

Population sex ratio and dispersal in experimental, two-patch metapopulations of butterflies

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Summary

1. Sex-biased dispersal, that is, the difference in dispersal between males and females, is thought to be the consequence of any divergent evolutionary responses between sexes. In anisogamous species, asymmetry in parental investment may lead to sexual conflict, which entails male–male competition (for sexual partner access), female–female competition (for feeding or egg-laying habitat patches) and/or male–female competition (antagonistic co-evolution).

2. As competition is one of the main causes of dispersal evolution, intra- and intersexual competition should have strong consequences on sex-biased dispersal. However, very few experimental studies, if any, have simultaneously addressed the effect of biased sex ratio on (i) each dispersal stage (emigration, transience, immigration), (ii) the dispersal phenotype and (iii) the colonization success of new habitat in order to fully separate the effects of varying male and female density.

3. Here, we used the Metatron, a unique experimental system composed of 48 interconnected enclosed patches dedicated to the study of dispersal in meta-ecosystems, to investigate the effect of sex ratio on dispersal in a butterfly. We created six populations with three different sex ratios in pairs of patches and recorded individual movements in these simple metapopulations.

4. Emigration was higher when the proportion of males was higher, and individuals reached the empty patch at a higher rate when the sex ratio in the departure patch was balanced. Males had a better dispersal success than females, which had a lower survival rate during dispersal and after colonization. We also showed that sex and wing size are major components of the dispersal response.

5. We did not observe sex-biased dispersal; our results thus suggest that female harassment by males and male–male competition might be more important mechanisms for the dispersal of females and males, than the search for a mating partner. Furthermore, the demonstration of a differential mortality between males and females during dispersal provides causal hypotheses of the evolution of sex-biased dispersal.

Key-words: colonization success, corridor, dispersal propensity, dispersal success, timing of emigration, inter- and intraspecific competition, metapopulation dynamics, Metatron, *Pieris brassicae*

Introduction

Sex-biased dispersal, that is, the difference in dispersal between males and females, has generated much interest

over the past 30 years, ever since it was proposed as a means to avoid inbreeding (the inbreeding hypothesis; Moore & Ali 1984; Pusey 1987) or to reflect sex-specific competition and/or needs (Dobson 1982; Waser 1985; Perrin & Mazalov 2000; Gros, Hovestadt & Poethke 2008). The inbreeding hypothesis has been progressively expanded (Gros, Hovestadt & Poethke 2008; Baguette

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et al. 2012; Matthysen 2012), with the evolution of sex-biased dispersal now considered as the consequence of inbreeding avoidance or any divergent evolutionary responses between sexes (e.g. Gros, Hovestadt & Poethke 2009). In particular, the asymmetry in parental investment may lead to sexual conflict (e.g. Chapman *et al.* 2003), which entails male–male competition (for sexual partner access), female–female competition (for feeding or egg-laying habitat patches) and/or male–female competition (antagonistic co-evolution). As competition is one of the main causes of dispersal evolution (Gandon & Michalakis 1999; Travis, Murrell & Dytham 1999; Cadet *et al.* 2003), intra- and intersexual competition should have strong consequences on sex-biased dispersal (Perrin & Mazalov 2000; Darden & Croft 2008; Rankin 2011). Theory of sex-biased dispersal indeed predicts that dispersal rates will be higher in the sex that suffers more from local competition (Perrin & Mazalov 2000), local competition being likely to occur when one of the two sexes is less abundant. Variations in sex ratio are thus expected to induce sex-biased dispersal. For example, female harassment by males in populations with a male-biased sex ratio may promote female dispersal as an escape behaviour to avoid potential costs such as physical injury, energy loss, infanticide, etc. (in primates: Sterck 1997; in insects: Baguette *et al.* 1998; in lizards: Le Galliard *et al.* 2005). The literature highlights that the nature of a population disequilibrium, such as a biased sex ratio (i.e. the over-representation of individuals of one sex in the population), influences (i) the phenotype of the dispersing individual (McPeck & Holt 1992; Chaput-Bardy *et al.* 2010), (ii) the success of the dispersal movement (Chaput-Bardy *et al.* 2010) and (iii) the colonization success of new habitat patches (Freedberg & Taylor 2007). Indeed, not all individuals respond to intraspecific competition the same way (Cote, Clobert & Fitze 2007). Consequently, it is likely that the phenotype of dispersing individuals will strongly depend on the nature of the population disequilibrium (Clobert *et al.* 2009). We therefore expect that individuals with different phenotypes (here sex and size) will show differences in dispersal behaviour according to variation in sex ratio.

However, empirical studies provide mixed validations of the above predictions on the effects of population sex ratio on dispersal (e.g. Pruettt-Jones & Lewis 1990; Krupa & Sih 1993; Le Galliard *et al.* 2005). Overall, theoretical and empirical studies show that not only density *per se* but also the density of males and females separately need to be considered as main drivers of dispersal. Understanding effects of sex ratio disequilibrium on the overall dynamics of spatially structured populations (metapopulations) is becoming nowadays increasingly important as anthropogenic population structure disequilibrium may in turn affect population persistence, metapopulation functioning and the potential for colonization (Baguette *et al.* 2012; Le Galliard, Massot & Clobert 2012).

