

## **Interrelations Among Habitat Use, Behavior, and Flight-Related Morphology in Two Cooccurring Satyrine Butterflies, *Maniola jurtina* and *Pyronia tithonus***

**Thomas Merckx<sup>1,2</sup> and Hans Van Dyck<sup>1</sup>**

*Accepted February 7, 2002; revised April 1, 2002*

---

*Mobility, activity patterns, habitat use, and some morphological traits of two often cooccurring satyrine butterflies of grasslands—the meadow brown (*Maniola jurtina*) and the hedge brown (*Pyronia tithonus*)—were studied by a mark-release-recapture method at two sites. Additionally, some flight-related morphological traits of a series of collected females of *P. tithonus* were compared between recently colonized and permanent populations. The more active, but less mobile *P. tithonus* got faster wing damage than did *M. jurtina* and had more, and more symmetrically spread eyespots on the wings. For both species, the microdistribution was affected by shelter, long vegetation, and nectar, but this was more pronounced in *P. tithonus*. It is hypothesized that *P. tithonus* may traverse the same landscape at a slower rate than *M. jurtina*.*

---

**KEY WORDS:** movements; flight morphology; eyespot pattern; butterflies; *Maniola jurtina*, *Pyronia tithonus*.

### **INTRODUCTION**

Cooccurring related species have often been the focus of research on resource use, habitat sharing, and interspecific competition. Within a habitat,

<sup>1</sup>Laboratory of Animal Ecology, Department of Biology, UIA, University of Antwerp, Belgium.

<sup>2</sup>To whom correspondence should be addressed. Fax: + 32 3 820 22 71. E-mail: thomas.merckx@ua.ac.be.

those species may use different resources, or use the same but in a different way or at a different time. In butterflies, cooccurrence of species may include spatial (host-plant species, host-plant part, microclimate, adult feeding resources) and temporal variation (phenology and voltinism) (e.g., Porter *et al.*, 1992). The meadow brown butterfly *Maniola jurtina* (L.) and the hedge brown butterfly *Pyronia tithonus* (L.) often co-occur in different kinds of grassland habitat (Bink, 1992). These European satyrines are univoltine with largely overlapping flight periods (Brakefield, 1987) and use several grasses in common as host plants (Bink, 1992).

Although both species often cooccur in Belgium, *P. tithonus* appears to be less frequent than *M. jurtina*, at both the regional and local scale (Maes and Van Dyck, 1999). However, a few of the vacant sites have recently been colonized. At the local scale (*i.e.*, within distribution grid cells of  $5 \times 5$  km), *P. tithonus* may be very abundant at one site, but lacking at another site having similar habitat at a distance of only a few kilometers (Maes and Van Dyck, 1999), while in *M. jurtina* there is no such pattern. A preliminary analysis of landscape features in occupied and vacant areas at a rather coarse-grained level of  $1 \times 1$  km (including percent cover by grassland, length of hedgerows, etc.), failed to explain the difference (T. Merckx, D. Maes, and H. Van Dyck, unpublished). Hence, these observations may point at larger, or even subtler, intrinsic interspecific differences regarding mobility and habitat use.

This paper reports on a comparative study examining interspecific variation in flight- and activity-related morphology, behavioral variation (including levels of flight activity and movements), variation in habitat use (including microdistribution with respect to shelter and nectar sources), and interrelations between these factors in males and females of *M. jurtina* and *P. tithonus* at two sites. In particular, variation in adult size and eyespot patterns on the wings is analyzed in relation to the level of flight activity and movements. Larger insects have often been thought to be more mobile and hence being better capable of covering larger distances and colonizing (new) sites. *M. jurtina* is clearly larger than *P. tithonus*, which would lead to the simple prediction that *M. jurtina* is a "better flier," covering, on average, larger distances than *P. tithonus*. For example, individuals of *P. tithonus* were more often recaptured at the same location, whereas *M. jurtina* was more often recaptured elsewhere (Dover *et al.*, 1992). Both species have been considered to be fairly sedentary (Brakefield, 1979, 1982; Warren, 1992; Wynhoff, 1992; Pollard and Yates, 1993; Dover *et al.*, 1997), but movements covering wider distances occur (Dover *et al.*, 1992, 1997).

Satyrine butterflies, particularly *M. jurtina*, have been extensively studied for their variation in eyespot patterns on the ventral hindwings (Brakefield, 1984; Brooke *et al.*, 1985; Owen and Smith, 1990, 1993; Shreeve

*et al.*, 1996). These small spots serve as deflecting devices for attacks by visual predators, like birds (Blest, 1957; Brakefield *et al.*, 1992). The model of Brakefield (1984) based on observations in *M. jurtina*, predicts more eyespots and a more symmetrical eyespot pattern for butterflies that are more active, and hence in greater need to deflect attacks. Mark-release-recapture (MRR) studies provide evidence that butterflies with more eyespots, on average, move farther (Brakefield, 1982, 1984), but the functional correlation is not clear, unless larger movements (dispersal) reflect a general rise in activity and hence a larger susceptibility to predators. Besides size and eyespot pattern, wing damage is also included. With respect to habitat use, we studied whether the presence of long grasses, bushes/trees, and nectar availability affected the two species differently. Bushes and trees may provide shelter for adults, particularly on arable land (Dover, 1996; Dover *et al.*, 1997). Although this is largely a comparative study, we also included an additional data set on *P. tithonus* females that were collected in recently colonized populations versus permanent populations to compare their morphology (cf. Hill *et al.*, 1999); it is expected that colonizing individuals are larger than resident individuals.

## MATERIALS AND METHODS

### Study Species

The meadow brown butterfly (*Maniola jurtina*) and the hedge brown butterfly (*Pyronia tithonus*) are typical Satyrinae (Nymphalidae), having small wing eyespots and brownish wings. In Belgium, both species occur in several grassland habitats and, based on coarse-grained distribution data, their distribution is widespread (Maes and Van Dyck, 1999). Mean life-span based on MRR data ranges from 5 to 12 days in *M. jurtina* (Brakefield, 1984) and 3.5 to 8 days for *P. tithonus* (Brakefield, 1979). The flight period of *M. jurtina* proceeds this of *P. tithonus* but there is a considerable overlap. Both species are protandrous.

### Study Areas

The comparative MRR study was conducted at two sites in Lembeek (Belgium): the nature reserve Grote Zenne (GZ) and TGV meadow (TG). Both sites contained meadows bordered with shrubs and trees. Each site was subdivided by a grid system (grid cells 10 × 10 m), and in each grid cell the following habitat characteristics were recorded: (1) vegetation height (*i.e.*,

short versus long grass), (2) presence/absence of shrubs, and (3) presence/absence of flowering plants. The shortest distance between the sites is 1200 m., thus exchange was within the limits of dispersal capacities for both species.

