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Population biology of two satyrine butterflies, *Erebia meolans* (de Prunner, 1798) and *Erebia aethiops* (Esper, 1777) (Lepidoptera : Satyridae)

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Summary

In 1986 population dynamics and size of one population, each of *Erebia meolans* and *Erebia aethiops* were investigated in Grindelwald (Switzerland) with the capture-recapture method. Both species flew over a period of about three weeks, *meolans* in July and *aethiops* in August. Maximum estimate by the Lincoln-Index was 66 males for *meolans* and 458 for *aethiops*. Females appeared in both species only in the second half of the flight period in smaller numbers. Analysis of habitat use of the *aethiops* males showed a preference for a steep meadow with tall grass at the edge of a wood interspersed with bushes and small trees.

Zusammenfassung

Im Sommer 1986 wurden in Grindelwald (Schweiz) je die Dynamik und Grösse einer Population von *Erebia meolans* und *E. aethiops* mit der Fang-Wiederfang-Methode untersucht. Die Dauer der Flugzeit betrug für beide Arten ca. drei Wochen, *meolans* im Juli und *aethiops* im August. Bei beiden Arten traten die Weibchen erst in der zweiten Hälfte der Fangperiode in geringerer Zahl auf. Für die Männchen von *meolans* wurde mit dem Lincoln-Index ein maximaler Wert von 66 Tieren geschätzt, für *aethiops* hingegen 458 Tiere. Es konnte gezeigt werden, dass die *aethiops* Männchen im Untersuchungsgebiet eine deutliche Präferenz für ein von Wald begrenztes und mit Gebüsch und jungen Bäumen durchsetztes Stück Wiese zeigten.

Introduction

Major factors contributing to the disappearance of butterflies are agricultural intensivation (Blab & Kudrna, 1982 : 45-46 ; SBN, 1987 : 82-85) and abandonment of agricultural use, both with profound effects on vegetation.

In the long term, both lead to impoverishment of botanical and zoological diversity (Ehrhardt, 1982 ; Briemle *et al.*, 1987). Another factor is the lack of knowledge on the compatibility of environmental changes i.e. human interventions and the ecology of invertebrates. How determinant such knowledge can be, was shown clearly in the case of the Large Blue (*Maculinea arion*), whose extinction in Great Britain was caused, among other factors, by lack of knowledge of the intrinsic relationship between the butterfly, its ant-host and sheep grazing on their habitats (Thomas, 1980). The same fate could be reserved for a number of our butterflies if ecological research on their biology and the influence of environmental changes on them is not undertaken immediately.

The aim of the present study was to investigate and compare the population dynamics and size of two species of the satyrid genus *Erebia* : *E. meolans* (De Prunner, 1798) and *E. aethiops* (Esper, 1777). *E. aethiops* is found mainly in man-made environments, prone to intensivation or abandonment, while *meolans* lives in more natural habitats, but also in man-made habitats such as road verges. Thus both species are good examples of butterflies influenced by recent changes in alpine regions. The importance and value of the obtained results for nature conservation are discussed.

Material and methods

Location and species

The study was conducted at Grindelwald, Switzerland, in the summer of 1986. *E. meolans* is on the wing from May until the end of July and prefers short-turfed, rocky and rather dry hillsides. The population investigated was found at the "Grosse Scheidegg" at an altitude of about 1450 m along a steep, dry bank bordering a road interspersed with rocks, bare ground and short-turf vegetation.

Erebia aethiops is a species that appears later and flies from July until September. It can be found in a wide variety of man-made habitats, such as dry meadows, pastures with tall grass above the timberline and light woodland interspersed with clearings. The investigated population was found in an extensively used pasture at "Bachhalten" at an altitude of about 1450 m (Fig. 1).

Mark-recapture

Both populations were visited on 6 days over a period of three weeks, *E. meolans* between July 1 and July 21 and *E. aethiops* between July 28 and August 21. Towards the end of July after a period of adverse weather no more *meolans* individuals were found at that site. At the end of August, field observations were stopped and therefore the end of the flying period of *E. aethiops* was not followed.

