Abstract

Current metapopulation models assume that migration rate remains constant from one generation to the other, leading to a constant population foundation rate. In the butterfly *Proclossiana eunomia*, the mating behaviour is a main factor affecting individual migration. In a field study, male harrassments induced female emigration at high male density. Males moved away in search of mates at low female density. Simulations of male-female movements based on behavioural data from the field revealed that changes in mate density will induce sex-biased emigration. Assessement of migration within a metapopulation in the field during 2 years supported these predictions. Such bias in migration has been reported earlier in other butterfly species with a similar mating system. Consequences of sex-biased emigration on metapopulation dynamics may be spasms in population foundation as these occur only when density oversteps a certain threshold. Patterns of colonization in a region where *P. eunomia* did not occur naturally correspond to this prediction. Variability in the rates of emigration and population foundation between generations may affect metapopulation viability analysis by current models.

Sex-biased density-dependent migration in a metapopulation of the butterfly *Proclossiana eunomia*

Michel Baguette*, Christian Vansteenwegen, Isabelle Convié, Gabriel Nève

Université catholique de Louvain, Unité d'Écologie et de Biogéographie, Place Croix du sud 4, B-1348 Louvain-la-Neuve, Belgium
* Corresponding author (fax 32 10 47 34 90; e-mail baguette@ecol.ucl.ac.be)

Abstract – Current metapopulation models assume that migration rate remains constant from one generation to the other, leading to a constant population foundation rate. In the butterfly *Proclossiana eunomia*, the mating behaviour is a main factor affecting individual migration. In a field study, male harrassments induced female emigration at high male density. Males moved away in search of mates at low female density. Simulations of male-female movements based on behavioural data from the field revealed that changes in mate density will induce sex-biased emigration. Assessment of migration within a metapopulation in the field during 2 years supported these predictions. Such bias in migration has been reported earlier in other butterfly species with a similar mating system. Consequences of sex-biased emigration on metapopulation dynamics may be spasms in population foundation as these occur only when density oversteps a certain threshold. Patterns of colonization in a region where *P. eunomia* did not occur naturally correspond to this prediction. Variability in the rates of emigration and population foundation between generations may affect metapopulation viability analysis by current models. © Elsevier, Paris

1. INTRODUCTION

A crucial issue in the study of metapopulation dynamics is the degree to which exchanges of individuals between habitat patches are constant from one generation to the next. Current metapopulation models assume that this migration rate, i.e. the proportion of dispersive individuals in each generation. remains constant [7, 8, 9, 10, 11]. However, the question remains about changes in individual migration leading to variation in migration patterns between generations.

We studied behaviour and emigration patterns of individually marked Bog Fritillaries (*Proclossiana eunomia* ESPER) in a fragmented landscape. As in this butterfly female emigration could depend on male harassment [2, 3], we investigate here how the mating behaviour promote the variation of migration patterns observed at the metapopulation scale.

Bog Fritillary butterflies have a polygyny mating system which is a characteristic of explosive breeding butterflies having only one short breeding period per year [15]. Due to the short reproductive period (mean residence time was about 5 days for males and 7 days for females) [2], males have little time to maximise their number of matings with virgin females. After

mating, females will maximise their time investment in selecting good oviposition sites [e.g. 15, 18]. As a result, males court all the females they meet whereas mated females refuse further courting males by adopting a mate-refusal posture or by fleeing away. Thus, we hypothesise the following situation: at high male densities, females are often harassed by ardent males, inducing female-biased emigration: at low male densities, females are less harassed and tend to stay in optimal feeding or egg-laying habitat patches. On the other hand, at low female densities, males need to move more to find unmated females, inducing male-biased emigration: at high female density, males tend to stay in the patch, inducing low male emigration.

The purpose of this paper is to assess (1) the relation between emigration and mating behaviour, and (2) the relation between density and migration pattern within a metapopulation.

2. MATERIAL AND METHODS

2.1. The species

Proclossiana eunomia is a glacial relict occurring in highly fragmented populations all over Europe [14].