### Mark-Release-Recapture

Data were collected July 3–August 18, 1998. During each survey (*i.e.*, all days with suitable weather conditions), all grid cells were checked in a varying order (cf. Dover, 1989) for *M. jurtina* and *P. tithonus*. Butterflies were captured by a handnet and individually marked at first capture by writing a unique number on the ventral side of the left hindwing with a fine, nontoxic, permanent marker (Staedtler Lumocolor 313). They were released at the place of capture. For each capture we recorded (1) species and sex; (2) date, time, and exact position; (3) marking number, and (4) behavior (three classes: flying, foraging, and resting). Distances of movements between captures were measured on detailed grid maps and calculated as the shortest distance between the centers of the grid cells. Two movement measures were calculated: distance covered between the first and the last capture and cumulative covered distance. Both distances were  $\log_{10}$  transformed prior to the analyses. The maximal movements that could be recorded within GZ, within TG, and between both sites were 427 m, 309 m, and 1700 m, respectively.

### Morphology: Wing Length and Eyespot Patterns

Forewing length (from article to tip) was measured using calipers (accuracy  $\pm 0.09$  mm). Wing wear was assigned to one of three classes: (1) no or very little wear, (2) moderate wear, and (3) heavy damage. Three eyespot characteristics were recorded; (1) eyespot number, (2) mean eyespot position, and (3) eyespot pattern. Eyespot patterns (*i.e.*, combination of eyespot number and position) were given a code according to Brakefield (1984). This typology, based on McWhirter and Creed (1971), distinguishes 13 of 64 types theoretically possible for *M. jurtina*. Since some of the observed eyespot patterns were not included, we extended the system (Table I). Eyespot position was recorded as a binary code from the anal wing side to the costa. Repeated measurements yielded a high repeatability of eyespot scores. Besides contingency tables ( $\chi^2$ ), we used multivariate generalized regression models (with type III sum of squares), using SAS software (SAS, 1996). Starting from a full model containing the factors and interaction terms,

**Table I.** Overview of Eyespot Patterns on Ventral Hindwings as Applied by Brakefield (1984) and How It was Extended in This Paper<sup>a</sup>

Name (description)	Brakefield (1984) ( <i>M. jurтина</i> )		This study ( <i>M. jurтина</i> + <i>P. tithonus</i> )	
	Position	Code	Position	Code
Nought	000000	0	000000	0
Costal 1	000010	C1	000010	C1
Costal 2	000011	C2	000011	C2
Costal 3	010011	C3	010011	C3
Costal 4	011011	C4	010111/011011	C4
Anal 1	010000	A1	011111	C5
Anal 2	110000	A2	010000	A1
Anal 3	110010	A3	110010	A3
Anal 4	111010	A4	010010	S2
Splay 2	010010	S2	110011	S4
Splay 4	110011	S4	111111	S6
Median 3	011010	M3	111011	SA5
All 5	111011	all 5	110111	SC5
			011010	MA3
			010110	MC3

<sup>a</sup>Codes for the presence (1) or absence (0) of each possible spot (anal to costal position)

model selection was done by backward elimination of the nonsignificant factors.

### Collected Samples in Recent Versus Permanent Populations

We compared flight morphology of *P. tithonus* females from six different populations: four had been colonized recently (Lembeek, Halle, and two sites in Sint-Pieters-Leeuw), and two were permanent populations (Solresur-Sambre and Herentals). In each site at least 10 females were collected. Specimens were dried to constant mass at 60°C. Total dry mass, thorax mass, and abdomen mass was measured with a microbalance (Sartorius 1207 MP2), and forewing length and area were measured by an image analyzing system (Optimas 5.2 Software). Morphological measures were log<sub>10</sub> transformed prior to analysis. As a measure of relative thorax mass and abdomen mass, residual values, when regressed on total mass, were used. This dataset was analyzed by a mixed regression model using sites as random effect nested by the fixed effect recent versus permanent (Mixed procedure in SAS). The degrees of freedom of *F* tests of the fixed effects were approximated with Satterthwaite’s procedure (Verbeke and Molenberghs, 1997).

## RESULTS

## Inter- and Intraspecific Morphological Variation: Size and Eyespot Position and Number

The full regression model for wing length ( $\log_{10}$ ) with species, sex, date, site, and all interaction terms showed a significant three-way interaction ( $P=0.03$ ). Hence, the analysis was first split by species and then also by sex. Females of both species had larger forewings than males (*P. tithonus*:  $F_{2,293} = 166.42$ ,  $P = 0.001$ ;  $F = 319.3$ ,  $P = 0.0001$  and *M. jurtina*:  $F_{5,595} = 214.52$ ,  $P = 0.0001$ ;  $F = 17.66$ ,  $P = 0.0001$ ); additionally, this difference decreased over time in *M. jurtina* ( $F = 17.60$ ,  $P = 0.0001$ ). Males and females of *M. jurtina* had significantly shorter wings in GZ than in TG (males:  $F_{2,217} = 15.63$ ,  $P = 0.0001$ ;  $F = 12.74$ ,  $P = 0.0004$ , and females:  $F_{2,377} = 38.00$ ,  $P = 0.0001$ ;  $F = 75.59$ ,  $P = 0.0001$ ) (Fig. 1). *P. tithonus* that emerged later in the flight period had shorter forewings ( $F = 38.11$ ,  $P = 0.0001$ ), while in *M. jurtina* this was only the case in females ( $F_{2,377} = 38.00$ ,  $P = 0.0001$ ;  $F = 6.74$ ,  $P = 0.00098$ ). There was a reversed tendency in *M. jurtina* males ( $F_{2,217} = 15.63$ ,  $P = 0.0001$ ;  $F = 11.60$ ,  $P = 0.0008$ ).

Eyespot position differed significantly between the species ( $\chi^2_5 = 191.67$ ,  $P = 0.001$ ); *P. tithonus* more frequently had costally or symmetrically placed

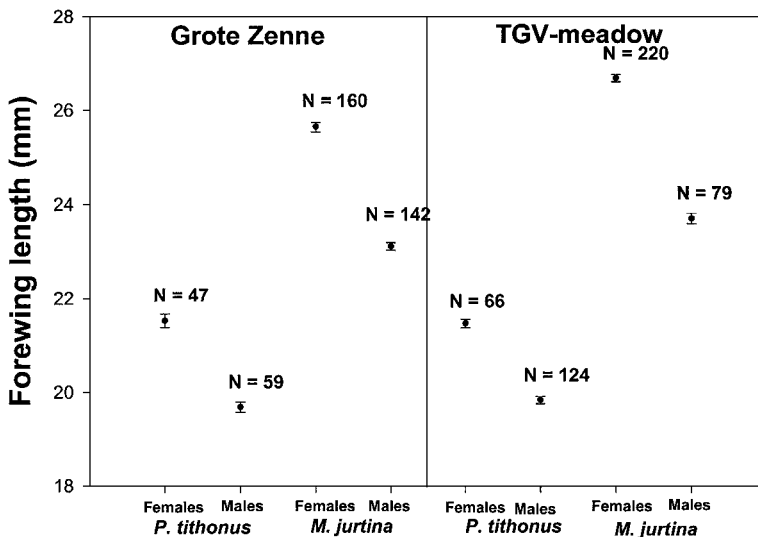


Fig. 1. Mean forewing length  $\pm$  SE of males and females of *P. tithonus* and of *M. jurtina* in both sites. Sample sizes are indicated for each mean.

eyespots, while additional anal patterns occurred in *M. jurtina*. In *P. tithonus*, males had more costally placed eyespots than females whose eyespots were more spread over the wing margin ( $\chi^2_5 = 40.14$ ,  $P = 0.001$ ) (Fig. 2a,b). The opposite relationship was found in *M. jurtina* ( $\chi^2_5 = 78.55$ ,  $P = 0.001$ ) (Fig. 2c,d). On average, *P. tithonus* had more eyespots than *M. jurtina* ( $\chi^2_6 = 522.31$ ,  $P = 0.001$ ), but again there were sexual differences with opposite patterns among the species. *M. jurtina* males had more eyespots than females ( $\chi^2_5 = 178.57$ ,  $P = 0.001$ ) (Fig. 3c,d), and the opposite relationship was found in *P. tithonus* ( $\chi^2_5 = 10.68$ ,  $P = 0.046$ ) (Fig. 3a,b).