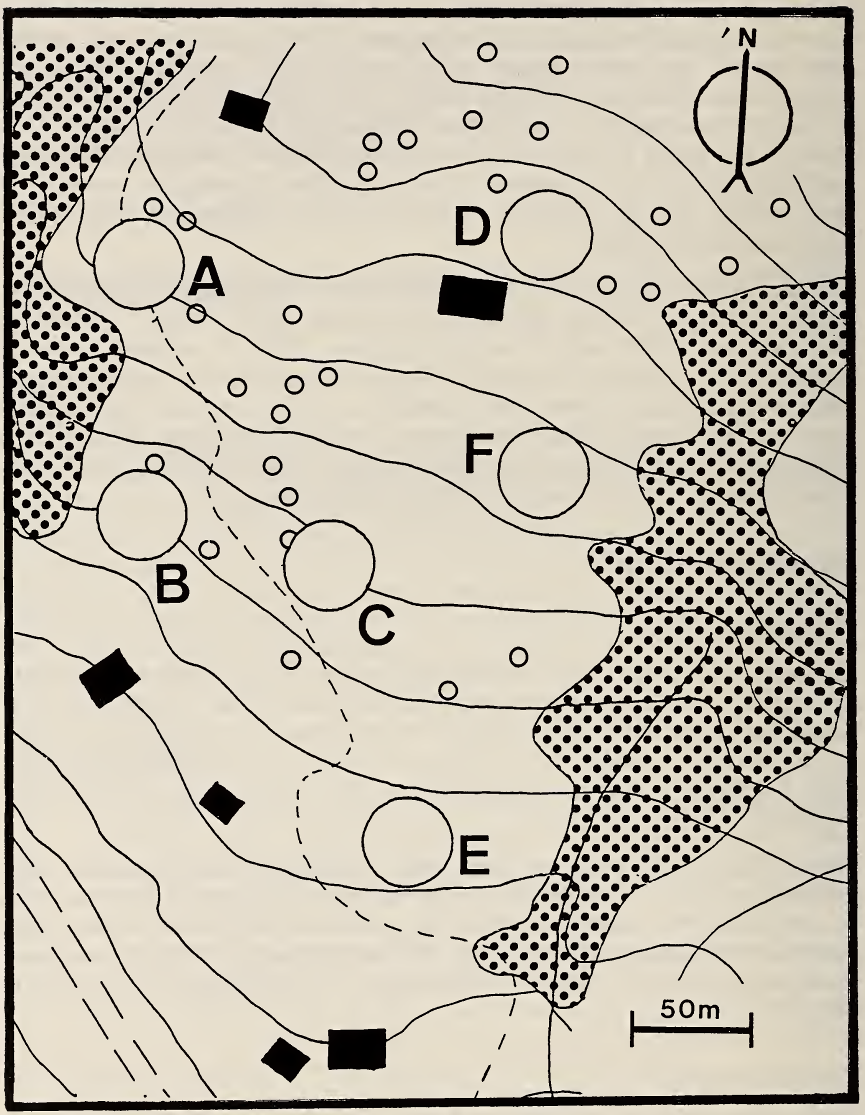

Fig. 1. Study site of the *aethiops* population at Bachhalten (Grindelwald). Dotted area = Wood ; Dotted line = Path ; Small Circles = Single trees ; Big empty circles = Subsites A-F.

Butterflies were netted by hand and marked individually by descaling the discoidal cell of the left hindwing underside and painting a number on the bare cuticle with an acryl cloth paint and a fine paint brush. Paint was preferred over the commonly used felt tip pen (Gall, 1985), because on the darkly coloured wings of Erebias such markings were not readable. Only three out of 280 marked specimens lost their markings. They were not included in the analysis. The butterflies were kept in a cool-box for several minutes after marking before being released in order to prevent an eventual "netting trauma" (Watt *et al.*, 1977). In the *meolans*-population, butterflies were caught by waiting at a particular site, where they had been observed patrolling during the preceeding year, and catching all individuals passing by. At the *aethiops* site, six subsites were defined according to previous observations and were visited regularly. The subsites were denoted with letters A-F according to the order of appearance of butterflies at those sites (Fig. 1).

