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The hypothesis of sexual conflict postulates that the differential male-female spatial distribution in butterfly species in which males are not territorial or do not defend a resource is due to the effect of ardent males on female behaviour. In such species females are often an ephemeral resource as they usually mate once while males are capable of multiple matings. In this system males will maximise their reproductive success by gaining access to many females while reproductive success of females is increased by maximising the time spent in selection of optimal oviposition sites. We show here that at low male density the distance flown by the female depends on the behavioural pattern displayed immediately before and after her flight. This relation disappeared at high male density. Moreover high male density (1) decreased the duration and the frequency of behaviours related to oviposition and (2) increased the frequency and the duration of male-female interactions. We propose that these two factors contribute to promote female dispersal at high male density. The decision to disperse out of habitats with high density of males might be a trade-off between low-quality reproduction within such habitats and dangers of dispersal out of these habitats.

Male density affects female spatial behaviour in the butterfly *Proclissiana eunomia*

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Abstract

The hypothesis of sexual conflict postulates that the differential male-female spatial distribution in butterfly species in which males are not territorial or do not defend a resource is due to the effect of ardent males on female behaviour. In such species females are often an ephemeral resource as they usually mate once while males are capable of multiple matings. In this system males will maximise their reproductive success by gaining access to many females while reproductive success of females is increased by maximising the time spent in selection of optimal oviposition sites. We show here that at low male density the distance flown by the female depends on the behavioural pattern displayed immediately before and after her flight. This relation disappeared at high male density. Moreover high male density (1) decreased the duration and the frequency of behaviours related to oviposition and (2) increased the frequency and the duration of male-female interactions. We propose that these two factors contribute to promote female dispersal at high male density. The decision to disperse out of habitats with high density of males might be a trade-off between low-quality reproduction within such habitats and dangers of dispersal out of these habitats.

Keywords: Sexual conflict, density dependent dispersal, oviposition behaviour.

Résumé

L'hypothèse du conflit d'intérêt entre sexes prédit que la distribution différentielle des mâles et des femelles chez les Lépidoptères non territoriaux est due au harcèlement incessant des femelles par les mâles. Chez ces espèces, les femelles sont souvent une ressource éphémère car elles ne s'accouplent en général qu'une seule fois alors que les mâles peuvent réaliser plusieurs appariements. Le succès reproducteur des mâles va donc dépendre du nombre d'accouplements qu'ils réalisent au cours de leur vie, alors que le succès reproducteur des femelles sera en relation avec le temps passé à choisir des sites de ponte optimaux. Nous montrons ici que lorsque la densité des mâles est faible, la longueur du déplacement des femelles dépend du patron comportemental qu'elles accomplissent avant et après ce déplacement. Cette relation disparaît lorsque la densité des mâles est forte. De plus, une forte densité de mâles s'accompagne d'une diminution de la durée et de la fréquence des patrons comportementaux liés à la ponte et d'une augmentation de la fréquence et de la durée des interactions entre mâles et femelles. Notre hypothèse est que ces deux facteurs contribuent à déclencher la dispersion des femelles lorsque la densité des mâles est élevée. La décision prise par une femelle de quitter un habitat à forte densité de mâles pourrait résulter d'un compromis entre réaliser une reproduction de mauvaise qualité dans cet habitat et affronter les dangers de quitter un habitat favorable.

INTRODUCTION

"To date there has been little detailed analysis of flight behaviour in relation to density in species of butterflies" (SHREEVE, 1992). However, in species in which males are not territorial or do not defend a resource, adult density may be a key-factor determining spatial structure of butterfly populations. As in such species, fertile females are generally an ephemeral resource, males are engaged in scramble-like competition for mates (THORNHILL & ALCOCK, 1983). The link between male mate-locating behaviour and population structure relies on two mechanisms. First, male aggregation occurs as a by-product of male mate-locating behaviour. Within suitable habitats, males investigate all objects with a shape or a colour similar to a female. Consequences are frequent male-male chases, leading to male aggregation (ODENDAAL *et al.*, 1988). The other mechanism relies on the hypothesis of sexual conflict at high adult density: as fertile females are an ephemeral resource, ardent males try to mate at each female encounter and interfere with female behaviour. Consequences are differential male-female spatial distribution (SHAPIRO, 1970; WATT *et al.*, 1979; DENNIS & BRAMLEY, 1985; ODENDAAL *et al.*, 1989; BAGUETTE & NÈVE, 1994). These two mechanisms are not mutually exclusive: in *Euphydryas anicia*, both male aggregations and male-female differential distribution were observed (ODENDAAL *et al.*, 1988, 1989). In this paper we focus on the sexual conflict mechanism. Distribution of females in areas of low male density is often attributed to male harassment in other areas. However, there was no direct evidence of male density influence on female spatial behaviour. We present here such evidence.