### Flight Activity, Wing Length and Wing Damage

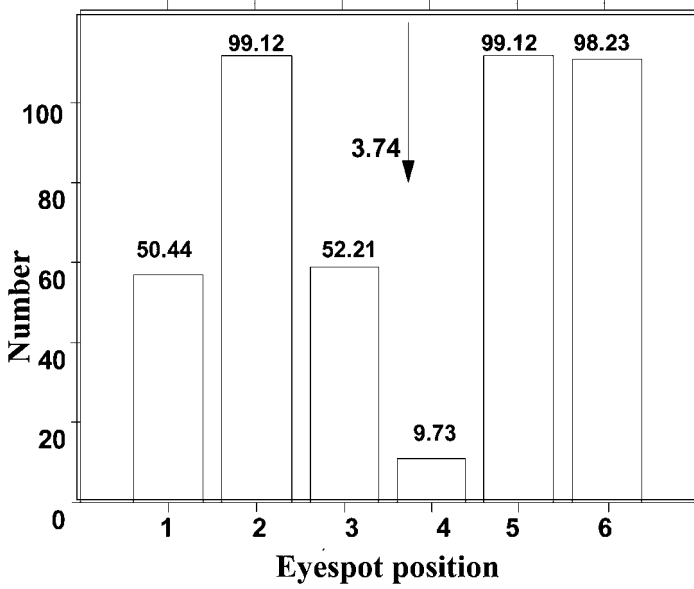
*P. tithonus* was observed more frequently at flight than *M. jurtina* ( $\chi^2 = 36.44$ ,  $P = 0.0001$ ), and overall males were observed more at flight than females ( $\chi^2 = 5.13$ ,  $P = 0.023$ ) (Fig. 4). The binary response “being at flight or not” before capture was analyzed in relation to wing length ( $\log_{10}$ ) and site (logistic regression). Males of *M. jurtina* were observed more frequently at flight in GZ compared to TG ( $\chi^2 = 4.60$ ,  $P = 0.03$ ), but this measure was not related to wing length ( $\chi^2 = 2.22$ ,  $P = 0.13$ ). For *M. jurtina* females and both males and females of *P. tithonus*, flight activity was not correlated with wing length and did not differ between the sites.

*P. tithonus* became more damaged than *M. jurtina* ( $F_{1,162} = 6.64$ ,  $P = 0.010$ ), and this effect increased over time ( $F_{1,162} = 40.43$ ,  $P = 0.0001$ ). Males of *M. jurtina* had more damage than females ( $\chi^2_2 = 7.28$ ,  $P = 0.026$ ), and the opposite relationship was found for *P. tithonus* ( $\chi^2_2 = 12.11$ ,  $P = 0.002$ ).

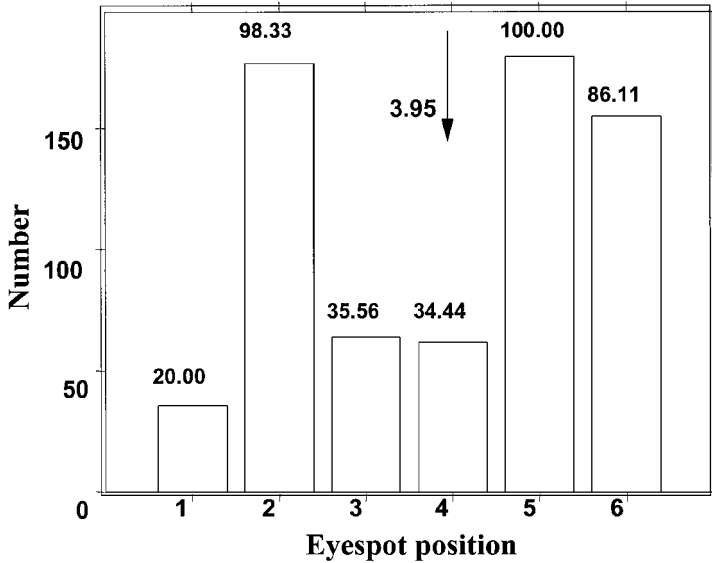
### Movements

The distance covered between first and last capture was analyzed starting with a full regression model containing species, site, and number of days during which the distance was covered. The final model retained species, site, number of days, and the interaction between species and site as significant terms ( $F_{4,256} = 12.83$ ,  $P = 0.0001$ ; time:  $P = 0.0001$ ; site:  $P = 0.0029$ ; species:  $P = 0.0001$ ; species  $\times$  site:  $P = 0.0006$ ). The distance covered increased with time between first and last capture. In GZ both species covered overall longer distances than in TG, and *M. jurtina* covered longer distances than *P. tithonus* (Fig. 5). The latter interspecific difference was larger in GZ than in TG explaining the interaction term. Next, the same analysis, but split by species, was done to evaluate sexual variation. For *M. jurtina* the effect of site was no longer significant. Since number of days was not

a)

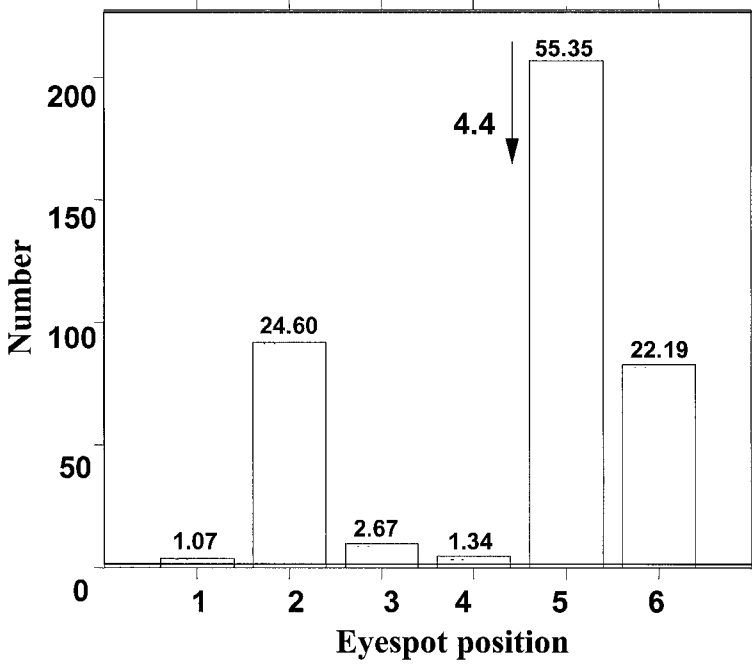


b)