One of the basic assumptions that has to be made with all mark-release-recapture-(MRR)-methods is the non-influence of marking on subsequent catchability. Morton (1982) however, shows that in some species marking does influence subsequent catchability. This was not tested in either *meolans* or *aethiops*, so it cannot be excluded to have played a role in the results. To analyse the MRR-data, both Jolly's stochastic method (Jolly, 1965) and the Lincoln Index (Lincoln, 1930) were used. Jolly's stochastic model allows direct estimation of N_i only for days 2 through i-1. The M_{i-1} estimation used by Watt *et al.* (1977) was used to estimate N_i on the last sampling date. Capture data for the two initial days of sampling were pooled and used as first estimate in both populations. Data were tallied on a pocket calculator (HP-41) using a program by M. Zimmermann (University of Berne). For the detailed *aethiops* MRR-data, proportions of recaptured individuals, at sites of marking and at other sites were calculated for all six sites in order to show an eventual preference for a site within the pasture.

Dispersal in aethiops

To analyse dispersal behaviour in *aethiops*, distances flown between capture points were measured as straight lines between the centres of the subsites. Then the following per individual dispersal statistics were calculated according to Gall (1984) :

n = number of individuals recaptured
r = number of recapture events
d = distance between successive recaptures
R = individual range (d between two most distant recaptures)

The following statistics were determined on a population basis :
$\hat{d}$ = mean distance between recaptures ($\Sigma_{i=1} \Sigma_{j=1} d_{ij}/r$)
$\hat{R}$ = mean range ($\Sigma_{i=1} R/n$)
$\hat{D}$ = mean total distance ($\Sigma_{i=1} \Sigma_{j=1} d_{ij}$)

Results

E. meolans

The MRR-data are presented in Tab. 1. During the three week period 56 butterflies, 42 males and 14 females were caught and marked. Sex ratio was biased towards males by 3 : 1 ($X^2 = 7.5$, $p < 0.05$). 40% of the males were recaptured at least once, whereas 27% or three female butterflies were caught a second time. Their flight activity was chiefly confined to the second half of the observation period while male captures were distributed evenly over the investigation period.

Tab. 1. Mark-recapture-data of the *E. meolans*-population at "Grosse Scheidegg"

Date of visit :	1.7.	2.7.	10.7.	14.7.	17.7.	21.7.
captured on day i	1	21	10	14	20	15
♂♂ captured on day i	1	18	10	11	14	10
already marked	—	1	2	8	5	6
♀♀ captured on day i	—	3	—	3	6	5
already marked	—	—	—	—	1	2
Σ marked individuals	1	21	29	35	49	56

Population size estimates were only computed for males (Fig. 2) as there were too few female recaptures to yield satisfactory results. Except for the estimate on July 10 of 66 males, estimated numbers remained rather stable around 35 individuals. In *meolans*, both males and females, patrol along well defined paths, using rocky short-turf ridges (personal observation).

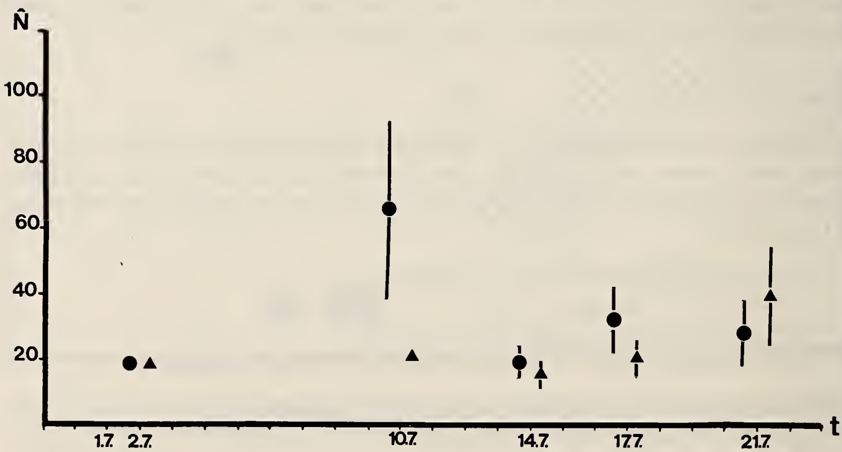

Fig. 2. Population size estimates for the male *meolans*-population at "Grosse Scheidegg" (Grindelwald) in 1986. ▲ = Jolly estimates, ● = Lincoln estimates.