A convenient approach to studying dispersal is to disentangle the dispersal process into three successive, but inter-related phases: departure out of a habitat (i.e. emigration), transfer within the landscape (i.e. transience) and settlement and reproduction in a new habitat (i.e. immigration), which may or may not be occupied by conspecifics (Stenseth & Lidicker 1992; Ims & Yoccoz 1997; Bowler & Benton 2005; Baguette & Van Dyck 2007; Clobert *et al.* 2009; Bonte *et al.* 2012). Very few studies, if any, have simultaneously addressed the effect of biased sex ratio on each dispersal stage within an experimental framework in order to fully separate the effects of varying male and female density (but see Le Galliard *et al.* 2005 for an approaching study). In particular, a direct assessment of the effect of sex ratio on the success of installation in another habitat after the decision to leave a patch has never been carried out. Here, we assume that the sex ratio in the initial population may impact not only the dispersal decision of the individual, but also its behaviour during the transience phase, as well as its decision to settle into an existing population or to colonize an empty patch. We also assume that the effect of sex ratio on the three different stages may vary according to the individual phenotypes (sex and size).

To tackle these issues, we tested for sex-biased dispersal in experimental metapopulations of the butterfly *Pieris brassicae* under varying population sex ratios. We used the Metatron, a large mesocosm specifically designed to study the dynamics of spatially structured ecological systems (Legrand *et al.* 2012). Butterflies are key in the study of dispersal (Stevens, Turlure & Baguette 2010) and metapopulation dynamics (Hanski 1998), and highly biased sex ratios have been reported in natural populations as a consequence of either parasitism by *Wolbachia* bacteria (Dyson & Hurst 2004) or protandry, that is, the emergence of males before females (e.g. Schtickzelle, Le Boulengé & Baguette 2002). *Pieris brassicae* is one of the most mobile butterfly species in Europe (Stevens *et al.* 2013), but previous works showed the coexistence of mobile and nonmobile individuals in natural populations (Ducatez *et al.* 2013). We assumed that only mobile individuals contribute to dispersal. Laboratory-bred adults were tested for mobility at emergence using the procedure designed by Ducatez *et al.* (2012). Mobile individuals were then released to create three different sex ratios (25%, 50% and 75% males) at constant density into paired patches connected by a narrow, S-shaped corridor, a design mimicking simple, two-patch metapopulations. We studied the dispersal of individuals from the release patch to the connected, previously empty patch using five variables: the dispersal propensity (emigration decision), the timing of emigration (the time between release and the first emigration from the release patch), the mortality in the corridors (mortality during the transience stage), the dispersal success (immigration within empty patches) and the survival after settlement in connected, previously

empty patches (the time between the first immigration within empty patch and death). We also examined, using the same experimental setting, how these five variables were affected by individual phenotype (i.e. sex and wing length, a proxy of body size).

Materials and methods

STUDY SPECIES: THE LARGE WHITE BUTTERFLY

Pieris brassicae is a common butterfly with a wide distribution in the Palearctic, encompassing at least 25° in latitude from the Maghreb to Scandinavia. It is considered as highly mobile and may also migrate, possibly covering several hundreds of kilometres per generation (Feltwell 1982). However, little is known about its migratory behaviour, which is believed to vary substantially across its range (Spieth & Kaschuba-Holtgrave 1996). Previous works on this species showed the coexistence of resident and dispersing individuals in France. These two strategies are reflected in a well-defined behavioural syndrome (Ducatez *et al.* 2012), and each has its advantage under particular climatic conditions and landscape settings (Ducatez *et al.* 2013).

STUDY SYSTEM: THE METATRON

The Metatron, developed in the Ariège, France, is a new infrastructure dedicated to the study of dispersal in metapopulations. It is composed of 48 100-m² patches covered with nets, interconnected by narrow 19-m-long S-shaped corridors (Legrand *et al.* 2012). Each corridor can be opened or closed following specific experimental requirements. Here, we used paired cages connected by fully open corridors. We selected cage pairs with similar habitat quality (same species in the herbaceous layer, comparable vegetation height). Within each cage, we placed 2 pots with nectariferous flowers for adult food resources and 1 pot with *Tropaolum majus* as a host plant (Feltwell 1982) to ensure favourable conditions. A specific precipitation regime was not implemented, and the roofs of the cages were fully open.

BUTTERFLY BREEDING AND MOBILITY TEST

Seven egg clutches of the large white butterfly (*P. brassicae*) originating from breeding lines in Visan (Vaucluse, France) were reared in separate incubators under controlled conditions until emergence in Moulis (Ariège, France). Larvae were fed with cabbage (*Brassica oleracea*) provided *ad libitum* in 15 × 5 × 5 cm boxes within a climate chamber. Temperatures were set at 23 ± 1 °C during the day and at 18 ± 1 °C during the night. The chosen photoperiod (light: dark 14: 10 h) induces direct development. Emerging butterflies were all marked with a specific number on their wings after they were completely dry.