Its specialized habitats in Middle Europe are wet meadows and some peat bogs where the bistort *Polygonum bistorta* L., the only food plant of the larvae in the region and the only nectar source of the adults is found. Wet meadows are early successional stages maintained by traditional agropastoral practices, abandoned since *c*. 1950. Such habitats are mostly transient and naturally patchy but patchiness has been increased by human-induced changes in the landscape after 1950. The species is classified as 'vulnerable' in Belgium, according to the IUCN criteria [1, 13] and protected by law in Southern Belgium (Wallonne region).

P. eunomia is a univoltine species that flies for about one month between the end of May and the beginning of July. Adult males emerge several days before adult females (protandry) which induces a skewed operational sex-ratio, male-biased at the beginning of the flight period, female-biased at its end. Extremes of sex-ratios are 100 % of males in the first days of adult emergence and 100 % of females during the last days of the flight season [2].

2.2. Study system

The main study area, les Prated along the Lienne river, southern Belgium (50°18´N, 5°49´E). The study system consists of a network of 19 small suitable patches separated by Spruce (*Picea abies* (L) Karst) plantations (with some trees more than 20 m high) or fertilised pastures. Previous work on this area has shown population turnover as well as a high rate of adult movements between suitable habitat patches at the local and the landscape scales [2, 14].

Behavioural data were collected in two other locations: la Fagne de Pisserotte (50°13´N, 5°57´E) and les Prés du haut Sommerain (50°10´N, 5°48´E).

2.3. Monitoring movements and population size

Butterfly movements were monitored by (i) tracking movement paths of individuals and (ii) a Mark-Release-Recapture (MRR) experiment. As males moved constantly and quickly in search of receptive females, their flight behaviour was described from only visual observations and MRR results. Females flew more slowly which allowed individual tracking. In 1994 (June 6 to July 1), 43 female tracks were performed for a total duration of 1 051 min (mean = 24.2 min, standard error = 3.4 min). Marked females were tracked for as long as possible. Movements were monitored by picking numbered flags at each landing place of the tracked butterfly. Afterwards, the coordinates of each flag were mapped by triangulation with a telemeter. This procedure allowed us to measure the distance between consecutive flags.

In the MRR experiment, the main study area was visited as often as possible, weather permitting, during the flight period (15 capture sessions in both 1992 and 1993). All adults observed were caught and individually marked with a thin-point permanent pen on the underside of the left hind wing before being released at the location of capture. In 1992 and 1993, 656 and 402 individuals respectively were marked. The wear of the wings, on a scale from 1 (very fresh) to 4 (extensive wing wear), the sex and the coordinates of the location of capture were recorded for each individual at each capture event. This method provided the distances moved between recapture times. The estimations of the *P. eunomia* populations size were computed using the JOLLY-SEBER method, as applied to open populations (program JOLLY) [12].

2.4. Manipulations

In 1994, 16 virgin females were reared from caterpillars in the laboratory and then released in the field. Their movements and behaviour were monitored by individual tracking (mean time = 132 minutes). In 1995, we manipulated adult densities by transferring marked individuals between patches within the study area. Two sets of males and females were introduced into a small empty patch (*c*. 50 × 50 m) of suitable habitat, isolated from other such patches by at least 300 m of unsuitable habitat. At day 1 (June 14 1995), we released 5 males-1 female; at day 2 (June 21 1995), 5 males-5 females. Adult behaviour immediately after release was recorded by 4 observers. The movements of these adults during the following days were determined using MRR data.

2.5. Mating behaviour

Dissections proved that females mated only once: on 20 field caught females, one was virgin and all the others had only one spermatophore in their reproductive tract [2]. Males were capable of multiple mating and were observed trying to copulate with another female immediately after a successful mating event.

Males located females by patrolling behaviour [e.g. 18]: they flew incessantly in suitable habitats looking for receptive females. This mate-locating flight differed from the oriented flights used when crossing unsuitable habitat or looking for nectar plants. Oriented flights were performed straight away at higher elevation (1.5 m above the ground or more). Mate-locating flight was a rather slow, low altitude flight (1 m and less), with frequent turns (approx. each metre). During this flight, all objects flying within 3 metres were investigated; all yellow or orange objects in the vegetation within the same range were also visited. When these objects proved to be *P. eunomia* females, males displayed insistent court-

ship by flying around the females and trying to copulate. If the female was not receptive, the duration of such courtship was variable and depended on the female behaviour. If the female was receptive, the copulation followed her first mate encounter, as proved by the experimental release of virgin females (16 virgin females released, 8 matings observed).