**Fig. 2.** Frequency of the presence of each out of six possible hindwing spots (anal to costal) in (a) *P. tithonus* females ( $N=113$ ), (b) *P. tithonus* males ( $N=180$ ), (c) *M. jurtina* females ( $N=374$ ), and (d) *M. jurtina* males ( $N=209$ ). Average eyespot patterns are indicated by the arrow.

c)



d)

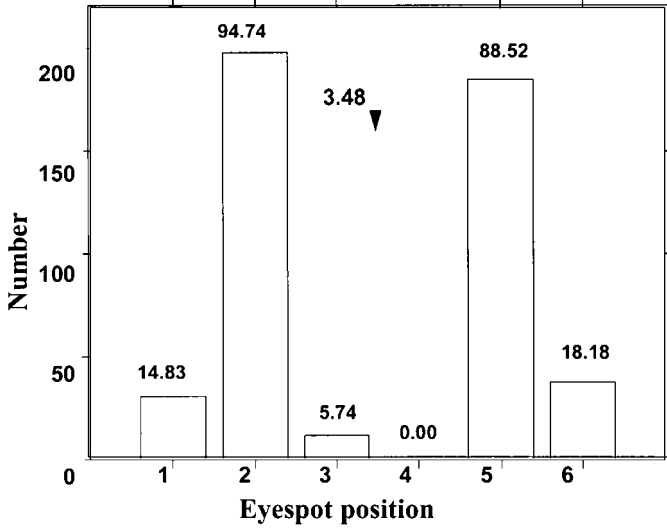
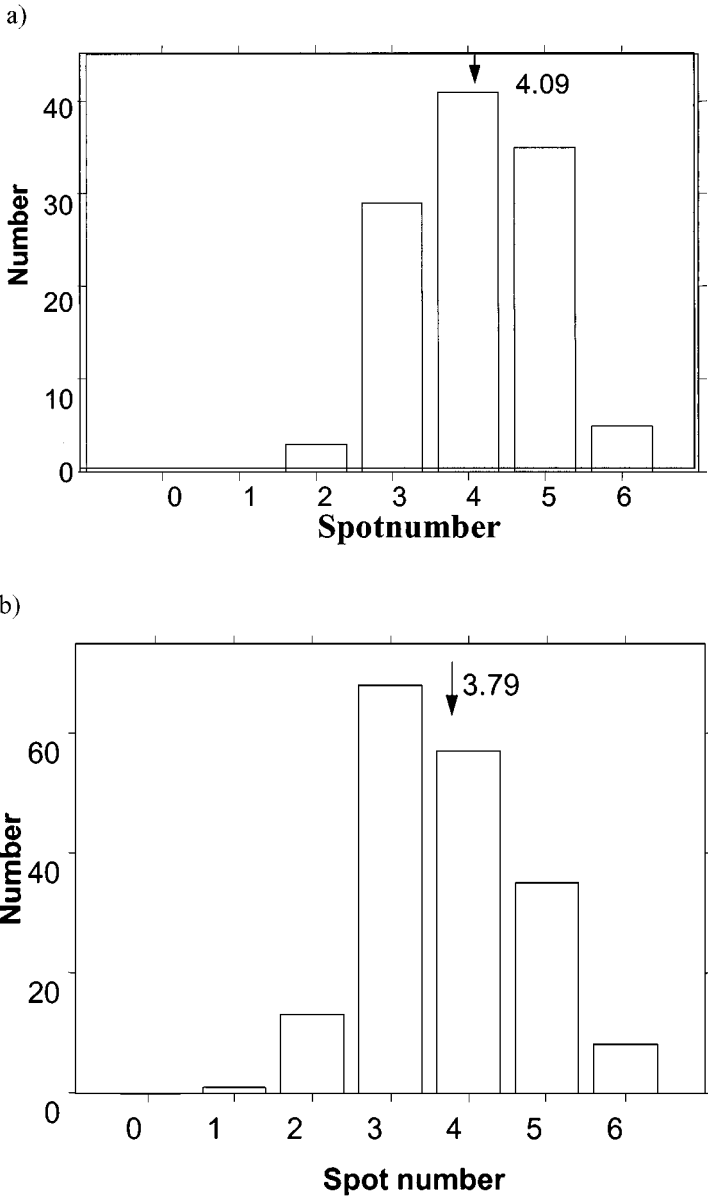
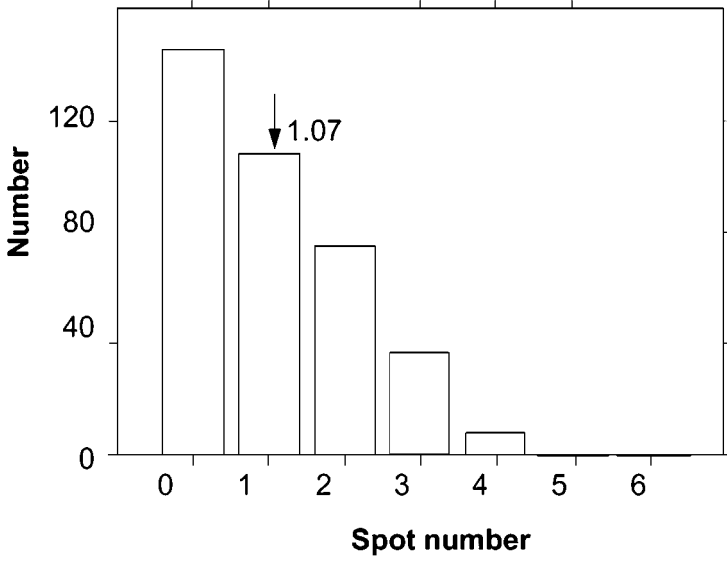


Fig. 2. (Continued)



**Fig. 3.** Frequency distribution of eyespot number on ventral hindwings in (a) *P. tithonus* females ( $N=113$ ), (b) *P. tithonus* males ( $N=180$ ), (c) *M. jurtina* females ( $N=374$ ), and (d) *M. jurtina* males ( $N=209$ ). Average eyespot numbers are indicated by the arrow.

c)



d)

