10 RESOURCE USE BY THE MEADOW BROWN (*MANIOLA JURTINA*) AND THE GATEKEEPER (*PYRONIA TITHONUS*) ON ARABLE FARMLAND

10.1 Introduction

In this chapter we present data from a mark-release-recapture study and from behavioural observations designed to investigate how two butterfly species, *Maniola jurtina* and *Pyronia tithonus*, meet their resource requirements on arable ~~farm~~land. Both species are typical of grassland and hedgerow habitat and maintained sizable populations on the experimental field margins at Wytham. The experimentally manipulated arable field margins provided the ideal framework for quantifying resource use by the two species; the effects of sowing and the timing of mowing were expected to exert major and measurable influences on resource availability for these butterflies. We use the patterns of response of these species to the different experimental treatments as a basis for predicting the potential effects of different field margin management strategies on these and other butterfly species.

The persistence of plant or animal populations depends on the extent to which the individuals' resource requirements are met by the habitat. Butterflies have complex requirements because each stage of their life history needs different resources. These resources differ for each species in a butterfly community. The basic requirements for persistence of a population are first, that males and females can find each other and mate, second, that adult females can deposit their eggs in such a way that the larvae can find their host plants, and third that adults can find food in order to live long enough to perform the above activities. Thus Wiklund (1977) describes three functional habitat types which must be included in the area occupied by a given population; a "mating habitat", an "oviposition habitat" and a "foraging habitat". The mobility of the species determines the size of the area which must contain all of the three functional habitat types.

Habitat utilisation differs according to the nature of the habitat itself. Intensively managed farmland presents many constraints on butterfly populations. Arable farmland consists of a fragmented mosaic of habitats which are prone to seasonal and inter-annual trauma (Macdonald & Smith 1991). The result is an unpredictable and scarce supply of resources. Typically, the plant community is impoverished through herbicide and fertiliser applications (see Chapter 1) and remaining nectar sources may be removed completely by cutting. Insecticide drift (Jepson & Cilgi, unpublished) and mechanical damage (Thomas 1984) contribute an additional unpredictable element in the probability of survival on arable field margins.

The distribution of adult and larval nutritional resources (Wiklund's 'foraging' habitat) is probably the major factor controlling the structure of non-migrating butterfly populations in both temperate and tropical areas (Ehrlich 1984). Both of these resources could be readily manipulated within the constraints of agricultural practices. Although the nutritional requirements of larvae tend to be more specific than those of the adults of most temperate species, they are often more readily available. In some habitats, and in particularly intensively managed arable farmland, suitable nectar sources may be at least as scarce as larval foodplants.

Since most adult butterflies must feed in order to survive, the availability of appropriate nectar sources is an essential requirement for butterfly populations. Nectar composition is an important factor in the biology of many Lepidoptera. Sugars in the diet have long been recognised to influence the fecundity and longevity of some butterfly species (Stern & Smith 1960, Murphy *et al* 1983, Hill 1989, Hill & Pierce 1989). Effects on longevity are particularly important for temperate species where unsuitable weather conditions may limit an individual's potential for mating and oviposition. Furthermore, butterflies are able to discriminate between sugar components in nectar, preferring sucrose and fructose over glucose (Watt *et al* 1974; Erhardt 1991, 1992), and compensation for sugar deficient diets by increasing intake has been found for *Pieris brassicae* (David & Gardiner 1961) and *Euploea corinna* (Hill 1989). The role of amino acids in the adult diet is less clear. They have been shown to increase fecundity in some long-lived pollen-feeding butterflies (Gilbert 1972, Dunlap-Pianka *et al* 1977) but to have no effect in short-lived nectar feeders (Murphy *et al* 1983) which may have accumulated sufficient nitrogenous reserves during the larval stage. However, even the most conservative view is that adult feeding is necessary for most butterflies to replenish energy reserves during the flight period. Nectar quality can therefore be considered to have two effects, influencing directly female reproductive potential, and indirectly influencing the proportion of an individual's time that must be devoted to feeding. Thus quality and quantity of nectar sources are likely to be important limiting factors determining population size even for the most generalist species. When nectar is in short supply, there is evidence that dispersal, especially of females, increases (Ehrlich *et al* 1980). In this chapter we examine the extent to which different parts of the field boundary and different sward types were utilised for foraging and the relationship between management and the availability of suitable nectar resources.