E. aethiops

MRR-data are presented in Tab. 2. 284 butterflies, 241 males and 43 females were caught and marked. The sex ratio in *aethiops* with 5.6 : 1 is strongly biased towards males ($X^2 = 79$, $p < 0.01$). The sex ratio is even more strongly skewed than in *meolans* ($X^2 = 3.26$, $p < 0.1$). 30% of the male butterflies were recaptured at least once, whereas only one female was caught a second time. Female butterflies were caught mainly in the second half of the study period, that is 10 days after the first males had been marked. The population size estimates of the male population augmented steadily during the observation period and reached a maximum by August 21 of 338 (± 116) by Jolly's stochastic method and 458 (± 114) by the Lincoln-Index. This maximum has to be considered with care, as at the end of the investigation period, population size was still augmenting (see Fig. 3), so that it cannot be excluded that population size increased even further after that date. However on the occasion of a visit at the site ten days later, only very few *aethiops* were observed.

Tab. 2. Mark-recapture-data of the *E. aethiops* population at "Bachhalten"

Date of visit :	28.7	30.7.	6.8.	9.8.	15.8.	21.8.
captured on day i	10	13	73	91	100	85
♂♂ captured on day i	10	13	71	86	86	62
already marked	—	1	13	27	28	21
♀♀ captured on day i	—	—	2	5	14	23
already marked	—	—	—	—	—	1
Σ marked individuals	10	22	82	146	218	281

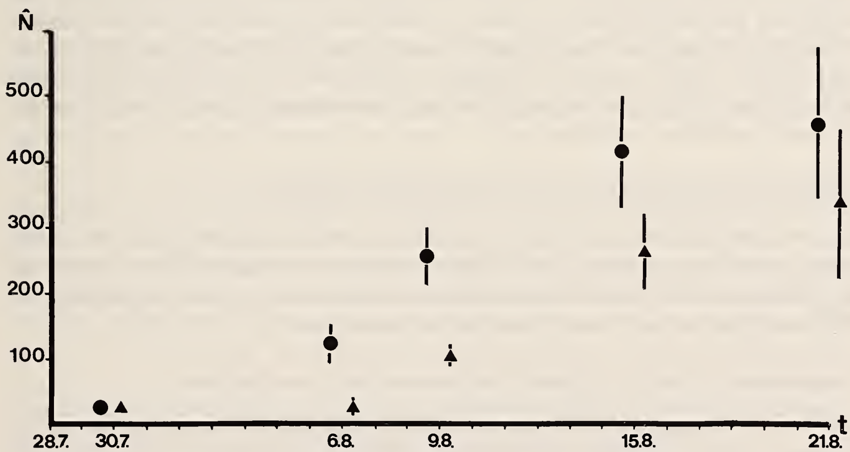

Fig. 3. Population size estimates for the male *aethiops* population at Bachhalten (Grindelwald) in 1986. ▲ = Jolly estimates. ● = Lincoln estimates.

Habitat use and dispersal in E. aethiops

Detailed MRR-data for the *aethiops* males are shown in Tab. 3. The same number of males was marked at subsite A as in the other five subsites together. 30% of the marked males at site A were recaptured at that same site, whereas only 14% were recaptured at another site. On the other hand at least as many recaptures at site A as on the original site of marking were made. Site A thus appears to be the very centre of activity of that male population. It is a fairly steep slope in the vicinity of a wood interspersed with bushes and small trees. Its size is about 15 by 30 meters.

Tab. 3. Detailed mark-recapture-data for the male *aethiops*-population at "Bachhalten" in 1986. Rows left of the double bar : number of individuals caught and marked at the sites. Rows to the right of the double bar : Individuals recaptured at the sites in %.

		Recapture at Site X in %				
Marked at Site X		Site A	Site B	Site C	Site D	Site E
Site A	126	31%	6%	2%	5%	1%
Site B	43	23%	14%	0	12%	0
Site C	10	33%	33%	0	10%	0
Site D	45	13%	7%	2%	0	0
Site E	17	18%	12%	0	0	0
Total	241	25%	9%	1%	5%	½%

The dispersal values for *aethiops* males yielded a mean distance between recaptures ($\hat{d}$) of 101 meters, a mean range ($\hat{R}$) of 108 meters and a mean total distance ($\hat{D}$) of 136 meters. Maximum distance flown by an individual over the whole investigation period was ca. 520 meters. Maximum distance flown on one particular day was ca. 260 meters. The size of the whole investigation area was 5 ha. Outside this area no *aethiops* were observed nearer than 1.5 km. There, another population was found, of which 270 individuals were marked in the same period. However, no exchange of individuals between the two populations was observed.