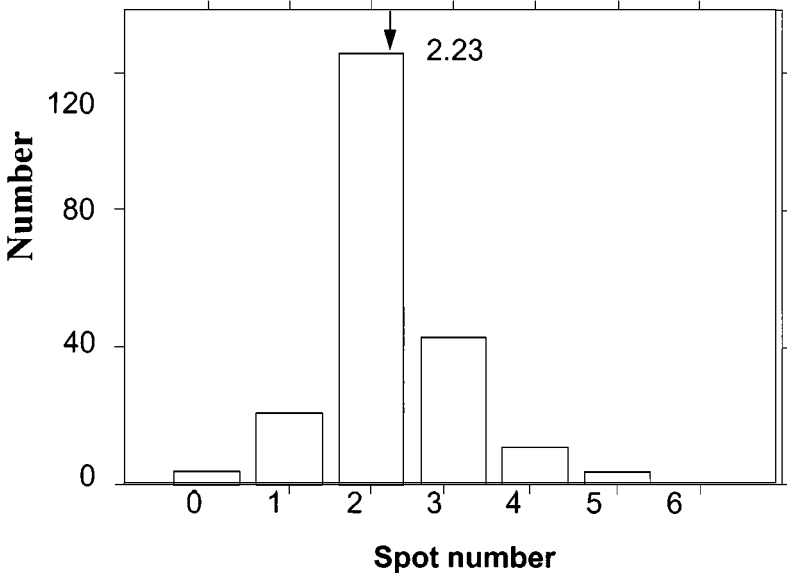
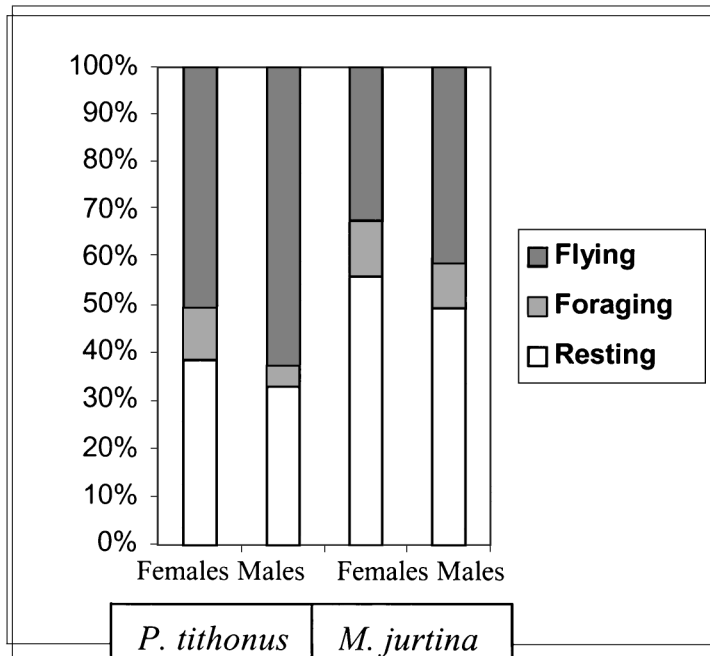


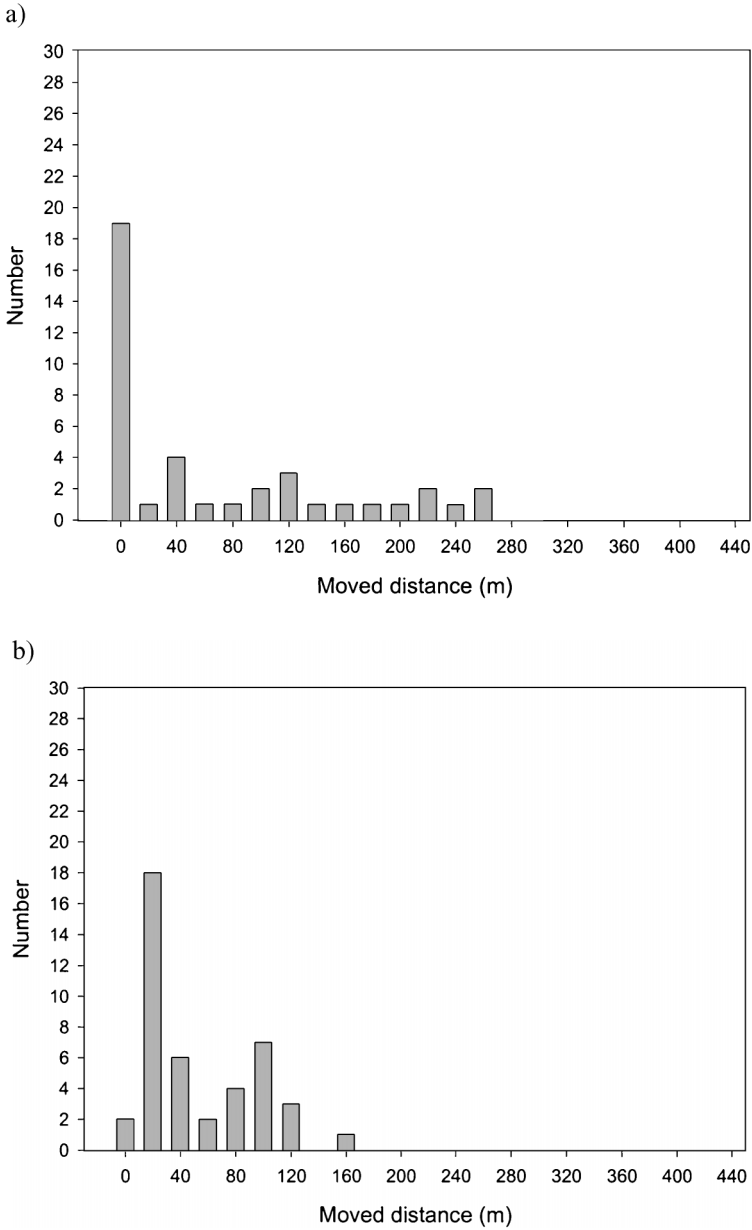
Fig. 3. (Continued)



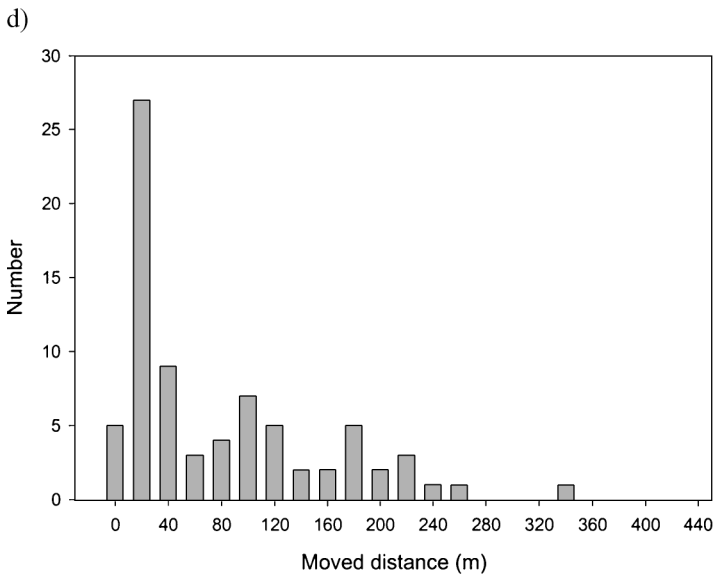
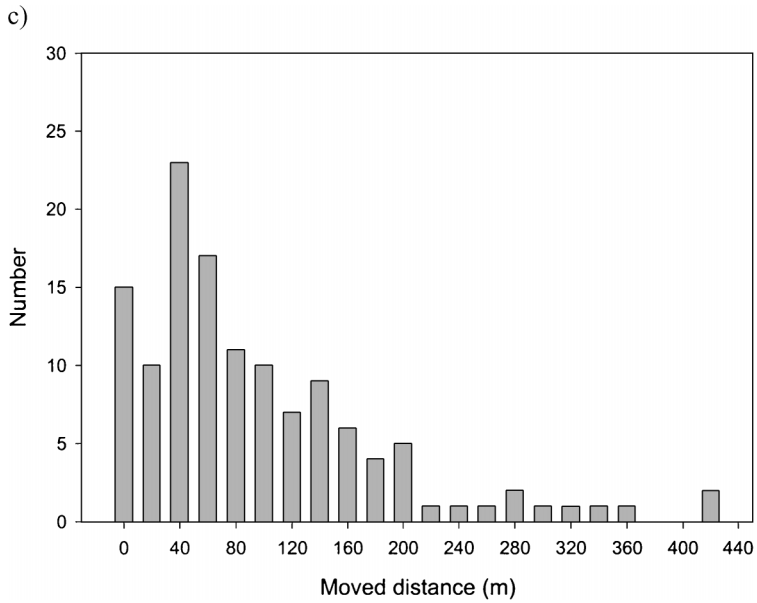
**Fig. 4.** Proportion of individuals observed in one of three behavioral categories (flight, foraging, and resting) before capture in males and females of *P. tithonus* and of *M. jurtina*.