Mating habitat may also be a limiting resource for a population. Mate location strategies in butterflies are dominated by two types of behaviour, perching and patrolling (Scott 1974). Patrolling males fly continuously in search of females but perching males take up stations and fly out to investigate passing butterflies, or even similar shapes. In a perching species, such as *Euphydryas editha*, characteristic perching sites may be a key resource for the population (Ehrlich 1984). Some species use a combination of both strategies (Dennis 1982) and it is possible that species may vary their strategies according to the habitat characteristics. For *M. jurtina* and *P. tithonus* in an agricultural habitat, we measured the extent of perching behaviour to assess whether the availability of perching sites was likely to be a habitat requirement for either species.

Suitable oviposition habitat is the third resource requirement for butterfly populations. The larvae of *M. jurtina* and *P. tithonus* species are grass feeders, but the extent to which the adults utilize different grass species for oviposition is not known. There are some discrepancies in reports of ovipositing habitat for *M. jurtina*; Baker (1978) reported that eggs were laid close to the ground amongst short turf but Brakefield (1982) disputes that this is a favoured oviposition habitat. In his studies of *M. jurtina* in three relatively undisturbed habitats near Liverpool he found that females preferred areas of fine-leaved grasses for laying their eggs and that the larvae were restricted to such areas. Reports of

P. tithonus oviposition sites are anecdotal. We therefore aimed to elucidate these important aspects of the ecology of *M. jurtina* and *P. tithonus* in the arable ecosystem.

There is widespread evidence that behaviour of male and female butterflies, including *M. jurtina* and *P. tithonus*, differs (Brakefield 1982; Dover 1989a) and that utilisation of habitat by the sexes can differ accordingly (Wiklund and Ahberg 1978). Many species of butterfly exhibit a male-female time lag in emergence known as protandry, where males may emerge up to several weeks before the females. A population in which the sex ratio changes as it ages could therefore shift its pattern of habitat utilisation through the course of the flight period. If resources such as nectar are more important for one sex than the other, there are implications for the timing of resource provision through management. We therefore examined sex-related differences in resource requirements and the implications of changes in the sex ratio during the season.

The accessibility of usable habitat to butterflies is determined by their mobility. A highly mobile species such as *Inachis io,* the peacock alternates cross-country migration with bouts of feeding, oviposition, territoriality and basking (Baker 1972, 1978). If resources are spatially separate rather than overlapping, the butterfly has to fly between them. For example, adult *Leptidia sinapsis* wood white in Sweden utilize woodland flowers for nectar and oviposit in adjacent meadows, even though they are weak fliers (Wiklund 1977). The unpredictable and patchy nature of resources on arable farmland may result in under-utilisation of the habitat by less mobile species, simply because they cannot move in response to changing resource distributions. Thomas (1984) concludes that only about 15% of British butterflies are highly mobile with open or migratory populations, while the remainder are relatively sedentary, needing minimum breeding areas of 0.5-50 hectares, depending on the species. In the discussion of this chapter we consider the implications of farmland habitat management for conserving butterflies of differing mobilities.

10.2 Results

In this section we describe first, analyses of the mark-release-recapture data together with those of the behavioural activities observed at the time of capture and, second, the detailed behavioural observations made on individual butterflies (see Chapter 2.2.5.3). The mark-release-recapture data are used to examine the distribution of butterflies between the different zones of the field boundary and between the different experimental treatments on the field margins. They are then used to examine the distances moved by the butterflies and the ways in which treatments were used differentially for different types of activities and by the two sexes. Finally they are used in conjunction with data on the abundances of potential nectar sources to examine foraging preferences amongst the plant species available on the field margins. The detailed behavioural observations provide additional and more direct information activity budgets of male and female butterflies, including data on display in males and oviposition in females.