Previous works on *P. brassicae* showed (i) extensive variation in mobility across individuals, which was consistent across time (Ducatez *et al.* 2012), and (ii) a relationship between mobility and dispersal in the Metatron, the most mobile individuals dispersing significantly more from their release patch to other patches than the less mobile individuals (Legrand, Trochet, Moulhérat, Calvez, Stevens, Clobert & Baguette, unpublished; Legrand *et al.* 2012). To ensure that this variation in mobility did not interfere with

dispersal responses due to sex ratio, all butterflies used in the experiment were scored for their performance using a flight mobility test devised by Ducatez *et al.* (2012). One day after emergence, individuals were marked and introduced into a 25 × 10 × 10 cm plastic chamber perforated at its base and fixed to a rapid agitator (Vortex Genie 2; Scientific Industries, New York, USA). Each individual was allowed to acclimate for 1 min. The vortex was then switched on, generating strong vibrations preventing the butterfly from perching on the chamber's wall. The behaviour of the butterfly was observed over 1 min. During the test, each individual could fly or lay uncomfortably at the bottom of the chamber. We recorded the total time an individual spent flying during the test, high values indicating good flight capacities. All experiments were performed at 25 ± 1 °C. We retained 243 individuals (129 females and 114 males) with good flight ability, that is, more than 50 s of flight during the 1-min test.

Wing length (in mm) was measured for each of the tested butterflies ($n = 243$) by the same experimenter using a calliper to control for the effect of morphology.

EXPERIMENTAL DESIGN

Data on the density of *P. brassicae* in natural populations are not available to our best knowledge. Shapiro (1970) mentioned densities ranging from five individuals per 100 m² in low-density populations to 800 individuals per 100 m² in very dense populations of the Pierid *Colias eurytheme*. He also reported a density of 720 individuals per 100 m² in a natural population of *Pieris protodice*. As individuals were confined in the cages of the Metatron and were thus unable to escape harassment, we chose a rather low density of 20 individuals per 100 m². We created three sex ratio treatments (number of males divided by the total number of individuals), hereafter called 'sex ratio treatment': 0.75, 0.5 and 0.25. For each sex ratio treatment, 20 butterflies were released into the Metatron following the experimental design presented in Fig. 1: sex ratio = 0.75 (15 males, five females), 0.5 (10 males, 10 females) and 0.25 (five males, 15 females). We performed two replicates for each sex ratio treatment. On 23 May 2011, each group of 20 butterflies was released at the centre of a patch connected to another empty patch. Butterflies from the seven families were randomly distributed into the treatment groups. In total, the experimental design was composed of six sets of two interconnected patches (three sex ratio treatments, two replicates). The selection of the release was randomly determined (Fig. 1). To keep densities and sex ratios constant within release patches, dead butterflies and emigrants were replaced during new release sessions. A pilot experiment showed that the daily capture probability within the Metatron was 0.82 for females and 0.75 for males (Legrand *et al.* 2012). Thus, the probability that a living butterfly was not captured after 2 days was rather low (0.06). Accordingly, butterflies not observed over two consecutive days were also replaced to keep densities constant in release patches. In total, four additional release sessions were performed from 25 May 2011 to 29 May 2011. A total of 199 butterflies (103 females and 99 males) were monitored until 1 June 2011 during capture sessions. Capture sessions were performed twice a day (10.30 and 16.30) weather permitting to record the position of butterflies: release patch, corridor or empty patch (Fig. 1). In total, 15 capture sessions were performed, and the age at release into the Metatron varied from 2 to 9 days.

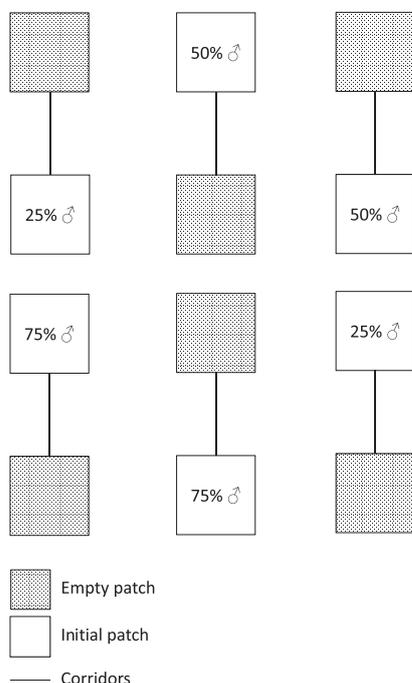


Fig. 1. Experimental design. Groups of 20 butterflies with varying sex ratio were randomly released within initial patches, each of them being connected to one empty patch through corridors. Each sex ratio treatment had two replicates. Empty patches at the beginning of the experiment are in grey.