In this release experiment of 16 virgin females, the behaviour of 8 subsequently mated females showed the same sequence: after release, they first stood inside the vegetation, then climbed on a leaf or a flower and remained immobile with open wings until detected by a flying male. After the climbing, females copulated with the first courting male. The time lag between female release and mating was variable (mean = 40.5 min, S.E. = 12.6 min) due to the influence of weather conditions on male flight activity. However, the mating time remained constant (mean = 29.3 min, S.E. = 1.5 min). Virgin females released after more than 2 d since emergence (n = 3) showed non receptive behaviour: two repeatedly refused copulation while the third one laid unfertilised eggs. The remaining females (n = 5) were not detected by any males during the observation time.

Adult females mated shortly after emergence from the pupa, as estimated from the wear of their wings: all females observed *in copula* in the field (n = 12) were in class 1 (very fresh).

After copulation, females were inclined to stay in the same area: in our MRR experiment, the first recapture of females observed *in copula* and subsequently recaptured was in all cases in the patch where the mating had occurred (n = 6, with a time lag between capture and recapture between 2 h and 12 d). Female tracking provided rough estimates of their mean flying speed: 0.75 m·s^{-1} (n = 43). Flying females courted by pursuing male(s) escaped by performing complex flight patterns. During such pursuits we observed females leaving patches of suitable habitat.

2.6. Computer simulation

To test whether the observed behavioural events could actually lead to sex-specific migration patterns, we designed a simple simulation model. Movements of both sexes of *P. eunomia* were simulated into a square of 200 × 200 space units, corresponding to meters in natural situations. Initial coordinates of males and females were assigned randomly inside the surface. Initial direction of flight was also random. Time steps corresponded to minutes.

Males moved at a constant speed which was set at 5 m·min^{-1}, as estimated from comprehensive male catch in the metapopulation (1 242 male catches). They did a turn of $90°$ on the left after 1 min and of $90°$ on the right after the next min in order to simulate

the zigzag trajectory of the patrol flight. If a female occurred within 3 m of the male trajectory, an encounter event was assigned to each mate. If a male came on the border of the square without any female encounter between his initial position and the border, he was considered as a disperser and disappeared from the square. If he had encountered a female along his way, he was considered as motivated to stay in the square and remained inside by a collision on the border. Deviation between the arrival and the departure trajectory was randomly chosen. The male had to encounter another female to stay in the square at his next border encounter, otherwise he was considered a disperser.

Females moved in the same way as males but at lower speed (0.75 m·min^{-1}), corresponding to their lower observed speed. Female movements were not directly dependent on encounters with males, but after a fixed number of such encounters a female was considered to become a disperser and disappeared from the square. We carried a sensitivity analysis of the critical number of encounters by changing this threshold: 1, 2, 3, 5 and 10 encounters were tested.

The simulation procedure allowed variation of three parameters: (i) the initial number of males, (ii) the initial number of females and (iii) square size. The initial number of individuals was chosen in order to simulate the change in the daily sex-ratio during the flight season. Three different situations were used: (a) the appearance of females in the population during the early flight season, with a high number of males and a low number of females: 50 males and 5 females, (b) equal number of both sexes: 50 males and 50 females and (c) a situation corresponding to the end of the flight season with a high number of females coexisting with a few males: 5 males and 50 females.

The change of migration probability in relation with the population size of the same sex was also evaluated. Migration probability was computed from an initial population size of 5 and 50 individuals after 200 min; the opposite sex population size ranking from 5 to 50 by step of 5 individuals.

Simulation results were scored as the mean proportions of dispersers after 200 min.