10.2.1 THE MARK-RELEASE-RECAPTURE STUDY

During the sampling period 656 *M. jurtina* individuals were captured and marked. 57% (377) of these were female and 43% (279) were male, giving a significant departure from an expected sex ratio of unity ($X^2_{(1)}=12.785$, $P=0.003$). 154 butterflies were recaptured once, 49 were recaptured twice, 20 a third time, 12 a fourth time and seven a fifth time. One individual was captured on eight occasions. 84 (54.5%) butterflies recaptured were female and 70 (45.5) recaptures were male. There was no significant difference in the probability of recapturing males and females ($X^2_{(3)}=0.538$, $P=0.4633$). During the *P. tithonus* sampling period, 785 individuals of *P. tithonus* were marked. Of these, 282 were recaptured at least once, 82 were recaptured twice, 22 were recaptured a third time, and four butterflies were recaptured on a fourth occasion. Of the 785 marked individuals 400 (51%) were female and 385 (49%) were male ($X^2_{(1)}=0.287$, $P=0.59$) and of the recaptured individuals, 150 (53.2%) were female and 132 (46.8%) were male. The relative proportions of recaptured males and females did not differ significantly from that of marked butterflies ($X^2_{(1)}=0.599$, $P=0.4388$), in contrast to the results from several studies of other species (Ehrlich 1965; Watt *et al* 1977, 1979).

The distribution of butterflies on the field margins

Distribution between habitat zones Table 10.1 shows that of the 656 marked *M. jurtina*, the largest percentage, 80.8% (530), was captured in the field margin zone (as opposed to the boundary feature, sterile strip or crop, see Chapter 2.2.5.3). *P. tithonus* showed a similarly close association with the field margin zone, with 76.6% (601) butterflies captured there. *P. tithonus* utilised ditches to a greater extent than *M. jurtina*, with just over 17% of butterflies being captured there compared with 6.6% for *M. jurtina*. In contrast, the sterile strip and the crop accounted for less than 2% of captures of *P. tithonus* but over 10% of *M. jurtina* were found in these two zones. The differences between zones in the numbers of captures was highly significant for both *M. jurtina* and *P. tithonus* ($X^2_{(6)}=1164.26$ and 1332.9 respectively, $P<0.001$). This resulted from the high numbers associated with the field margin, relative to its availability, and correspondingly low numbers associated with the other zones, in particular the crops, sterile strips and tracks.

Distribution between experimental treatments *M. jurtina* showed an aggregated microdistribution on the field margins, with heavy concentrations of captures occurring on particular treatments. Analysis of variance of mean total numbers caught on each treatment, excluding those caught on associated features, was highly significant ($P<0.001$; Table 10.2). A three-way analysis of variance showed that cutting had a highly significant effect on butterfly distribution ($P<0.001$). The effect of sowing on the distribution of butterflies was not quite significant ($P=0.055$), but butterfly numbers were higher on sown than on unsown swards. Mean numbers of butterflies were significantly higher on treatments that were not cut in the summer (spring and autumn cut or uncut) than on those that were cut in the summer ($P<0.001$). Spring and autumn cut treatments did not differ significantly from treatments which remained uncut. Planned comparisons showed that numbers of butterflies on sprayed treatments were not significantly different from those on either cut or uncut treatments.

The experimental treatments also had a significant overall effect on the distribution of captures of *P. tithonus* ($P<0.05$, Table 10.3). As with *M. jurtina*, some treatments attracted greater numbers of *P. tithonus* than others and the pattern of preference was similar. Cutting had a highly significant effect ($P<0.001$) with higher mean numbers of butterflies captured on swards which were not cut in summer ($P<0.001$). There was no significant difference between sown and unsown swards, and in contrast to *M. jurtina*, the unsown, uncut swards had higher mean numbers of butterflies than sown uncut swards. Again, the numbers of butterflies on sprayed plots did not differ significantly from those on either cut or uncut plots.

Probability of remaining on treatment type of first capture

Marked individuals were classified according to the combination of their capture locations on their first and subsequent capture to test whether they showed a tendency to remain on the same treatment type, regardless of whether or not it was the same plot. In order to increase sample size treatments were grouped in the following categories: sown and not cut in summer, sown and cut in summer, not sown and not cut in summer, not sown and cut in summer.