In the Bog Fritillary *Proclissiana eunomia* (ESPER), females usually mate only once during their life span while males are able to mate repeatedly (BAGUETTE & NÈVE, 1994; BAGUETTE, CONVIÉ, VANSTEENWEGEN, WAEYENBERGH & NÈVE, unpubl.). Sex-biased dispersal was detected between suitable habitats at the landscape scale, in agreement with the hypothesis of sexual conflict: females dispersal between habitats was higher at high male density (BAGUETTE & NÈVE, 1994; NÈVE *et al.*, 1996; BAGUETTE, CONVIÉ, VANSTEENWEGEN, WAEYENBERGH & NÈVE, unpubl.).

We compare here female behaviour and movements in two suitable habitat patches of similar size, shape and host-plant density. This procedure relies on a between-site comparable habitat quality; as we selected sites with a similar habitat structure, host-plant density and nectar source density, this may be regarded as a reasonable assumption. Butterfly density is generally not a good indicator of site quality, as population levels fluctuate drastically with local weather conditions (POLLARD, 1988) or parasitism (WARREN, 1992). We preferred to use such a "natural experiment" rather than density manipulation in order to avoid adult fleeing after translocation. We test the effect of male density on (1) length of female movements in association with behavioural patterns, (2) duration and (3) relative frequency of female behavioural patterns. The null hypothesis is that male density has no effect on female behaviour.

STUDY SYSTEM AND METHODS

P. eunomia is an univoltine species with adults flying in wet meadows and peat bogs between May and July. Bistort *Polygonum bistorta* L. is the only host plant of both larvae and adults. The mating

system is polygynous (BAGUETTE & NÈVE, 1994; BAGUETTE, CONVIÉ, VANSTEENWEGEN, WAEYENBERGH & NÈVE, unpubl.). Male mate-locating behaviour is patrolling (SCOTT, 1974; RUTOWSKI, 1984, 1991; SHREEVE, 1992; BAGUETTE, CONVIÉ, VANSTEENWEGEN, WAEYENBERGH & NÈVE, unpubl.).

Female individual behaviour was recorded in two sites of the same size (1 ha) differing in adult density by a ratio of 1 to 10, as estimated by Mark-Release-Recapture (MRR) and transects of adult counts. MRR population estimates used the Jolly-Seber method, as applied to open populations (HINES, 1988). The low density site was a patch in the Lienne valley (50°18'N, 5°49'E) while the high density site was located in the Pisserotte peat bog (50°13'N, 5°57'E). Because behaviour and habitat use are linked to the spatial structure of habitats, including the distribution pattern and abundance of hostplants and nectar sources, it is essential that sites used in such a comparative study are truly comparable in these aspects. The vegetation in both sites belonged to the same association, namely the *Deschampsia cespitosa* – *Polygonetum bistortae* NOIRFALISE. Within this vegetation, bistort occurred in discrete monospecific patches separated by tussocks of *Deschampsia cespitosa* and *Juncus effusus*. We checked the similarity of bistort cover (ca. 50%) between sites. The spatial pattern of patches was similar in both sites. Bistort flowers, the only nectar source of adult butterflies, were present within patches at the same density (1-5 flowers/m²).

In 1994 (6 June-1 July), 43 females tracks were performed (20 in the low density site, 23 in the other) for a total duration of 1051 minutes (mean = 24.2 minutes, SE = 3.4 minutes). As butterfly behaviour, especially flight activity, is linked to solar radiation and windspeed, we gathered data in optimal weather conditions within each site (table 1).

TABLE I. – Mean (SE) of daily sunshine duration (in min) and windspeed (in km/h) in study sites. Both parameters are not significantly different between sites (Wilcoxon 2-sample test, normal approximation, $S = 27.5$, $Z = 0.57$, $P = 0.57$ for sunshine duration and $S = 27$, $Z = 0.49$, $P = 0.63$ for windspeed).