3. RESULTS

3.1. Migration at the metapopulation scale

In 1992, the total estimated size of the metapopulation amounted to 1 374 individuals (613 males and 761 females, JOLLY estimates). The between-patch migration over more than 200 m was significantly female-biased: 42 of the 285 recaptures (15 %) of females took place in a patch of *Polygonum bistorta* separated by at least 200 m of unsuitable habitats to

the one where they had been captured before. The similar ratio was significantly different for males (16/407, 4 %, $c_1^2 = 25.5$, $P<0.001$). Mean displacement between two successive catches, showed an asymmetry between male and female movements: it was higher for females (female mean 123 m, S.E. = 12, n = 285; male mean 59 m, S.E. = 5, n = 407, $F_{1.690} = 29.58$, $P<0.001$).

In 1993, the metapopulation size decreased to 644 individuals (338 males and 306 females, JOLLY estimates). The between-patch migration over more than 200 m of unsuitable habitats was not significantly biased (3/64 females, 5 % vs. 23/280 males, 8 %, $c_1^2 = 0.93$, P = 0.34). The mean displacement between two successive catches was similar: 63 m for females (S.E. = 14, n = 64) and 75 m for males (S.E. = 8, n = 280, $F_{1.342} = 0.44$, P = 0.51).

The ratio of individuals moving across unsuitable habitats to the total number of individuals within the metapopulation was similar in 1992 and 1993 (8 %). The between-year comparison of adult spatial behaviour showed that the ratio of males dispersing between patches separated by at least 200 m of unsuitable habitats to the total number of male recaptures within the metapopulation was significantly higher in 1993 (16/407, 4 % in 1992 vs. 23/280, 8 %, in 1993, $c_1^2 = 5.7$, $P<0.05$) whereas the ratio of female dispersing between patches separated by at least 200 m of unsuitable habitats to the total number of female recaptures within the metapopulation varied in the opposite way (42/285 in 1992, 15 % vs. 3/64, 5 % in 1993, $c_1^2 = 4.7$, $P<0.05$). The mean displacement between successive catches was significantly lower for females in 1993 ($F_{1.347} = 5.28$, $P<0.05$) and higher for males in 1993 ($F_{1.685} = 2.98$, P=0.08).

3.2. Density manipulation

We released 5 males and 1 female at day 1. The males did not detect the female in the patch during the 2 h observation time. Male migration from the patch occurred rapidly: 20 min after release 4 males had crossed a line 50 m around the patch. All males left the patch and then returned. They came back after a flight over unsuitable habitats at irregular intervals. Outside the patch we recorded direct flights only while inside the patch males switched to patrolling flight. After such returns, the mean time stayed within the patch was 174 s., S.E. = 49, n = 5. Movements of released individuals within the metapopulation were recorded the day after (*table I*); all the individuals were caught again.

The release of 5 males and 5 females at day 2 allowed us to observe male harassment inducing female migration: after 3 interactions in flight with 3, 1 and 1 male successively (15, 2 and 2 s. respectively)

Table I. Density manipulation. Movements of individuals after release within the population as shown by MRR data.

Distance between the release patch and the next recapture	Experiment 1 Release of 5 males, 1 female	Experiment 2 Release of 5 males, 5 females
0 m	1 female	1 female, 1 male
300 m	4 males	2 females
500 m	–	1 female
700 m	1 male	–
1100 m	–	1 female

a female left the patch in direct flight. As in the previous experiment, movements were recorded the day after (*table I*). All the females, but only 1 out of the 5 males, were recaptured.

3.3. Model predictions

We investigated the effect of the number of male-female encounters leading to female migration by varying the threshold number of encounters. Male migration into the simulation conditions did not depend on this threshold value: all males left the patch before 200 min (*figure 1* A). Female migration rate decreased from 36 % (one encounter before leaving the patch) after 200 min to 0.2 % (10 encounters before leaving the patch). We selected 3 as a critical number of encounters which produced an intermediate migration rate of 18 % (*figure 1* B).

Figure 2 shows that the time-courses of male and female population decreases were different depending on the initial population size in a patch of 200 × 200 m. For each sex, we define t_{50} as the number of minutes needed to reach 50 % of the initial population size. In the case of males, at a given initial male population size, t_{50} increased as the initial number of females increased. Dispersal in males was inversely related to female density: male migration decreased if the female initial population size increased. Conversely, for females, t_{50} increased if the initial density of males decreased. Consequently, female migration was directly related to the initial male density.