A chi-squared analysis was performed on the data. For each initial capture category, the subsequent distribution on recapture was tested. Table 10.4 shows that, for *M. jurtina*, a second capture distribution for individuals initially captured on either sown, uncut treatments or on unsown, uncut treatments was significantly different from the expected random distribution ($\chi^2_{(3)}=33.85$, $P<0.001$ and $\chi^2_{(3)}=18.03$, $P<0.001$ respectively). By contrast, when initial capture was on sown and cut treatments the distribution of following captures was not significantly different from random ($\chi^2_{(1)}=3.267$, $P=0.07$ and $\chi^2_{(1)}=0.6$, $P=0.44$ respectively when grouped as shown). Similarly, when initial capture was on unsown, treatments which were cut in summer the distribution of following captures was also not significantly different from random ($\chi^2_{(1)}=0.059$, $P=0.81$ and $\chi^2_{(1)}=0.529$, $P=0.47$ respectively when grouped as shown). The results indicate that having been captured on an uncut treatment, whether sown or unsown, there was a high probability that an individual would be recaptured on a similar treatment. There was no evidence that butterflies first captured on cut treatments showed any tendency to remain on those treatment types; however, the sample sizes of the captures on these treatment groups were much smaller, and the possibility cannot be ruled out that, had the samples been larger, a pattern similar to that on the uncut treatments would emerge.

P. tithonus showed a similar pattern of behaviour (Table 10.5). The distribution on recapture for each initial capture category was again tested using a chi-squared analysis. The second capture distribution for individuals initially captured on sown, uncut treatments was significantly different from the expected distribution ($\chi^2_{(3)} = 26.31$, $P<0.001$) and also for those captured first on unsown, uncut treatments ($\chi^2_{(3)} = 60.4$, $P<0.001$). The magnitude of the χ^2 value was in both cases due to a tendency of butterflies to remain on the same treatment type and, in contrast to *M. jurtina*, was highest for the unsown, rather than sown, swards. When initial capture was on unsown, cut treatments the subsequent capture distribution was again significantly different from an expected random distribution ($\chi^2_{(3)}= 11.66$, $P<0.01$), but in this case the magnitude of χ^2 was largely due to the movement of butterflies away from the unsown, cut treatments on to unsown, uncut ones. When butterflies were first caught on sown, cut treatments the second capture distribution was not significantly different from random ($\chi^2_{(1)}$= 0.053, P=0.819 and $\chi^2_{(1)}$ = 0.053, P=0.44 respectively when grouped as shown) but, again, the small sample size makes this result inconclusive.

The data for both species were re-analysed after removing from the sample those butterflies which remained on the same treatment type and the same plot. This tested for any biases due to butterflies having a tendency to remain on a plot, irrespective of treatment type. Although some of the resulting sample sizes were too small to be amenable to chi-squared analysis, even when treatment types were grouped, the trends were very similar to those from the above analyses. The results are shown in Tables 10.6 and 10.7.

Distances between capture locations

The shortest line distances between the locations of consecutive captures of butterflies were determined by assigning co-ordinates to each treatment in each block. A distance of zero metres indicated that a butterfly was recaptured on the same treatment in the same block as its previous capture. Other distances represented capture locations on different treatments and/or blocks.

Over 80% of *P. tithonus* were recaptured within 150m of their previous capture and over 70% of *M. jurtina* were recaptured within 200m of their previous capture (Table 10.8). Analyses of distances between capture locations for *M. jurtina* where the time interval between captures was one, two, or three days are shown in Table 10.9. Where there was a one day interval between captures, analysis of the sample showed the mean distance travelled between captures was 186.19m (S.E.=36.9) for female *M. jurtina* and 148.1m (S.E.=29.5) for males. This did not represent a significant difference in dispersal distances between males and females (Wilcoxon 2-sample Test, Z=0.055, P=0.956). Mean distances travelled by *P. tithonus* between captures of a one day interval were less than *M. jurtina* (Table 10.9); females travelled a mean of 89.76m (S.E.=16.8) and males travelled a mean of 109.03m (S.E.=25.2). Again, there was no evidence of a difference in dispersal distances between the sexes (Wilcoxon 2-sample Test, Z=0.817, P=0.414). There was little increase in the distances between captures when there was a longer interval between captures (Table 10.9).