significant for *P. tithonus* and was the only effect in the final model for *M. jurtina* ( $F_{1,189} = 15.88$ ,  $P = 0.0001$ ), the latter probably caused the overall time effect in the former analysis. So, independent of sex and site, *M. jurtina* covered longer distances within larger time windows. Independent of sex and time, *P. tithonus* covered longer distances in TG compared to GZ ( $F_{1,68} = 9.26$ ,  $P = 0.0033$ ).

Next, analyses were repeated with cumulative covered distance. The final model kept time, species, and the interaction between species and site as significant terms ( $F_{4,256} = 14.03$ ,  $P = 0.0001$ : time:  $P = 0.0001$ ; species:  $P = 0.0001$ ; site  $P = 0.062$ ; site  $\times$  species:  $P = 0.0017$ ). In GZ, butterflies tended to fly overall longer distances than in TG (Fig. 5). The other relationships were identical to the analysis with distance covered between first and last capture. As before, the analysis was split by species to evaluate sexual variation. Again *P. tithonus* ( $F_{2,67} = 5.00$ ,  $P = 0.0095$ ) covered longer distances in TG compared to GZ, without any significant differences between the sexes. However, cumulative distance did increase over time in



**Fig. 5.** Frequency distributions for movements (i.e., cumulative distance in meters between first capture and final recapture) of (a) *P. tithonus* in GZ, (b) *P. tithonus* in TG, (c) *M. jurtina* in GZ, and (d) *M. jurtina* in TG.



**Fig. 5.** (Continued)

*P. tithonus*. In *M. jurtina*, individuals covered longer cumulative distances with time since capture, and longer distances in GZ compared to TG (model:  $F_{4,186} = 7.94$ ,  $P = 0.0001$ ; site:  $P = 0.038$ ; time since capture:  $P = 0.0001$ ). There was no significant difference in covered distance between the sexes.

### Habitat Use

*M. jurtina* was significantly more abundant per grid cell than *P. tithonus* ( $\chi^2_5 = 51.69$ ,  $P = 0.001$ ). The distribution of *P. tithonus* and *M. jurtina* among grid cells tended to be differently affected by the presence of the resources. In *P. tithonus*, all three variables were univariately significant: it occurred more frequently in cells with long vegetation ( $\chi^2_1 = 5.30$ ,  $P = 0.021$ ), shelter ( $\chi^2_1 = 7.81$ ,  $P = 0.005$ ) and nectar ( $\chi^2_1 = 9.64$ ,  $P = 0.002$ ). *M. jurtina* occurred significantly more frequently in sheltered cells ( $\chi^2_1 = 4.53$ ,  $P = 0.039$ ), but there were tendencies only for long vegetation ( $\chi^2_1 = 3.19$ ,  $P = 0.074$ ) and nectar ( $\chi^2_1 = 3.12$ ,  $P = 0.077$ ). Comparing frequencies of occurrence in grid cells providing all three resources, *P. tithonus* was more restricted to them than *M. jurtina* ( $\chi^2 = 44.67$ ,  $P = 0.0001$ ), but no sexual differences were found.

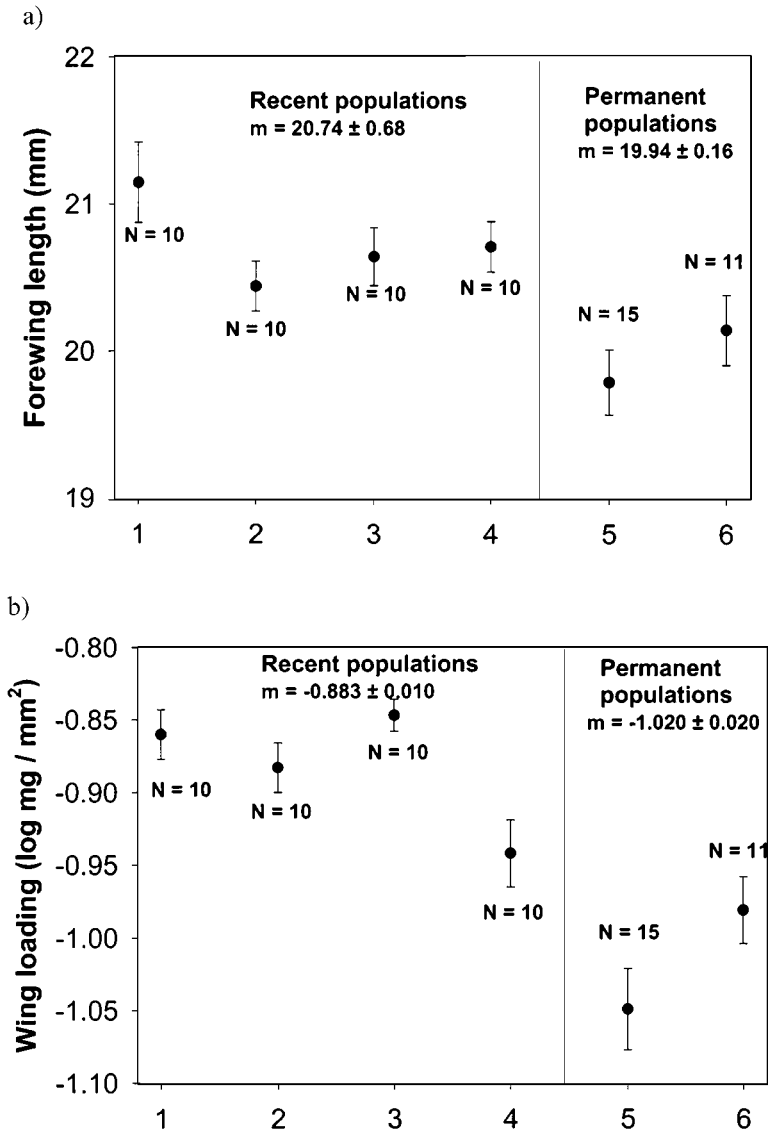
### Recent Versus Permanent *P. tithonus* Populations: Differences in Female Size

Females of the recently colonized populations had significantly larger forewings ( $F_{1,3.48} = 11.34$ ,  $P = 0.034$ ) and forewing areas ( $F_{1,3.96} = 9.55$ ,  $P = 0.037$ ) than those of the permanent populations (Fig. 6a). Recent population females were significantly heavier ( $F_{1,3.88} = 13.76$ ,  $P = 0.021$ ) and had significantly higher wing loading ( $F_{1,3.82} = 12.66$ ,  $P = 0.025$ ) compared to permanently occupied populations (Fig. 6b). There were no significant effects of relative thorax mass ( $F_{1,3.46} = 0.12$ ,  $P = 0.74$ ), relative abdomen mass ( $F_{1,64} = 0.44$ ,  $P = 0.50$ ) and aspect ratio ( $F_{1,3.67} = 0.28$ ,  $P = 0.62$ ) between both groups of populations.

