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Hilltopping as a mate location strategy in a Mediterranean population of *Lasiommata megera* (L.) (Lepidoptera, Satyridae)

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Abstract

Data collected on the distribution of male *L. megera* at different elevations in the Old Fort, Corfu town, reveal that they establish territories on hilltops as part of their mate location repertoire. Both the act of hilltopping and perching are regarded as mechanisms to increase the probability of contacts between males and unmated females. Selection of hilltops appears to be unrelated to any bias in the distribution of male or female resources, which are evenly spread over the area studied.

Male *L. megera* are flexible in mate location behaviour. In the process of obtaining mates they both perch and patrol, displaying a range of activity from territorial defence to the more passive acceptance of competitors during longer periods of flight over wider areas (see Dennis 1982). There are clear indications that behaviour varies at both the population and individual levels, relating to environmental (habitat differences ; weather), demographic (population density ; sex ratio), physiological (age of individuals) and genetic (inherited bias) factors. A distinctive aspect of their mate location behaviour, as for other butterflies which also establish territories, is their use of topographic vantage points. Typically, edges of habitats are selected, the territories being sited on patches of bare ground, walls, fences, stones, piles of gravel and other landmarks. This process has been likened to hilltopping by the author (Dennis 1982, Dennis & Bramley 1985) because all these landscape elements provide "visual peaks" which have the effect of concentrating resources, in particular males for females and females for males. It has been argued that the process is particularly necessary for a butterfly like *L. megera* whose wing pattern and colouration, subject to conflicting selection pressures, is dull (Dennis 1982). The sombre colour of the butterfly (cryptic against its background habitat) is almost certainly an adaptation to predation by birds as attested by wing damage data (pers. obs.). To offset this, courtship requires strategies that increase the apparency of mates for each other.

Hilltops provide one of several medium scale landmarks that butterflies can use as mate location cues. Some species are known to use linear structures

such as gullies (*Polygonia zephyrus* and *Amblyscirtes oslari*; SCOTT 1968) and edges, particularly physical structures such as buildings and walls but also boundaries between vegetation types (*Inachis io* and *Aglais urticae*: BAKER 1972. *Vanessa atalanta, Nymphalis antiopa* and *Polygonia comma*; BITZER & SHAW 1979, 1983). Hilltopping, described in a detailed paper by SHIELDS (1967), is in some ways more unusual, inasmuch as several species of butterfly have been known to use the same feature for mate location at the same time. Hilltopping species include a heterogeneous taxonomic and behavioural assemblage, habitual patrollers as well as perchers. Males congregate on hilltops and the females visit these situations to be mated. The strategy is almost certainly used to facilitate mating and fertilisation. The sites investigated to date by SCOTT and SHIELDS have not been particularly characterised by other resources such as moisture, nectar, larval hostplants, shelter and warmth. SCOTT (1968) argues that hilltropping is a mating mechanism that aids survival in species with low density populations, although some exceptions appeared in his work which he was unable to explain. Male density is distinctly higher on hill tops in hilltopping species and an abnormally high percentage of conspecific females are virgin. Moreover, SHIELDS (1967) has demonstrated "homing in" behaviour to summits of both males and females in a series of experiments on *Papilio zelicaon*.

The present observations arise from a brief visit to the Old Fort, Corfu town, Kerkira. It became obvious during the visit that male *L. megera* were more common at the summit than at lower elevation in the fort. The Old Fort, which lies to the east of the town, rises in a series of levels (embattlements) to two towers, one (Castell Nouo) higher than the other (Castell Vechio), to a total elevation over 55 m. The population of *L. megera* is to a large extent isolated to the fort (approximately 200 × 400 m in area), surrounded as it is by sea and the town. Data on the density of *L. megera* were obtained, during a second visit on July 19, 1986, by taking counts over five minute periods at five different levels and 7 locations, from level 1 (10 metres above sea level) to level 5 (the summit). Each level was separated by at least 10 metres in elevation. Sites 1 to 5 extended up the side of Castell Nouo; site 7 is the summit of Castell Vechio and site 6 the level ground separating the two towers. The areas and habitats (levelled stone enclosures covered in scrubby patches of desiccated herbs and grasses, mainly *Deschampsia* spp.) of each site were very similar, usually affording two complete transects; however the tower of Castell Nouo had the smallest area. Care was taken to count each specimen seen only once.