STATISTICAL ANALYSES

We used generalized linear mixed-effects models (GLMM) with fixed and random effects to study the impact of the sex ratio on five response variables detailed below, each being characteristic of a particular stage of the dispersal process. In all analyses, the behaviour of individuals was treated as independent from that of others (an individual was considered as one observation).

Emigration stage

- 1 The *dispersal propensity*: emigrants ($n = 78$; 33 females and 45 males) were defined as individuals emigrating at least once from the release patch to the corridor or to the empty patch. Residents ($n = 121$) were thus defined as individuals staying in the release patch until death. Individuals that were never recaptured after their release sessions were excluded from the analyses.
- 2 The *timing of emigration*: the number of days between the release and the first emigration from the release patch ($n = 60$; 36 females and 24 males). Individuals that were not recaptured the session before they dispersed were excluded from the analyses as their timing of emigration could not be ascertained.

Transience stage

- 3 The *mortality in the corridors*: among emigrants, we recorded individuals dead in the corridors (i.e. during the transience stage). Emigrants were considered dead in the corridor when

individuals were directly found dead in the corridor or when individuals were recorded for the last time in a corridor (thus never recaptured within either patch).

Immigration stage

- 4 The *dispersal success*: successful emigrants ($n = 37$; 12 females and 25 males) were defined as individuals that reached the empty patch at least once. Emigrants that died in the corridor or returned to the release patch before reaching the empty patch (they only visited the corridor) were thus considered unsuccessful. We considered the dispersal success as an estimator of the colonization success. Only a couple of individuals moved back from the previously empty patch to the release patch. We did not consider these movements in the analyses.
- 5 The *survival after settlement*: the number of days between settlement in the empty patch and death among successful emigrants ($n = 37$; 12 females and 25 males).

To test for the effects of the sex ratio treatments, we constructed two sets of GLMM. First, the sex ratio was included as a factor, and second, the sex ratio was included as a continuous variable allowing the testing of quadratic effects. Because Akaike Information Criterion (AIC) values were always lower in the second set of models, we only present the results using sex ratio as a continuous variable. Models were thus built as follows:

Dispersal propensity or timing of emigration or mortality in the corridors or dispersal success or survival after settlement \sim sex + sex ratio + sex ratio² + life span + wing length + first-order interactions + patch identity (random) + family identity (random) + error

A binomial distribution and a logitlink were used in the model describing the *dispersal propensity*, the *mortality in the corridors* and the *dispersal success*, and a Poisson distribution and a log link were used in the model describing the *timing of emigration* and the *survival after settlement*. The patch identity into which butterflies were released and the family were included as random factors (random intercepts). All first-order interactions were tested.

Emergences of *P. brassicae* from the same family are not synchronous. As a result, butterflies were of different ages when released, between 1 and 9 days (mean \pm SE: 3.43 \pm 0.11 days). This age at release was defined as the time spent in the laboratory after the emergence of the adult and before its release into the Metatron. We observed that this time in the laboratory negatively impacted the life span of individuals in the Metatron (ANOVA: $F_{1,197} = 44.46$, $R^2 = 0.18$, $P < 0.001$). To incorporate this effect in models, both the age at release and the life span should be added as variables. However, this would lead to overparameterization of models. We thus decided to correct life span by the age at release taking the residuals of the linear model: *total life span* \sim *age at release* + error.

Analyses were done using R 2.12 (R Development Core Team 2008). The LME4 R-package (Bates, Maechler & Dai 2008) was used to run the saturated models. Model selection was performed using backward selection. Interactions were removed first when they were not significant, and the less significant variable was then removed step by step. Between each step, successive models were compared using likelihood ratio tests (LRT) to determine the significance of the variable removed as recommended by

Burnham & Anderson (2002). If the effect of this variable was not significant, the new model was kept and the backward selection was continued. The procedure was stopped when all explanatory variables had a significant effect on the response variable.

Results

Among the 199 recaptured individuals (103 females and 96 males), 78 were emigrants (33 females and 45 males) and 121 were residents. 24.24% of emigrants were from patches with sex ratio treatment = 0.25, 37.5% from patches with sex ratio treatment = 0.5 and 57.38% from patches with sex ratio treatment = 0.75 (Fig. 2a). We observed a positive relationship between the *dispersal propensity* and sex ratio, meaning that both males and females were more likely to emigrate when the proportion of males increased (Table 1 and Fig. 2a).

The *timing of emigration* varied between 0 and 11 days (mean \pm SE: 2.05 ± 0.33) and was not different between males and females (males: 1.78 ± 0.36 and females: 2.46 ± 0.62 days, sex effect not significant). A positive relationship was found between the *timing of emigration* and *wing length* (Table 2). Butterflies with shorter wings emigrated earlier than those with longer wings. The *timing of emigration* was however not affected by the sex ratio treatment, even among the first-order interactions.