	Lienne (low density site)	Pisserotte (high density site)
Sunshine duration	611 (58) n = 6	667 (129) n = 5
Windspeed	10 (1) n = 6	12 (2) n = 5

Females were individually marked (methods in BAGUETTE & NÈVE, 1994) and tracked for as long time as possible by a team of two observers. Movements were monitored by marking the landing place of the tracked butterfly by a numbered flag. Afterwards, the coordinates of each flag were mapped by triangulation with a telemeter. This procedure allowed us to measure the distance between consecutive flags. When the female alighted, we recorded her behaviour pattern(s) and its duration. Seven patterns of female behaviour were identified: (1) wing-shivering, (2) basking, (3) resting, (4) foraging, (5) sexual interactions, (6) searching for oviposition site and (7) egg-laying.

For each landing, we computed two parameters: (1) the distance which preceded the first behaviour pattern recorded after landing (hereafter Dist1) and (2) the distance which followed the last behaviour pattern recorded before flying (hereafter Dist2). This procedure provided a set of Dist1 and Dist2 for each behaviour pattern.

The three variables (Dist1; Dist2 and the duration of the behavioural pattern) were compared using sites and behavioural patterns as classification levels. Data were analysed by variance analysis, correlations and (likelihood ratio) Chi-square tests using the SAS package (SAS Institute Inc., 1989).

RESULTS

Total adult density was estimated to 21 males and 18 females/ha by MRR in the low density site. Daily population size estimated by the Jolly-Seber method was correlated to the transect counts (Pearson correlation coefficient $r=0.73$, $n=15$, $P<0.01$ for females and $r=0.71$, $n=15$, $P<0.01$ for males, figure 1). We used this relation to predict adult density in the other site. This extrapolation provided a relative estimation of 220 males and 180 females/ha in the high density site on the whole flight season.

At low adult density, both distance parameters (Dist1 and Dist2) were significantly dependent on the behavioural pattern which followed/preceded the



FIG. 1. – Relation between Jolly-Seber estimates of daily population size and transect counts.

flight (for Dist1: $F_{6,358} = 3.62$, $P < 0.01$, for Dist2, $F_{6,357} = 2.70$, $P < 0.05$). At high adult density, we could not detect a significant effect of behaviour on distance parameters (for Dist1: $F_{6,217} = 1.31$, $P = 0.25$; for Dist2, $F_{6,216} = 1.10$, $P = 0.37$) (table 2).

TABLE II. – Mean (SE) distances flown (in m) before (Dist1) and after (Dist2) a given behavioural pattern in the low/high density site.

Patterns	Dist1		Dist2	
	Low	High	Low	High
Wing-shivering	6.36 (0.79) n = 26	4.30 (1.11) n = 68	5.38 (0.74) n = 123	3.54 (1.21) n = 66
Basking	6.05 (1.14) n = 65	5.07 (2.17) n = 27	4.64 (0.96) n = 65	2.03 (0.76) n = 28
Resting	2.77 (0.68) n = 63	8.25 (4.92) n = 39	2.94 (0.61) n = 60	9.30 (5.30) n = 36
Foraging	6.72 (1.10) n = 46	4.15 (0.93) n = 23	6.58 (1.54) n = 50	3.14 (0.68) n = 27
Sexual interaction	1.68 (1.10) n = 38	0.26 (0.13) n = 58	2.23 (1.30) n = 39	2.16 (0.94) n = 59
Searching for oviposition sites	2.96 (1.26) n = 22	1.67 (1.67) n = 3	7.29 (1.94) n = 22	0.41 (0.41) n = 3
Egg-laying	0.10 (0.10) n = 5	0 (0) n = 5	12.34 (5.43) n = 5	3.98 (1.56) n = 4

Comparison of behaviour duration showed that male-female interactions were significantly longer in high density site (mean = 5.4 sec, $n = 63$ vs., mean = 2.2 sec, $n = 39$, $F_{(1,99)} = 4.01$, $P < 0.05$). Comparison of the proportion of each behavioural event indicated that male-female interactions were more than twice as frequent at high density (24.31% of the female total activity) than at low density (10.26%). In the same time female activity devoted to searching oviposition sites decreased from 6.05% in the low density level site to 1.96% when density increased (table 3). This change in the relative frequency of the two patterns is significant between sites (Likelihood ratio Chi-square₍₁₎ = 5.72, $P < 0.05$).

Proportion of resting bouts after an interaction with a male and after other behavioural patterns was significantly different between sites; resting due to such interactions occurred more frequently in the high density site (table 4, Chi-square₍₁₎ = 4.09, $P < 0.05$). Comparison of the duration of resting bouts showed that resting after an interaction with a male was not significantly different from resting bouts following other behavioural patterns (in the high density site mean = 194 sec, $n = 11$ after an interaction vs mean = 175 sec, $n = 29$, $F_{(1,38)} = 0.05$, $P = 0.82$; in the low density site mean = 296 sec, $n = 7$ after an interaction vs mean = 221 sec, $n = 56$, $F_{(1,61)} = 0.28$, $P = 0.60$). Duration of resting bouts after an interaction with a male was not significantly different between sites ($F_{(1,17)} = 0.85$, $P = 0.37$).

