with different activities, such as mate location, food acquisition or oviposition (SCOTT, 1975; WIKLUND, 1977; DAILY *et al.*, 1991; SHREEVE, 1992b; LÖRTSCHER *et al.*, 1995). In a previous study several Lepidoptera species exhibited different activity patterns in different sections of the study site (LÖRTSCHER, unpubl.). In *L. coridon*, males were most often observed flying in the mown, species rich meadow section, whereas the females were often observed in the abandoned grassland, mainly visiting flowers. The large number of marked females in the abandoned grassland and the movements between the mown meadow and the abandoned grassland corroborate these patterns. In addition, eggs of *L. coridon* were mainly found on the species rich section of the meadows; no known larval foodplant of this species occurred in the abandoned grassland site. Therefore, females of *L. coridon* appear to use the abandoned grassland as a food habitat and the meadow as a reproduction habitat. Males flew through the whole area, including the abandoned grassland, a behaviour that is most likely explained by the patrolling mate locating behaviour in this species.

Males of *M. galathea* were mainly found in areas with dense vegetation or in the vicinity of the edges of the woods, whereas females were mostly confined to the area of the species rich meadow, the upper pasture and the abandoned farm, which fit well the habitat preferences of this species (BLAB & KUDRNA, 1982; SBN, 1987; EBERT, 1991). The wider distribution and the less sectorary behaviour exhibited by the males can largely be explained by their patrolling mate locating strategy (SHREEVE, 1992a). As supposed, this species reacts rather finely to the mowing of the meadow and moves to undisturbed sites.

The preference of *M. jurtina* for cultivated grassland is largely in accordance with literature (SBN, 1987; EBERT, 1991) and with a previous study on the same site (LÖRTSCHER, unpubl.). Males were mostly observed moving about in the cultivated meadows. The sectors where most females were marked and recaptured are characterized by the presence of dense, grassy vegetation. The microdistribution of this species was largely governed by the presence of such areas in combination with sites rich in nectar plants (BRAKEFIELD, 1982a; WYNHOFF, 1992).

In contrast to several mostly anecdotal reportings (SHREEVE, 1992b) and the study by DOWDESWELL *et al.* (1949) on *M. jurtina*, the physical barriers made up of shrubs and birch stands, separating the marking sector in Alpe di Poma from the sectors on Alpe di Pree, constituted no barrier to the three butterfly species studied. Frequent movements to and from that sector were recorded in all three species.

The movement patterns found in this study confirm as to how a richly structured landscape is partitioned between butterfly species and even between the sexes of the same species. In fact, movements between different habitat types were frequently observed and differed markedly due to the specific needs of males and females. Thus, the present study points to the necessity of a richly structured agricultural landscape for the survival of the three butterfly species studied, and with them many other species of invertebrates as well.

ACKNOWLEDGEMENTS

We would like to thank the following persons for their support during this study: A. STAMPFLI, F. GUGGISBERG, C. ANTOGNOLI, A. VALSANGIACOMO, and M. ZIMMERMANN as well as B. WALTHER and U. KRONBACH for their assistance with butterfly marking. J. LOONEY and anonymous reviewers greatly improved the English of earlier versions. This study was part of a multidisciplinary project on unfertilized meadows and pastures of the Canton Ticino (Switzerland), managed by Prof. O. HEGG of the Botanical Institute of the University of Berne, and financially supported by the Swiss NF Project 31–9096.87 and by grants from the governments of Switzerland (BUWAL) and of the Cantone Ticino (Dipartimento dell' Ambiente), respectively, as well as from the Lega Svizzera per la protezione della natura (Sezione Ticino).

ZUSAMMENFASSUNG

In einer landwirtschaftlich traditionell genutzten Landschaft wurden die lokalen Verbreitungs- und Bewegungsmuster der drei häufigen Wiesenschmetterlingsarten *Maniola jurtina, Melanargia galathea* und *Lysandra coridon* mittels Fang-Wiederfang-Untersuchungen analysiert. Die drei Arten zeigten teils deutliche Unterschiede. *M. jurtina* hielt sich vorwiegend in den gemähten Wiesen auf, *M. galathea* bevorzugte vergandende Wiesen und die Weide und *L. coridon* kurzrasige, trockenwarme Wiesenpartien. Die vergandenden Wiesen wurden wiederholt von allen drei Arten besucht, obwohl beträchtliche Hindernisse überquert werden mussten. Die Männchen von *L. coridon* wechselten häufig ihren Aufenthaltsort zwischen den von ihnen bevorzugten Wiesenpartien. Die Weibchen von *M. galathea* und *L. coridon* waren sesshafter als die Männchen, während bei *M. jurtina* kein Unterschied festgestellt wurde. Die Männchen von *M. jurtina* und *M. galathea* verhielten sich klar protandrisch, wobei dies bei *M. jurtina* zu einer fast kompletten Separation der Phänologien der beiden Geschlechter führte.

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(received March 28, 1996; accepted after minor revision October 10, 1996)