Female density affected the mate encounter probability and therefore consequently female migration probability by changing the male density. *Figure 3* shows a set of simulations where the proportion of dispersers was computed after 200 min from an initial population size of 5 and 50 individuals: the population size of the opposite sex ranked from 5 to 50 by step of 5 individuals. The difference between the upper and the lower female curve indicated the effect of female density on female migration: at higher female density, the mate encounter probability increased and therefore female migration increased. The same held true for
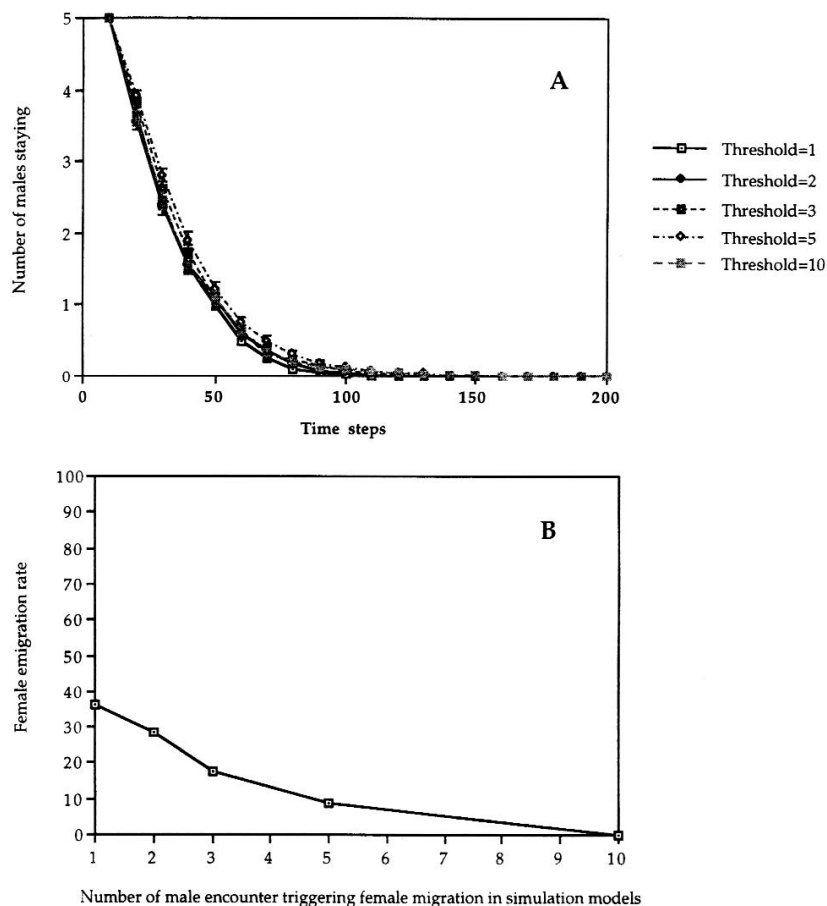
Figure 1. Variation of migration following changes in the critical number of mate encounter leading to female migration: simulations of five males and five females moving within a small patch of 50 × 50. A: Decrease of males during 200 min. Results are the mean and the standard error of 100 runs for each threshold value. B: Female migration rate in % of the initial population computed from the mean number of females remaining in the patch after 200 min with 100 runs for each threshold value.

males (*figure 3*). The difference between the upper and the lower male curve indicated the effect of male density on male migration: at higher male density, the mate encounter probability decreased and therefore male migration increased.