TABLE III. – *Proportion of behavioural patterns in the low/high density site.*

Pattern	Low density	High density
	(n = 380)	(n = 253)
Wing-shivering	33.95%	29.80%
Basking	17.63%	14.11%
Resting	16.58%	15.69%
Foraging	14.21%	12.16%
Sexual interaction	10.26%	24.31%
Searching for oviposition sites	6.05%	1.96%
Egg-laying	1.31%	1.13%

TABLE IV. – *Proportion of resting bouts after an interaction with a male and after other behavioural patterns in the low/high density site.*

	Low density	High density
Resting after interaction	7 (11%)	11 (26%)
Resting after other behavioural patterns	58 (89%)	32 (74%)

DISCUSSION

Male density clearly affects female behaviour. At low density, each behavioural pattern of females is associated with a particular spatial activity: the flight length depends on the behavioural pattern displayed by the female immediately before and after her flight. Two behavioural patterns are followed by especially long flights: egg laying (12.34 m) and searching for oviposition sites (7.29 m), contrasting with the much shorter flights preceding these patterns. At low male density, females are able to perform such long distance flights without being chased by ardent males.

Behavioural pattern and length of the flight are not related at high male density. Mean distances associated with each behavioural pattern are shorter (albeit not significantly) at high density than at low density in all cases but of one: resting behaviour. Females displayed this behaviour during cloudy and/or windy weather but also immediately after male chases. Distances flown before/after female rests are much longer at high density, which can be related with longer duration of male-female interactions (more than twice as long, 5.4 sec. vs. 2.2 sec.). During longer chases females are more prone to leave patches of flowering bistorts and they have to move more to return to their preferred places.

Change in duration of male-female interactions can be explained by an easier access to females at high density; therefore, males may invest more time in interactions. At high male density, female dispersal out of suitable habitat patches increases (BAGUETTE, CONVIÉ, VANSTEENWEGEN, WAEYENBERGH & NÈVE, unpubl.), which means that shorter within-habitat movements are associated with more frequent between-habitat dispersal. However, this paradoxical conclusion is not in contradiction with the sexual conflict hypothesis. Two proximal mechanisms contribute to promote the female dispersal process at high male density. Longer and more frequent male chases may increase the rate of female emigration outside

the habitat, as chased females performed complex flights to escape their pursuer(s) (e.g. SHREEVE, 1992 for a description of such flights). Departures from the study sites caused by male-female chases were observed during several female tracks (7/20 in the high density site, 0/23 in the low density site).

Moreover, as females flew to detect suitable oviposition sites, pursuing males actively impeded females to perceive such sites. Therefore the cost of male-female interactions in flight could be high for the female. High male density decreased the proportion of female activity devoted to the search of oviposition sites (only 3 searching events observed, less than 2% of the total behavioural patterns). Female resting bouts after interactions were also more frequent. As the reproductive success of fertile female is likely to depend on the time spent in selection of optimal oviposition sites (e.g. WIKLUND & AHRBERG, 1978; WIKLUND & FORSBERG, 1985), the decision to disperse out of habitats with high density of males might be a trade-off between low-quality reproduction within such habitats and dangers of dispersal out of these habitats.

The tactic of female dispersal at high male density might be selected for in species living in transient habitats. Years of high adult abundance, such a dispersal process insures a flow of mated females out of populated habitats, increasing the colonisation probability of empty habitats at the landscape scale. Studies of very small, isolated habitats with a huge extinction probability of *P. eunomia* populations revealed that recolonisation events are not scarce (NÈVE *et al.*, 1996). Moreover, introduction experiments have proved that the colonisation rate of empty habitats by *P. eunomia* is high (DESCIMON, 1976; DESCIMON & NAPOLITANO 1992; NÈVE *et al.*, 1996). An alternative tactic allowing ardent male avoidance is a switch in habitat selection between mated and unmated females. WIKLUND & AHRBERG (1978) reported on the low encounter rate between males and mated females in *Anthocharis cardamines* due to a change in female habitat selection after mating. However, we can expect that the latter tactic will be selected only in more generalist species than *P. eunomia*.

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