The between-capture distances were different between the two species (Table 10.9). The distances recorded between subsequent captures of one, two, or three day intervals were significantly greater for *M. jurtina* than *P. tithonus*. For example, of the sample of individuals which had a one day interval between captures, *P. tithonus* were located a mean of 96.74m (S.E.=14.23) from their initial point of capture and *M. jurtina* were located a mean of 168.6m (S.E.=24.33) from the initial capture location. This represented a significant difference in dispersal distances between *M. jurtina* and *P. tithonus* (Wilcoxon 2-sample Test, Z=2.70, P=0.007).

The effects of experimental treatment and of sex on activity patterns

M. jurtina and *P. tithonus* individuals were classified according to their activity at time of capture, and the percentages of butterflies engaged in each activity on each treatment were calculated (Table 10.10, Figures 10.1 and 10.2). The results showed that behaviour of individuals of both species differed according to their sex and the treatment on which they were located.

Analysis of resting activity of *M. jurtina* showed that, of the butterflies present on each treatment type, a significantly greater proportion of butterflies was resting on some treatments than others ($F_{(9,1)}=6.01$, $P<0.01$; Table 10.11). However, the numbers of butterflies resting when captured did not differ significantly between the treatments (Table 10.12). Treatments cut in the summer were utilised for resting more than those cut in spring and autumn or left uncut (planned comparisons). Unsown swards also had a higher percentage of resting butterflies than sown swards. Females rested significantly more than males ($F_{(9,1)}=7.73$, $P<0.05$).

The treatments did not differ significantly in the proportion of butterflies which were flying when captured ($F_{(9,1)}=1.62$, $P=0.2415$), but males flew significantly more than females ($F_{(9,1)}=14.27$, $P=0.0044$).

The number of butterflies feeding when captured showed a highly significant difference between treatments ($F_{(9,1)}=17.38$, $P<0.001$) (Table 10.13). Butterflies fed significantly more on the uncut treatments than on those cut in the summer ($P<0.001$). Sown swards were utilised for feeding more than unsown swards ($P<0.05$). The rank order of the treatment means is almost exactly the reverse of that for resting activity (Table 10.11, above). Females fed significantly more than males ($F_{(9,1)}=12.67$, $P<0.01$).

Over all treatments, 35% of captured females were resting, 24% were flying and 40% were feeding. 1% were interacting with other butterflies. Males spent less time resting and feeding (25% and 31% respectively) but more time flying and interacting with other butterflies (38% and 7% respectively).

In contrast to *M. jurtina*, the proportion of *P. tithonus* resting did not differ significantly between treatments ($P=0.113$). The percentage of butterflies flying when captured was also unaffected by treatment ($P=0.066$). As in *M. jurtina*, female *P. tithonus* rested significantly more than males ($P<0.001$) and males flew significantly more than females ($F_{(9,1)}=126.17$, $P<0.001$).

The difference between treatments in the proportion of butterflies feeding when captured was not quite significant ($P=0.051$, Table 10.14). However, the treatments which were left uncut, or cut in spring and autumn were utilised more for feeding than any other treatments. Treatments cut in the summer had lower mean percentages of butterflies engaged in feeding. In contrast to the results for *M. jurtina*, which preferred sown swards for feeding, sowing had no significant effect on *P. tithonus*, and numbers feeding on unsown swards were higher than those on sown swards. Females fed significantly more than males ($P=0.001$).

P. tithonus, like *M. jurtina*, showed an overall difference in activities according to sex. Over all treatments 37% of females captured were resting, 26% flying and 36% feeding. Thus resting and feeding were equally important activities for females. Only one quarter were flying. In contrast, 20% of males were captured were resting, 48% were flying and 20% feeding. Thus flying was the most frequent activity. Resting and feeding were equally important activities but less frequent than for females.

Nectar source preferences

The frequencies with which different plant species were utilised as nectar sources by *M. jurtina* and *P. tithonus* were calculated for all butterflies which were feeding when captured (Table 10.15).