4. DISCUSSION

4.1. Migration and mate density

Behavioural observations in the field together with an experimental change of adult density (albeit on a small sample) allowed us to forecast an effect of mating behaviour on migration. During the first experiment (release of 5 males, 1 female), male emigration rate was 100 %, as released males were located the next day in other patches while the female being undetected by males, remained in the release patch (*table I*). During the second experiment (release of 5 males, 5 females), female emigration occurred, but did not involve all individuals. Several observations of male harassment leading to female emigration confirmed that courting males actively triggered female emigration. Simulations confirmed that such behavioural processes can lead to a sex-biased emigration, posi-
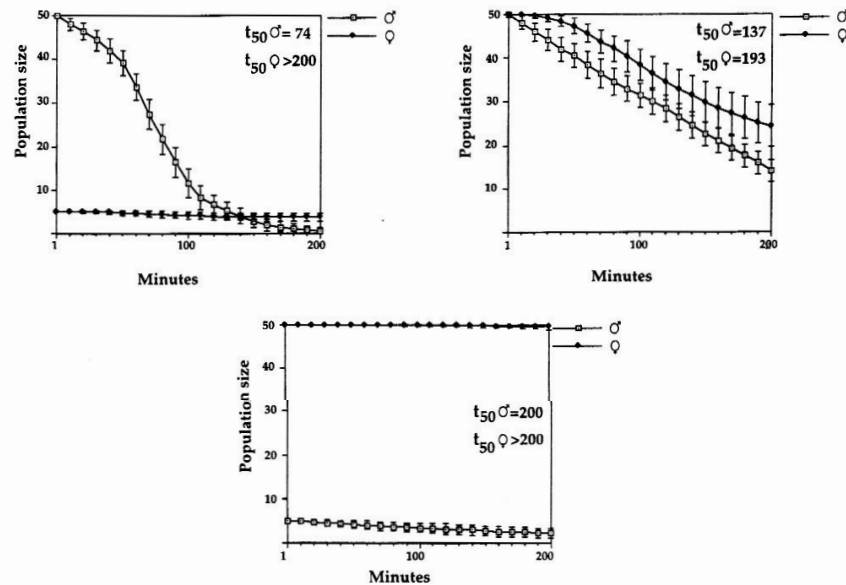
Figure 2. Change of migration probability in relation to population size of the opposite sex. The initial number of individuals was chosen in order to simulate the evolution of the daily sex-ratio: (i) simulation of the appearance of females in the population, with a high number of males and a low number of females, (ii) a situation with equal number of both sexes and (iii) a situation corresponding to the end of the flight season with a high number of females coexisting with a few males. t_{50} is the number of minutes needed to reach 50 % of the initial population size of each sex. Patch size was 200 × 200. Results are the mean and the standard error of 100 runs for each minute.

tively related to the density of the males for females and negatively to the density of females for males. Model predictions fitted well the asymmetric patterns of movements between two years at the metapopulation scale: more females moved (and they moved further) at higher male and female densities while more males moved (and they moved further) at lower male and female densities.

Migration frequencies in the simulation (e.g. 100 % of males dispersing within hours and up to 36 % of all female dispersing in this period) could look as too high to be relevant to the metapopulation system under study (e.g. 4-8 % of males migration over the flight season). However, as shown by the density manipulation experiments, adults left the patch but return a few minutes later. Therefore, the 'instantaneous migration rate' provided by the simulation model cannot be compared with the results within the metapopulation, as obtained from MRR data. Simulation results are of the same magnitude than field observations of this 'instantaneous migration rate'.

The model predicted also that sex-biased migration would occur in the population from the early emergence of males until their decrease. Migration would

be male-biased first, at the time when no or only a few females occur. Afterwards, females would disperse until the decrease in male numbers. Such a time-course of migration could not be observed in our field data. The effect of density on migration was detected only at the metapopulation scale with all the movements pooled by year. Several factors could contribute to hide the intra-year temporal pattern of migration due to the phenological change in sex-ratio over the season. The between-patch variation in adult emergence at the metapopulation scale hindered the division of the whole flight period into units corresponding to the different states of the operational sex-ratio. However, a change in male spatial behaviour was observed in *Euphydryas editha*, another explosive breeder related to *P. eunomia*, before and after the appearance of a significant number of females [4]: males flew shorter distances after the emergence of females. This change in male spatial behaviour is in agreement with the predictions of our model.