More males were seen at the top of the towers than at other locations (Table 1). A minimum of 10 males were noted on the towers compared to

two at lower sites during the five other observation periods. A minimum of seven males is recorded for Castell Nouo for the five minute observation period as it was difficult to determine whether insects rising up the cliffs were the same or different individuals. Two other males were observed in transit making their way up the side of Castell Vechio. Even including these latter two individuals in the assessment as occupying lower ground, there is a significant bias by *L. megera* males for summit locations (Fisher Exact test, $p = 0.025$). It was interesting that the higher but smaller Castell Nouo had many more males than the lower but larger Castell Vechio. Five prominent territories were established on the sloping embattlement walls of Castell Nouo and other males were constantly rising up the precipitous cliffs in attempts to establish territories of their own. The only other two territorial males were found in the saddle (site 6) between the two summits on a surrounding wall. Both were heavily worn, rather weak and lacked aggression, being easily approached by an observer and each other. The only other relatively common butterfly at the fort was *Pieris rapae*. This was noted patrolling at lower sites but was absent at the two summits.

Table 1. Records of *L. megera* during five minute observation periods for 7 sites and 5 levels of elevation on the Old Fort, Corfu town, July 19, 1986 (see text for sampling details).

Site	Elevation	Males	Females
7	4	3	0 Castell Vechio
6	3	2	0
5	5	7-10	0 Castell Nouo
4	4	0	0
3	3	0	0
2	2	0	0
1	1	0	0 (1 on 16/7/86)

All but two of the males observed had either established territorial perches or were competing for them. The two individuals observed on the slopes of Castell Vechio were effectively engaged in patrolling although apparently en route for the summit. On Castell Nouo, territorial males were evenly spaced (minimum distance 3 metres ; maximum 7 metres) along a 32 metres section of the south facing sloping embattlements and the adjoining roof of a building. None were found on the north facing side. Two of the ten territorial males had established territories in shade, the remaining eight in sunshine. All were angled to the sun (facing directly away from it), those in shade with their wings open, those in bright sunshine with their wings closed, minimising the impact of direct sunlight. Male-male encounters at territorial sites involved tight spiral interactions much as those observed for the butterfly

elsewhere (DENNIS 1982) and for *Pararge aegeria* (DAVIES 1978 ; WICKMAN & WIKLUND 1983, SHREEVE 1984). No minor landscape features determined the precise location of perches for males but one male at site 6 selected the observer's white pad placed casually two metres away from its perch on the wall, its territory being distorted as a result (cf., DENNIS & WILLIAMS, in press).

At least two important questions emerge from the present observations. Why do *L. megera* males hilltop at the fort and why do they establish territories ? As it is, these observations on hilltopping and territoriality complement each other and our knowledge of *L. megera*. Several ideas have been put forward to explain hilltopping : (i) hilltops are emergence sites for females and males congregate there ; (ii) adult resources (foraging sites) occur more commonly on hilltops and males await females there ; (iii) hilltops are one of several topographic vantage points which, providing visual peaks, can be used as cues for courtship in species occurring at relatively low density. Potential emergence sites for *L. megera* occur over much of the fort area (cf., DENNIS 1983) and adult resources were no more abundant at the summits than elsewhere. Indeed, because of the small area involved both nectar and hostplants were most limited in the tower of Castell Nouo. In any case, the concentration of mate location at foraging sites could be deleterious to both sexes, as males would waste valuable energy soliciting unreceptive females, and females would be harrassed whilst egg laying (MORTON 1985, p. 223). However the butterfly was in low density at the fort (less than 20 insects seen in 1 hr within an area of 80,000 m^2) and over Corfu island generally and only one female was seen (at site 1) in two visits. These points support the third hypothesis.