## DISCUSSION

### Wing Morphology in Relation to Flight Activity and Mobility

The results from behavioral snapshot observations of flight activity differed from those from MRR movement recording since *M. jurtina* was less



**Fig. 6.** Morphological differences between *P. tithonus* females from recently colonized and permanent populations (1: Sint-Pieters-Leeuw A; 2: Sint-Pieters-Leeuw B; 3: Lembeek; 4: Halle; 5: Solre-sur-Sambre, and 6: Herentals): (a) forewing length and (b) wing loading. ( $m = \text{mean} \pm \text{SE}$ ).

frequently observed in flight, but did cover significantly larger distances than *P. tithonus*. Hence, activity levels do not appear to be a good indicator of mobility. Are these differences reflected by interspecific differences in morphology? The more mobile *M. jurtina* was larger. However, there is evidence for cooccurring butterflies that interspecific variation in size is not always related to differences in movements, like dispersal between habitat patches (Baguette *et al.*, 2000), but since *M. jurtina* and *P. tithonus* are closely related species, this difference may be of higher significance. A preliminary study on flight speed, based on videotape recordings, showed a tendency towards higher flight speed in *M. jurtina* (C. Debaer and H. Van Dyck, unpublished). Physiological differences (e.g., energy supply) may be of large significance for interspecific differences in mobility, but very little is known about this.

The more active, but less mobile *P. tithonus* had more, and more symmetrically spread, eyespots on the wings than *M. jurtina*. This makes sense in terms of the model of Brakefield (1984) that predicts a positive correlation between spotting and activity. Males were seen more frequently flying than females in both species, but males of *M. jurtina* only had more (and more symmetrically spread) eyespots than females and the reverse was true in *P. tithonus*. Male butterflies spend most of their time locating mates and are generally more active than females (Pollard, 1981; Brakefield, 1982; Shreeve, 1992). Females usually mate only once, which leaves them more time available for resting, nectar feeding, host plant selection and oviposition (Wynhoff, 1992).

Both species were more heavily damaged with age, but *P. tithonus* received damage faster, which agrees with its higher level of activity. In *M. jurtina* males had, on average, more damage than females, and vice versa for *P. tithonus*. Hence, within each species, the sex with the most, and most symmetrically spread, eyespots was on average most damaged. Eyespot patterns did not differ between the study sites, but males of *M. jurtina* (unlike females and both sexes of *P. tithonus*) were more frequently seen flying in GZ. In the latter site males of *M. jurtina* were significantly smaller than in TG. Thus, these differences in activity and size are again an indication of a lack of correlation between being larger and more active, but at the intraspecific level.

According to the first mobility measure, *P. tithonus* covered shorter distances than *M. jurtina*. In *M. jurtina* we found for both sexes and sites a significant time effect: distance increased with the number of days between first and final capture. There was no such effect in *P. tithonus*. The second mobility measure yielded largely similar results. For both species, distance covered increased with time. Our results on interspecific differences for movements agree with Dover *et al.* (1992, 1997). *P. tithonus* covered longer distances in

TG compared to GZ. For both sexes of *M. jurtina*, covered distances were larger in GZ, but only with the second measure. Probably differences in habitat structure may be responsible for this (Shreeve, 1990). *M. jurtina*, with more eyespots covered longer distances, similar to the findings of Brakefield (1982), but size had no effect. In *P. tithonus* however, eyespot number had no effect, but size did so with respect to the second mobility measure: larger individuals covered longer distances. This is in agreement with the finding that recently colonized populations of *P. tithonus* consisted of females with larger forewings compared to permanent populations. Furthermore, in spite of the difference in wing length (and flight activity) between the sexes, sexes in both species did not differ in mobility, indicating the absence of a relationship between wing length and mobility.

### Habitat Use

Within the sites, grid cells with long vegetation, shrubs, and nectar were more likely to be occupied by *P. tithonus*. This points to the combined importance of shelter and nectar supply and probably oviposition sites (Dover, 1997; Dover *et al.*, 1997). *M. jurtina* is less tightly associated with those structures but makes use of it when wind speed rises relatively high. Hedges with flowers are strongly preferred (Dover *et al.*, 1997). According to a study by Wynhoff (1992), the distribution of *M. jurtina* is determined by the presence of nectar plants. In our study, *M. jurtina* occupied only the sites with shelter more frequently than those without it, and there were only tendencies for the two other parameters. This suggests, similar to Dover *et al.* (1997), that *P. tithonus* is more tightly associated to those structures and resources than *M. jurtina*. The latter moved around more and used the habitat in a more extensive way compared to *P. tithonus*, which is less mobile and more restricted to the sites with long vegetation, shelter, and nectar.

### Distribution and Colonization Capacity

Regarding the intriguing observation that both species frequently cooccur, but that *P. tithonus* is also often lacking, our results indeed point to rather subtle differences in mobility and habitat use. Although both species are relatively widespread in Belgium, they mainly occur as small (meta)populations. In particular, due to the intensification of agriculture, flower-rich grasslands have become fragmented into tiny bits and pieces scattered in an intensively used landscape (Maes and Van Dyck, 2001). From our results we hypothesize that *P. tithonus* will traverse the same landscape at a slower rate than

*M. jurtina* because of its lower level of mobility and slightly higher need for shelter and nectar. Consequently, within a network or metapopulation context (which often applies for both species), it can be expected that patches remain vacant longer for *P. tithonus* than for *M. jurtina* (Thomas *et al.*, 1992). The type of the landscape matrix between patches can be of further differential importance between the species, but remains to be examined. It has recently been shown that *M. jurtina* does not move randomly when it is outside a habitat patch, but rather adopts a systematic searching behavior (Conradt *et al.*, 2000). It seems reasonable to assume that other localized butterflies behave in a similar way in this respect, but cues that are used and interactions with particular landscape features are likely to be rather species-specific. Moreover, there is also evidence that butterfly dispersal is not only a matter of nonrandom patterns, but also of a nonrandom sample of individuals (Hill *et al.*, 1999) going for a nonrandom walk. Similarly, we found *P. tithonus* females of recently founded populations to be of larger size and of higher wing loading than permanent populations.

### ACKNOWLEDGMENTS

We thank Dirk Maes (Institute of Nature Conservation), Erik Matthysen (University of Antwerp), and Johan Billen (University of Leuven) for their support during this study. Access to the study sites was kindly provided by Mr. Tramasure (TG) and the Flemish Ministry of Forestry (GZ). This research is funded by the University of Antwerp (GOA15R/3942). T. M. is research aspirant and H.V.D. postdoctoral fellow with the Fund of Scientific Research Flanders-Belgium (F.W.O.).