Table 1. β estimates with associated standard error for explanatory variables with significant effects on the *dispersal propensity* after backward selection (likelihood ratio test: $P = 0.081$, $\chi^2 = 3.045$, d.f. = 1). For each explanatory variable, a positive effect means an increase in the probability to emigrate

	Estimate	Standard error	<i>z</i> value	Pr(> <i>z</i>)
Intercept	-1.82	0.77	-2.35	0.019 *
Life span	0.51	0.12	4.42	< 0.001 ***
Sex ratio	2.82	1.42	1.98	0.047 *

***: $P < 0.001$; **: $0.001 < P < 0.01$; *: $0.01 < P < 0.05$.

Among the 78 emigrants, 35 individuals died in the corridors. The probability of dying during transience was thus 0.41 in this experiment. The *mortality in the corridors* showed a negative correlation with the interaction between sex and sex ratio and also with the interaction between *wing length* and sex ratio (Table 3). As the sex ratio increased, fewer males died in the corridors; however, females were found to die more frequently in the corridors (Fig. 2b). Moreover, *wing length* of emigrants that died in the corridors also decreased with the increasing sex ratio, meaning that dead emigrants had larger wings than surviving emigrants for female-biased sex ratio and the reverse for male-biased sex ratio (Fig. 2c).

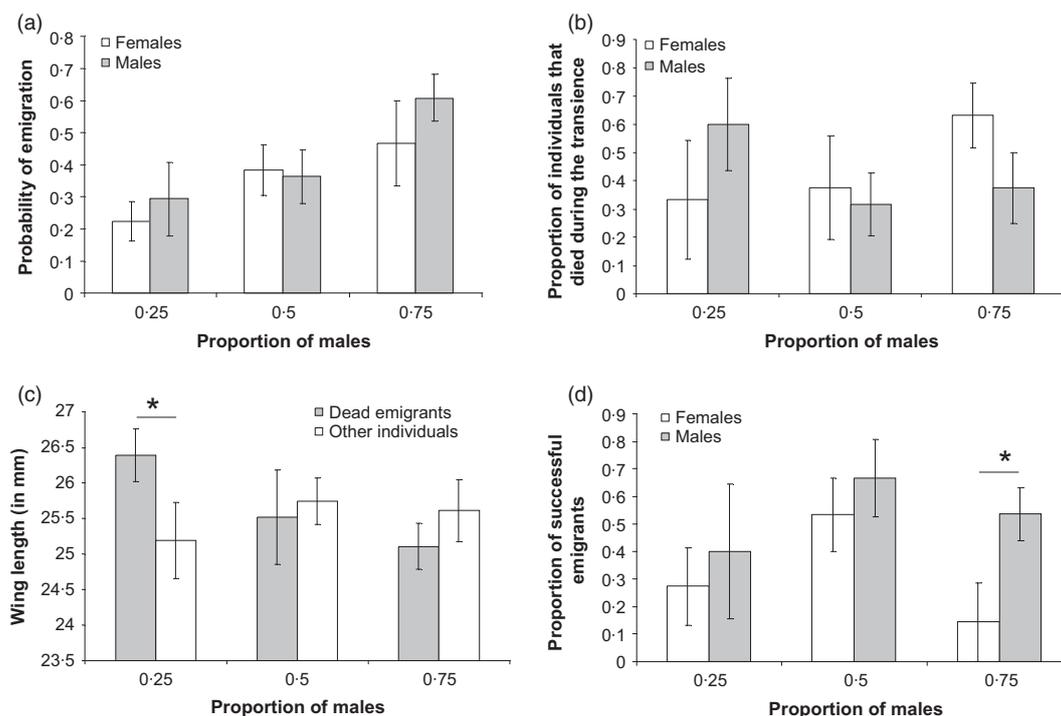


Fig. 2. (a) Probability of emigration according to sex ratio treatments (i.e. proportion of males in patches) and sex. The total number of individuals in patches was 66, 72 and 61 for sex ratio treatment = 0.25, 0.5 and 0.75 respectively. Bars represent standard errors. (b) Proportion of individuals that died during transience for each sex ratio and sex. The total number of dead individuals in the corridors was 8, 9 and 18 for sex ratio treatment = 0.25, 0.5 and 0.75 respectively. (c) Mean wing length (in mm) of emigrants that died in the corridors and of the other individuals according to sex ratio treatment. Bars represent standard errors. Significant difference among groups is represented by an asterisk (*). (d) Proportion of successful emigrants (individuals reaching the empty patch at least once) for each sex ratio treatment and sex. Bars represent standard errors. Significant difference among groups is represented by an asterisk (*).