Perching (wait and sit tactic), as opposed to patrolling, may also occur for several reasons (cf., DENNIS, in press) : (i) males have insufficient energy supplies to remain patrolling ; more specifically, energy used in patrolling begins to exceed that used in defence (BAKER 1972) ; (ii) ambient conditions are inadequate for sustained flight which lowers body temperatures (SHREEVE 1984) ; (iii) the ratio of available females to males is substantially reduced and patrolling becomes less effective than perching at vantage points, regardless of energy resources. Although these explanations are not mutually exclusive, it is possible to separate them. Observations at the fort were carried out in the early morning when energy levels in the butterflies should be high. Moreover, other species were involved in incessant patrolling (*P. rapae ; I. podalirius*). In Britain, *L. megera* tends to patrol more in the warmer conditions after midday. But in Corfu shade temperatures exceeded 30°C, evidently close to optimal conditions, as thermoregulation by butterflies in the sun was geared to reducing (wings closed and body area covered) not

raising (wings open) body heat. On the other hand, females were undoubtedly in short supply and in such circumstances scrambling for a resource (females) over a wide area becomes expensive (in terms of energy expenditure) and ineffective.

It is argued then that the establishment of territorial perches and hilltopping are mechanisms intended to increase mating success by increasing the density of individuals and the probability of contacts and by minimizing energy losses. The act of territoriality does not conflict with the maintenance of high male density at hilltops, since males continually rise up to the summit to challenge incumbents (latent density greatly exceeds visible density) and females are therefore never lost for partners there. Although it would be expected that both strategies would be most effective for butterfly populations occurring at low density, there is no reason why overall density levels should necessarily contrast for hilltopping and non-hilltopping species. Butterflies differ in a number of other important respects, for instance physically (size, apparency, defence mechanisms and speed of flight ; life span), behaviourally (patrol-perch spectrum) and ecologically (abundance, aggregation and coincidence of larval and adult resources ; significance of nectar and moisture to adults ; predictability of topographic vantage points within habitats ; nature of predators), and are probably capable of making a range of adjustments to low density. Nevertheless, in the case of the sparse population of cryptically patterned *L. megera* on Corfu Old Fort, both strategies would seem to have a high premium.

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Book reviews – Buchbesprechungen – Analyses

E. PALM : Nordeuropas Pyralider. 18 × 25 cm, 287 pp., 8 colour plates, 264 figs and ca. 400 distribution maps, Apollo Books, Lundbyvej 36, DK-5700 Svendborg, Denmark, 1986, DKr. 400,- (ISBN 87-88738-04-3).

This book is the third volume in the series "Danmarks Dyreliv" (Vol. 1 : Diptera, Syrphidae and Vol. 2 : Lepidoptera, Geometridae) of which many volumes are in preparation. The author gives the characteristics of the family Pyralidae and then treats all of the North European Pyralidae species in the same way : description of the adult, distribution in northern Europe, habitat, phenology, flight period, food plant and larval behaviour. There are two distribution maps for almost all species : one of North Europe and one of Denmark. The identification of sibling species is facilitated with drawings of genitalia or wing venation. The colour plates depict all of the treated species. The Phycitinae are somewhat enlarged and the other subfamilies slightly reduced. This does not hamper the identification of specimens, except maybe for the Scopariinae.

Unfortunately, the main body of the book is written in Danish and this could prevent a wide distribution of this interesting study. To solve this problem partly, a very short summary in English is given for each species. The book is of interest for all entomologists studying Pyralidae. Subscribers to the whole series profit from a discount of 15% on all volume prices.

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