A range of flowers was utilised as nectar sources in the study area. Members of the Compositae were particularly heavily utilised for nectar by both species. Of the plants in the wild flower seed mixture *Leucanthemum vulgare*, *Knautia arvensis* and *Centaurea nigra* and *Centaurea scabiosa* were the most popular nectar sources, but *Cirsium arvense*, *Cirsium vulgare* and *Carduus acanthoides* together were the plants most frequented for nectar. *P. tithonus* was associated with hedge and ditch species such as *Rubus* spp. and *Pulicaria dysenterica* (L.) Bernh. common fleabane to a greater extent than *M. jurtina*. The number of plant species recorded as nectar sources was similar for both species. Although females of both species fed more than males, we were unable to detect any significant differences in the plant species utilised as nectar sources by the two sexes in either species. However, because of the differences in flight periods of males and females within each species, and thus the different availability of nectar sources for each sex, the comparable samples available were too small for statistical testing of this hypothesis.

The frequency of nectar source use was analyzed together with data on the abundance of potential nectar sources (see Chapter 2.2.5.1). In July and August a maximum of 99 species was recorded as being in flower on the field margins. Only 15 of these species (or groups of species where appropriate) were recorded as nectar sources for *M. jurtina* and *P. tithonus* (Table 10.15 above). The butterflies were never observed feeding on a number of highly abundant species, such as *Galium aparine*, *Myosotis arvensis* (L.) Hill Field Forget-me-not, and *Geranium dissectum*. There was thus active discrimination against some plant species.

The butterflies also exhibited distinct preferences amongst the species that were utilised for foraging. We compared the actual number of visits to the plant species with the numbers expected on the basis of their relative abundance within the sub-set of utilised species. Where species were grouped for analysis (for example the Umbelliferae) the abundances of all the species in the group were totalled for the analysis. Chi-square goodness-of-fit tests were performed on the data for both *M. jurtina* and *P. tithonus* (Table 10.15). The results showed that, of the 15 species or groups of species which were utilised for nectar, some were preferred greatly over others. In particular, *M. jurtina* showed strong preferences for *Centaurea* spp., *Cirsium* and *Carduus* spp., and *K. arvensis*. *P. tithonus* preferred *Cirsium* and *Carduus* spp. and *P. dysenterica*; both butterfly species fed on these species significantly more than would be expected from their relative abundance in the study area.

Sex ratios and wing wear through the flight season

M. jurtina was the earlier of the two species and was first recorded on 2 July in 1991. Males reached their peak numbers on 10 July 1991 (61 males were caught and marked on this date) but females did not reach peak numbers until 2 August when 64 females were marked. The last female was marked on 22 August and the last male butterfly to be marked was caught on 20 August (Figure 10.3).

P. tithonus was not recorded until 22 July in 1991. One female and 14 males were marked on this date. Males rapidly reached a peak in numbers by 26 and 29 July. In contrast, but displaying a similar pattern to *M. jurtina*, female *P. tithonus* reached a peak on 8 August when 52 individual females were marked. Females were still being marked by 2 September but the last male was marked on 28 August (Figure 10.4).

The sex ratios and wing wear rating of males and females of *M. jurtina* and *P. tithonus* are shown in relation to progress of the flight season in Table 10.16. In both species the sex ratio shifted from a preponderance of males early in the flight season to one of females later in the season. This shift was relatively rapid; between 16 July and 5 August the composition of *M. jurtina* captures changed from 26% to 88% females. *P. tithonus* showed a similar pattern of emergence and there were only two weeks (from 5-11 August and from 26 August-2 September) when there was no significant difference in the number of males and females captured ($P>0.05$). The average wing wear rating increased progressively through the flight season: wing wear in females lagged behind that in males, as would be expected from their delayed eclosion. At the end of the season females were in better condition than males.

Because of the sampling intensity and the high recapture rate, butterflies with a wing wear rating of 4 or more on first capture were likely to be immigrants. The frequency of captures in each wing wear category for *M. jurtina* and *P. tithonus* are shown in Table 10.17. A number of first time captures, particularly of *M. jurtina*, were not in good condition, suggesting that there was a moderate level of immigration into the population.