Table 2. β estimates with associated standard error for explanatory variables with significant effects on the *timing of emigration* after backward selection (likelihood ratio test: $P < 0.001$, $\chi^2 = 12.585$, d.f. = 1)

	Estimate	Standard error	z value	Pr(> z)
Intercept	-3.70	1.32	-2.81	0.005 *
Wing length	0.18	0.05	3.63	< 0.001 ***
Life span	0.37	0.05	6.83	< 0.001 ***

***: $P < 0.001$; **: $0.001 < P < 0.01$; *: $0.01 < P < 0.05$.

Table 3. β estimates with associated standard error for explanatory variables with significant effects on the *mortality in the corridors* after backward selection (likelihood ratio test: $P < 0.0482$, $\chi^2 = 3.9016$, d.f. = 1)

	Estimate	Standard error	z value	Pr(> z)
Intercept	37.45	16.69	-2.24	0.025*
Sex (male)	-2.26	1.7	1.33	0.18
Wing length	-1.39	0.64	2.18	0.029*
Sex ratio	-68.1	27.93	2.44	0.015*
Sex (male) * sex ratio	5.73	2.92	-1.96	0.049*
Wing length * sex ratio	2.53	1.07	-2.36	0.018*

***: $P < 0.001$; **: $0.001 < P < 0.01$; *: $0.01 < P < 0.05$.

Among emigrants, 37 individuals (12 females and 25 males) reached the empty patch at least once. Emigrating males reached the empty patch more often than females. The *dispersal success* also showed a quadratic fit with sex ratio, meaning that individuals had more chance to colonize empty patches when they left a balanced sex ratio (Table 4 and Fig. 2d). Among the colonizers, males tended to have a better *survival after settlement* than females (Table 5), while the sex ratio treatment within release patches had no effect on postcolonization survival (sex ratio: $P = 0.51$, interaction between sex ratio and sex: $P = 0.62$).

Discussion

We will successively discuss the effect of sex ratio on each of the three dispersal stages (emigration, transience and immigration). We will then discuss how these Metatron results could expand our knowledge of the dispersal process despite the inherent limitations of this experimental system.

EMIGRATION: DEPARTURE FROM THE RELEASE PATCH

Relatively few experimental studies under semi-natural conditions have examined adult emigration as a consequence of the manipulation of mature adult sex ratio in a

Table 4. β estimates with associated standard error for explanatory variables with significant effects on *dispersal success* after backward selection (likelihood ratio test: $P = 0.095$, $\chi^2 = 2.792$, d.f. = 1). For each explanatory variable, a positive effect means an increase in the probability to be a successful emigrant

	Estimate	Standard error	z value	Pr(> z)
Intercept	-6.2	2.61	-2.37	0.018*
Sex (male)	1.23	0.61	2.02	0.044*
Life span	0.65	0.21	3.14	0.002**
Sex ratio	23.08	10.92	2.11	0.034*
Sex ratio ²	-22.67	10.6	-2.14	0.032*

***: $P < 0.001$; **: $0.001 < P < 0.01$; *: $0.01 < P < 0.05$.

Table 5. β estimates with associated standard error for explanatory variables with significant effects on *survival after installation* after backward selection (likelihood ratio test: $P < 0.0681$, $\chi^2 = 3.3281$, d.f. = 1)

	Estimate	Standard error	z value	Pr(> z)
Intercept	0.85	0.28	3.07	0.002**
Sex (male)	0.41	0.23	1.8	0.07

***: $P < 0.001$; **: $0.001 < P < 0.01$; *: $0.01 < P < 0.05$.

population. We are aware of one study on the common lizard; however, this study provides limited details of sex-biased dispersal (Le Galliard *et al.* 2005). Indeed, this study considered adult emigration, despite adult dispersal being the exception rather than the rule in natural populations of the common lizard (Clobert *et al.* 1994). Nonetheless, our results in *P. brassicae*, where adult dispersal is the rule (Feltwell 1982), concur with the study on the lizard: a biased sex ratio did not entail a higher emigration rate of the more abundant sex with respect to the less abundant sex. There is no tendency to balance a population sex ratio by emigration of the more abundant sex. Instead, we found a higher emigration rate for both sexes from a population with a male-biased sex ratio. Our results support the attainment of balance between intra- and intersexual competition as a driver of dispersal in this species rather than the mating probability-dependent emigration suggested by the theoretical work of Perrin & Mazalov (2000).

Several mechanisms can explain such sex-specific emigration responses regarding intra- and intersexual competition. Aggressive male-male interactions have been widely described in several groups and proposed as a major driver of male dispersal decisions in butterflies (e.g. Baguette *et al.* 1998), including Pierid butterflies (Shapiro 1970). Indeed, when the proportion of males is high, dispersal may become less costly than male intrasexual competition, leading to a higher emigration probability for males. Accordingly, we repeatedly recorded aggressive behaviours between males during flight or feeding periods in our experiment (data not shown). As a by-product, emigration may increase male mating probability if males

arising from a male-biased sex ratio reach a population with a female-biased sex ratio (Baguette *et al.* 1998). Within female-biased populations, higher female availability might also contribute to the decrease in male emigration as previously shown in several studies (e.g. Baguette *et al.* 1998). The relationship between emigration and the mating status of males would be interesting to investigate. Indeed, in two species of Pierid butterflies, Shapiro (1970) reported that young males were more prone to leave breeding areas with high male density.