Comparison of population size of aethiops *and* meolans

To compare the sizes of the two populations, their maximum estimates were tested according to White *et al.* (1982) with the two tailed Z-Test. The result ($Z = 22.7$, $p < 0.01$) confirms the impression that the *meolans* population in 1986 was much smaller than the *aethiops* population.

Comparison of Jolly's stochastic method and the Lincoln-Index

One of the essential assumptions of the Lincoln-Index is that neither birth or immigration nor death or emigration influence the population investigated (Begon, 1979). If such events occur, the Lincoln-Index yields systematic overestimations for both the first and the second capture event (Seber, 1982).

If there are only immigration and birth, the estimate concerns the second capture event and if there are only death and emigration it concerns both events (Begon, 1979). Therefore at the beginning of the investigation period the estimates should be pictured at the second capture date and in between towards the end. For a comparison of the Lincoln-Index and Jolly's stochastic model however, they were all pictured at the second capture date (Figs. 2 & 3). On all but one date the Lincoln-estimate was significantly higher than the Jolly-estimate ($Z_p < 0.05$).

Discussion

As all results concern one investigation period only, generalisations are difficult to make. Especially concerning population size estimates, one-year studies on population dynamics neglect possible yearly fluctuations in population size, a phenomenon usual in the Genus *Erebia* (Warren, 1936). Furthermore, as was pointed out by Ehrlich (1984), within-species diversity in ecological features such as population size, dispersal or larval foodplants can be rather great. However, there are some results that deserve further discussion. The present study shows that *E. aethiops* is confined to a rather limited well defined area which it rarely leaves. For *E. meolans*, from the population size and other observations one could presume the same. *E. aethiops* males showed a clear preference for a small area of tall-grass pasture surrounded by woodland and interspersed with bushes and small trees between which they patrolled, while *meolans* was mainly observed patrolling along well defined habitat structures such as rocky ridges at the border of meadows or roads. Sex ratios were more biased towards the male side in the *aethiops* population. From personal observations the author concludes that the main reasons for this are behavioural differences between the sexes in the two species. Males were mainly observed patrolling, but females on the other hand mostly resting or basking on flowers or in the vegetation. Consequently males were much more prone to capture, as only butterflies passing by were caught and marked. These behavioural differences were less pronounced in *meolans*, thus possibly accounting for the less skewed sex ratio.

Population size estimates differ greatly among the two species. The maximum estimate for the male *aethiops* population counted 458 individuals in 1986 whilst the male *meolans* population reached only 66 individuals. The small size in *meolans* raises the question whether this population is part of a metapopulation in the Grindelwald region as was shown for the checkerspot butterfly *Euphydryas editha bayensis* in the San Francisco Bay area (Harrison *et al.*, 1988). Through its small size it is constantly prone to extinction by chance events but may be recolonized by large, constant "mother"-populations. The Grindelwald region contains several other *meolans* populations (Schiess, 1988), so that this hypothesis would be worth further examination.

The observed population features, i.e. rather small size, restricted area, little dispersal (for *aethiops*), compare rather well with several other studies of different butterfly species (GALL, 1984 ; BRUSSARD *et al.*, 1974 ; EHRLICH, 1984). The only other study dealing with a representative of this genus by BRUSSARD & EHRLICH (1970) on *Erebia epipsodea* showed that it occurred in vast, effectively panmictic populations which may cover hundreds of square kilometers. On the limits of its distribution however, it apparently shows a more colonial population structure as a consequence of a patchy distribution of a resource, possibly a specific larval host (EHRLICH, 1984). This example shows that it would be very risky to draw conclusions about the population structure of *meolans* and *aethiops* from the small insight this study yields. Furthermore MURPHY *et al.* (1986) suggested that standard mark-recapture statistics alone are insufficient to reveal adult population features that distinguish species susceptible to extinction from those that are comparatively more secure. Much more should be known and that knowledge can only be obtained through long term studies over a large area of the species distribution. BERRY (1989) put these needs into words for his presidential address at the British Ecological Society by saying : "Ecology is concerned with dynamic interactions. These may lead to change or stability, but they can be recognized only by collecting observations over a period of time. Long-term data series are not fashionable ; they appear to funding agencies as an open-ended commitment. We must defend them, because they are our only way of actually determining what is going on in the real world around us".

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