### REFERENCES

- Baguette, M., Petit, S., and Queva, F. (2000). Population spatial structure and migration of three butterfly species within the same habitat network: Consequences for conservation. *J. Appl. Ecol.* **37**: 100–108.
- Bink, F. A. (1992). *Ecologische atlas van de dagvlinders van Noordwest-Europa*, Schuyt & Co Uitgevers en Importeurs bv, Haarlem.
- Blest, A. D. (1957). The function of eyespot patterns in the Lepidoptera. *Behavior* **11**: 209–255.
- Brakefield, P. M. (1979). Spot-number in *Maniola jurtina*—variation between generations and selection in marginal populations. *Heredity* **42**: 259–266.
- Brakefield, P. M. (1982). Ecological studies on the butterfly *Maniola jurtina* in Britain. I. adult behavior, microdistribution and dispersal. *J. Anim. Ecol.* **51**: 713–726.
- Brakefield, P. M. (1984). The ecological genetics of quantitative characters of *Maniola jurtina* and other butterflies. In Vane-Wright, R. I., and Ackery, P. R. (eds.), *The Biology of Butterflies*, Princeton University Press, Princeton, New Jersey, pp. 167–190.

- Brakefield, P. M. (1987). Geographical variability in, and temperature effects on, the phenology of *Maniola jurtina* and *Pyronia tithonus* (Lepidoptera: Satyrinae) in England and Wales. *Ecol. Entomol.* **12**: 139–148.
- Brakefield, P. M., Shreeve, T. G., and Thomas, J. A. (1992). Avoidance, concealment and defence. In Dennis, R. L. H. (ed.), *The Ecology of Butterflies in Britain*, Oxford University Press, Oxford, pp. 93–119.
- Brooke, M., De Lees, D. R., and Lawman, J. M. (1985). Spot distribution in the meadow brown butterfly, *Maniola jurtina* L. (Lepidoptera: Satyridae): South Welsh populations. *Biol. J. Linn. Soc.* **24**: 337–348.
- Conradt, L., Bodsworth, E. J., Roper, T. J., and Thomas, C. D. (2000). Non-random dispersal in the butterfly *Maniola jurtina*: Implications for metapopulation models. *Proc. R. Soc. London (Biol.)* **267**: 1505–1510.
- Dover, J. W. (1989). A method for recording and transcribing observations of butterfly behavior. *Entomol. Gaz.* **40**: 95–100.
- Dover, J. W. (1996). Factors affecting the distribution of satyridae in arable farmland. *J. Appl. Ecol.* **33**: 723–734.
- Dover, J. W. (1997). Conservation headlands: Effects on butterfly distribution and behavior. *Agricult. Ecosys Environ* **63**: 31–49.
- Dover, J. W., Clarke, S. A., and Rew, L. (1992). Habitats and movement patterns of satyrid butterflies (Lepidoptera: Satyridae) on arable farmland. *Entomol. Gaz.* **43**: 29–44.
- Dover, J. W., Sparks, T. H., and Greatorex-Davies, J. N. (1997). The importance of shelter for butterflies in open landscapes. *J. Insect Conserv.* **1**: 89–97.
- Hill, J. K., Thomas, C. D., and Blakeley, D. S. (1999). Evolution of flight morphology in a butterfly that has recently expanded its geographic range. *Oecologia* **121**: 165–170.
- Maes, D., and Van Dyck, H. (1999). *Butterflies in Flanders (N-Belgium): Ecology, Distribution and Conservation*, Stichting Leefmilieu vzw/KBC, Instituut voor Natuurbehoud & Vlaamse Vlinderwerkgroep vzw, Antwerp/Brussels (in Dutch).
- Maes, D., and Van Dyck, H. (2001). Butterfly diversity loss in Flanders (N-Belgium): Europe's worst case scenario? *Biol. Conserv.* **99**: 263–276.
- McWhirter, K. G., and Creed, E. R. (1971). An analysis of spot placing in the meadow brown butterfly *Maniola jurtina*. In Creed, E. R. (ed.), *Ecological Genetics and Evolution: Essays in Honour of E. B. Ford*, Blackwell Scientific Publications, Oxford, pp. 275–289.
- Owen, D. F., and Smith, D. A. S. (1990). Interpopulation variation and selective predation in the meadow brown butterfly, *Maniola jurtina* (L.) (Lepidoptera: Satyridae) in the Canary Islands. *Biol. J. Linn. Soc.* **39**: 251–267.
- Owen, D. F., and Smith, D. A. S. (1993). Spot variation in *Maniola jurtina* (L.) (Lepidoptera: Satyridae) in southern Portugal and a comparison with the Canary Islands. *Biol. J. Linn. Soc.* **49**: 355–365.
- Pollard, E. (1981). Aspects of the ecology of the meadow brown butterfly *Maniola jurtina* (L.). *Entomol. Gaz.* **32**: 67–74.
- Pollard, E., and Yates, T. J. (1993). *Monitoring Butterflies for Ecology and Conservation*, Chapman & Hall, London.
- Porter, K., Steel, C. A., and Thomas, J. A. (1992). Butterflies and communities. In Dennis, R. L. H. (ed.), *The Ecology of Butterflies in Britain*, Oxford University Press, Oxford, pp. 139–177.
- SAS (1996). *Version 6.11*. SAS Institute Inc., Cary, North Carolina.
- Shreeve, T. G. (1990). The movements of butterflies. In Kudrna, O. (ed.), *Butterflies of Europe, Introduction to Lepidopterology*, Volume 2, Aula-Verlag, Wiesbaden, pp. 512–532.
- Shreeve, T. G. (1992). Adult Behavior. In Dennis, R. L. H. (ed.), *The Ecology of Butterflies in Britain*, Oxford University Press, Oxford, pp. 22–45.
- Shreeve, T. G., Dennis, R. L. H., and Williams, W. R. (1996). Uniformity of wing spotting of *Maniola jurtina* (L.) in relation to environmental heterogeneity (Lepidoptera: Satyrinae). *Nota lepid.* **18**: 77–92.
- Thomas, C. D., Thomas, J. A., and Warren, M. S. (1992). Distributions of occupied and vacant butterfly habitats in fragmented landscapes. *Oecologia* **92**: 563–567.

- Verbeke, G., and Molenberghs, G. (1997). *Linear Mixed Models in Practice: A SAS-Oriented Approach*, Springer-Verlag, New York.
- Warren, M. S. (1992). Butterfly populations. In Dennis, R. L. H. (ed.), *The Ecology of Butterflies in Britain*, Oxford University Press, Oxford, pp. 73–92.
- Wynhoff, I. (1992). Micro-distribution and flower preference of the Meadow brown (*Maniola jurtina*) and the Ringlet (*Aphantopus hyperantus*). In Pavlicek-van Beek, T., Ovaa, A. H., and Van der Made, J. G. (eds.), *Future of Butterflies in Europe: Strategies for Survival*, Agricultural University Wageningen, Wageningen, pp. 177–185.