While intermale competition or female availability might explain our result for the increased male emigration with sex ratio, this explanation certainly does not hold for females. Indeed, female emigration also increased with male-biased sex ratio. We might expect that in a closed environment like the Metatron, the ability of females to escape from male harassment would be limited, thus impacting the effects of harassment on female dispersal decisions. Overall, dispersal rates might be lower or emigration might take more time, in the Metatron as compared to natural conditions, because individuals can only disperse through the corridor, whereas in nature, they have the opportunity to disperse in different directions. Harassment of females by males has often been presented as a consequence of an increase in male-biased sex ratio (Chapman *et al.* 2003; Le Galliard *et al.* 2005). In butterflies also, it has been suggested that one of the main drivers of female emigration was female harassment by males (e.g. Shapiro 1970; Baguette, Convie & Nève 1996; Baguette *et al.* 1998; Hovestadt & Nieminen 2009). Females should indeed suffer less from male harassment in a female-biased sex ratio and should therefore tend to stay. Interestingly, the presence of a high proportion of a given sex is not taken by the other sex as a sign of a good-quality patch (e.g. Stamps 1994; Léna *et al.* 1998).

We showed that the variation in sex ratio did not affect the *timing of emigration* for either sex. This result is quite intriguing since we would expect the dispersing individuals leave sooner with an increasing male-biased sex ratio if emigration was male competition and female harassment motivated. We suggest that the way *P. brassicae* males and females assess a population sex ratio could offer an explanation for this counterintuitive result. Understanding how individuals perceive population's characteristics, that is, using direct cues (conspecific density) or other more indirect or difficult systems (e.g. scents and/or the decrease of resources), might help to solve this issue. Otherwise, the absence of sex ratio effect on the timing of emigration could also be due to the time needed for individuals to locate corridors. It might even be that such a variation in sex ratio in natural populations of *P. brassicae* is rare, which might explain why males and females did not respond rapidly to the variation. However, huge variation in the sex ratio of natural populations of related Pierid species (7–44% of females) has been reported (Shapiro 1970). Moreover, this scenario is potentially in contradiction with the fact that the timing of emigration

is not independent of male and female phenotypes. Indeed, the timing of the first emigration was positively correlated to *wing length*, which is highly correlated to body size in butterflies (Garcia-Barros 2000). In butterflies, wing length is often used as a reliable proxy for dispersal ability at the interspecific level (e.g. Sekar 2012), and large-winged butterflies are considered as better dispersers. However, this shortcut is currently under debate, as it has been shown that an array of selected life-history traits is a much better predictor of dispersal than body size alone (Stevens *et al.* 2012). At the intraspecific level, Ducatez *et al.* (2012) showed that wing length was positively correlated to mobility in males of *P. brassicae*, but not in females. As a result, males with shorter wings may be less efficient during the transience stage. We showed here that *wing length* also has an impact on the *timing of emigration* for both sexes, individuals with shorter wings emigrating earlier than those with longer wings. However, the *timing of emigration* was not dependent on the interaction between individual phenotype and the population sex ratio, suggesting that the *timing of emigration* is, here, more phenotype dependent than environment dependent (Clobert *et al.* 2009), giving more credit to our above suggestion of slow sex ratio perception.

TRANSCIENCE: CORRIDOR CROSSING

Not all emigrating butterflies succeeded in reaching the empty patch. The analysis of mortality in the corridor revealed that females seemed to die in higher numbers than males. Moreover, males coming from populations with more females incurred higher mortality than those coming from populations with more males. This relationship was reversed in females, mortality in the corridor being higher in females coming from populations with more males. This strongly suggests that emigrating when the other sex is more abundant could be a wrong decision.

In females, it is likely that male harassment in male-biased populations caused damage to harassed females, which in turn decreased their likelihood for success during the transience stage. Such harassment is not a consequence of the experimental setting used here, as it has repeatedly been mentioned in the literature dealing with butterfly dispersal in natural populations (see review in Hovestadt & Nieminen 2009) and particularly in related *Pieris* species (Shapiro 1970). This scenario might further indicate that only some females could resist male harassment in male-biased populations, the others deciding to emigrate despite being less efficient. If dying within a Metatron's corridor can be assimilated to the mortality cost paid by emigrants during transience, our results also indicate that departure decisions are rather uncorrelated with success during transience.

The phenotype of the emigrants also influenced mortality during the transience stage in interaction with the sex ratio of the release population: large-winged individuals survived less in the corridor than short-winged individuals

when originating from male-biased populations, while it was the contrary for female-biased populations. This result confirms that it is more the phenotype (morphological, physiological and/or behavioural) of the emigrants in interaction with the characteristics of its population of origin that governs the transience and immigration into a new habitat patch (Cote, Clobert & Fitze 2007; Clobert *et al.* 2009). In other species as well, size, dispersal propensity and dispersal success were found to show different patterns and signs of association (Clobert *et al.* 2009) even at the within-population level (Sinervo *et al.* 2006; Cote, Clobert & Fitze 2007). Although strongly significant, this result is however difficult to explain since large-winged individuals are usually thought to have better dispersal capacities (Sekar 2012). It might indicate, as already suggested by interspecific comparisons (Stevens *et al.* 2013), that wing length is not the best predictor of dispersal success in butterflies. Other traits such as life-history traits (Stevens *et al.* 2012) or behavioural strategies (Cote *et al.* 2010) are indeed better predictors of dispersal success.