Female migration or long-distance movements have been observed in other butterflies. At high male density, females of *Pieris protodice* harassed by courting males left their habitat patches [17]. In *Lasiommata*
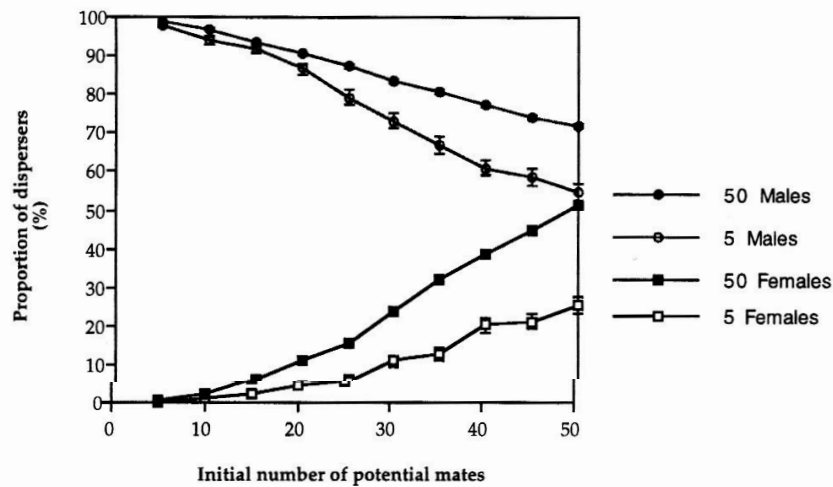
Figure 3. Change of migration probability in relation with the population size of the same sex. Dispersal probability was computed from an initial population size of 5 and 50 individuals after 200 min; the opposite sex population size ranking from 5 to 50 by step of 5 individuals. Results are the mean and the standard error of 100 runs for each minute. In this example, the simulation area was 200 × 200, corresponding to a real patch of 4 ha.

megera, the spatial distributions of males and females were also dissociated by female avoidance of courting males [5]. Female distribution in *Eurodryas anicia* depended on both host plant density and male harassment [15]. In the bivoltine *Colias philodice eriphyle*, sex-biased migration occurred at each generation but the disperser sex changed from one generation to the other. Males dispersed more in the first generation when overall density was low, while females dispersed more in the second generation at high overall density. This pattern is explained by the searching behaviour of males inducing male migration at low female density while female harassment by courting males resulting in female migration is more frequent at high male density [19]. This scenario corresponds to sex-biased density-dependent migration, which seems thus to be a process occurring in several butterfly species.

4.2. Density-dependent migration and metapopulation dynamics

Immigration and emigration rates are of major importance in metapopulation dynamics. This is especially true in the case of species living in transient habitats like *P. eunomia* whose main habitat in Western Europe is the first stage of the succession towards the river bank woodland. Nève et al. [14] reported on the metapopulation structure in *P. eunomia*. Large habitat patches with long-lived populations are connected via smaller ones acting as stepping stones, where extinction is likely to occur. In such a network, sex-biased density-dependent emi-

gration led to a high level of between-patch migration which indicates the importance of conservation of viable populations at the landscape scale in spite of the turnover of optimal habitats.

If emigration is sex-biased density-dependent, population foundation rate is not expected to be constant, as high female emigration rate will only occur at high butterfly density. Results of the experiment of *P. eunomia* introduction in the Morvan where the species never occurred naturally before are in good agreement with this prediction [6, 14]. Two introduction events (4 and 14 females respectively) were made in 1970 and 1974. Within 10 years, neighbouring sites were colonized and colonization first included sites close to introduction sites. Relationship between distance and time needed for colonization was proved to be non-significant during the first decade while this relationship became significant on the whole data (24 years since introduction) [14]. This pattern of colonization rate suggests that population foundation occurred only when butterfly density oversteps a certain threshold. Such spasms in population foundation did not correspond to the basic assumptions of constant migration rate of metapopulation dynamics models, which could affect metapopulation viability estimates produced by these models. As the colonization probability is a direct function of migration, changes in the migration rate from one generation to the next will modify the incidence function (i.e. the probability that patch *i* is occupied within the landscape) at each generation.

Acknowledgements

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Errata

After the proof stage, the text was altered whenever accents occurred.

The end of the acknowledgements should read : "Ministère de la Région wallonne (Belgium)"

Altered references are :

[1] Baguette, M. & Goffart, Ph., 1991. Liste rouge des Lépidoptères Rhopalocères de Belgique. Bulletin et Annales de la Société royale belge d'Entomologie, 127 : 147-153.

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