IMMIGRATION: DISPERSAL SUCCESS

The overall *dispersal success* defined here as the individual's ability to reach the other patch (emigration combined with survival during the transience) was influenced by both the sex and the population sex ratio. Males settled in the empty patches more often than females, even more so when they originated from a high sex ratio (in high male-biased sex ratio: LRT $P = 0.058$, $\chi^2 = 3.59$, d.f. = 1; see Fig. 2d). In comparison, only females from balanced sex ratio populations managed to reach the previously empty patch. Also, males had a slight tendency to survive better than females after settlement. Such sex-specific success in the ability to reach new patches may have important implications for the colonization process. Indeed, whenever an environmental change alters a population sex ratio, it will also alter the capacity of this population to ensure optimal colonization of surrounding empty patches since the resulting newly founded populations will all skew towards male-biased populations. Measures of sex ratio in natural populations of *P. brassicae* are unavailable. In other butterfly species, sex ratios biased towards females have been described as a consequence of infection by the male-killing bacteria *Wolbachia* (Hiroki *et al.* 2002; Dyson & Hurst 2004). More generally, male-biased populations are frequently observed in butterflies (Tabashnik 1980; Frey & Leong 1993; Underwood & Shapiro 1999) as a consequence of protandry (e.g. Schtickzelle, Le Boulengé & Baguette 2002). Although the presence of such disequilibrium in sex ratio remains to be determined in *P. brassicae*, our results show how simple changes in population parameters might change the dispersal success of individuals and provide interesting perspectives to studies of other species (e.g. Bergerot *et al.* 2012).

Conclusion

An experimental approach often requires the simplification of the real, natural world by controlling the variability of some environmental factors. Here, the dispersal of butterflies in the Metatron is approximated by the movement of individuals from one cage to the next by crossing narrow, S-shaped corridors. To what extent this simplification proves satisfactory for drawing sound conclusions on the whole dispersal process is obviously a key question. Overall, our results suggest that female harassment by males and male–male competition might be more important mechanisms for the dispersal of females and males, than the search for a mating partner. Despite the fact that we created populations by selecting individuals with good mobility performances, only one-third (32%) of the butterflies emigrated. The Metatron obviously imposed a strong constraint on the emigration stage by forcing emigrant candidates to use two small doors opening into the corridors, while in natural populations, emigrants are free to leave patches by flying in any direction. The transience stage was approximated by the crossing of a narrow, S-shaped corridor. Distance between habitat patches was thus traded off against the difficulty to move in the corridor. Interestingly, we detected a high mortality rate in the corridor, which suggests that the costs associated with the transience are high. This appears to be a general pattern in the real, natural world, as suggested by the review of Bonte *et al.* (2012). The demonstration of a differential mortality between males and females during the transience stage is particularly interesting in providing causal hypotheses of the evolution of sex-biased dispersal. Settlement was probably the dispersal stage that was the least constrained by the Metatron. The ability of individuals to reach other patches was male biased and is dependent upon the sex ratio for females, with a survival after settlement increased in males. *P. brassicae* is a migratory butterfly, with individuals flying northwards across Europe in spring and southwards in autumn. Populations in Northern Europe are founded each year by migrants, as the hibernation of caterpillars is not possible for climatic reasons. Given the clear-cut distinction between mobile and nonmobile individuals (Ducatez *et al.* 2012), we suggest that only mobile individuals contribute to the migration. Individuals from northern populations were indeed shown to be more mobile (Ducatez *et al.* 2013). This motivated our choice to restrict our experiment to the more mobile individuals. It would be interesting (i) to test the mobility of the migrant individuals reaching Northern Europe and (ii) to check the sex ratio in populations at the colonization front during these migrations. Our experiment suggests that both the stability of local populations and the success of colonization by both sexes are highly dependent upon the sex ratio and are favoured under balanced conditions. It would be interesting to ultimately establish how those individuals of lower flight ability (and perhaps lower intrinsic emigration propensity) respond to both total density and sex ratio.

Finally, experiments such as this are ideal for providing at least initial estimates for parameters that can be used in the new generation of dispersal models that are becoming available (Travis *et al.* 2012). Interestingly, while these models have rapidly incorporated more realism over the last few years, none has yet included emigration propensity as a function of sex ratio. Our results neatly illustrate how this type of experimental system can flag effects that modelling can then incorporate to test their potential importance. Existing models (e.g. Barton *et al.* 2012) could be easily extended to establish how sex ratio-dependent emigration propensities influenced range expansion dynamics under different strengths of Allee effects.

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