10.2.2 BEHAVIOURAL OBSERVATIONS

Detailed behavioural observations were made on a small sample of 64 (27 female and 37 male) *M. jurtina* and 24 (14 female and 10 male) *P. tithonus* individuals (Chapter 2.2.5.3). The mean observation lengths were 14.6 minutes for female *M. jurtina* and 10 minutes for males, and 27 minutes for female *P. tithonus* and 3.9 minutes for males. Observations were made at different times of day and under different weather conditions although the same criteria were followed for the conditions under which transects were recorded.

Activity patterns

The total amounts of time spent engaged in each of five behaviour categories were analyzed separately for male and female butterflies. Of a total of 396 minutes of observation of female *M. jurtina*, 178 minutes (44%) were spent feeding, 19 minutes

(4.8%) flying, 139 minutes (35%) resting with the wings closed, 54 minutes (13%) basking and 5.3 minutes (1.3%) ovipositing. The corresponding figures for male behaviour, derived from a dataset consisting of 370 minutes of observation, were 127 minutes (34.47%) feeding, 101 minutes (27.3%) flying, 87 minutes (23.5%) resting with closed wings and 54 minutes (14.7%) basking (Table 10.18).

Table 10.18 also shows equivalent data for *P. tithonus*. Observations totalled 387 minutes for female *P. tithonus*. Of these, 191 minutes (49.3%) were spent feeding, 26 minutes (6.8%) flying, 111 minutes (28.5%) resting with the wings closed, 46 minutes (12%) basking, and 13 minutes (3.4%) ovipositing. Male *P. tithonus* were observed for a total of 39 minutes of which 17 minutes (44.3%) were spent feeding, 18 minutes (46.2%) flying, 24 seconds (1%) resting with the wings closed and 3.3 minutes (8.5%) basking (Table 10.18).

Basking behaviour in *M. jurtina* and *P. tithonus*

Comparison of the time spent resting with wings closed and with them open (basking) showed a greater tendency towards basking behaviour in males than in females in both *M. jurtina* and *P. tithonus*. This result was much more pronounced in *P. tithonus*. In female *P. tithonus*, of the time spent resting, 70.4% was with the wings closed and only 8.4% basking with the wings open. In contrast, males basked for 89.9% of their resting time and only spent 10.71% of the time with the wings closed.

Basking by male butterflies frequently occurred on prominent vegetational structures, such as flower heads or hedges, while resting with the wings closed tended to occur predominantly at ground level amongst low vegetation, particularly on grasses. Females showed a smaller tendency to bask in prominent positions.

Resting or basking periods varied considerably in length from a few seconds to many minutes. If weather conditions became unfavourable, butterflies would cease activity. *P. tithonus* females rested with their wings closed for significantly longer periods than males (P=0.031; Table 10.19). They also basked for longer periods but this was not significant (P=0.074). *M. jurtina* females also rested and basked for longer periods than males, but neither result was significant (Table 10.19).

Nectar source use

M. jurtina was recorded feeding on nine species or groups of species (Table 10.20). The most frequently utilised nectar sources were *L. vulgare*, *Cirsium* and *Carduus* spp., *Centaurea* spp., and *K. arvensis*. *P. tithonus* individuals were recorded feeding on seven species or groups of species; six of these were also recorded for *M. jurtina* (Table 10.20). In addition, *P. dysenterica* was frequently utilised by *P. tithonus*. These results were similar to those from the mark-recapture data.

The lengths of time which butterflies spent feeding on individual flowers were analyzed for *M. jurtina* and *P. tithonus*. Mean feeding bout lengths differed according to the sex of the butterfly, but not the plant species on which the butterfly was feeding. Female *M. jurtina* individuals fed for significantly longer periods at each flower than males

(P=0.0095; Table 10.21). The plant species on which the butterfly was feeding had an effect on feeding bout length which approached significance (P=0.0696), with butterflies feeding for the longest periods on *Cirsium* and *Carduus* spp. and *Centaurea* spp., followed by *Tripleurospermum inodorum* (L.) Schultz Bip. Scentless Mayweed, *K. arvensis* and *L. vulgare*. There was no significant interaction between sex and plant species (P>0.05).

Females of *P. tithonus* also fed for longer periods than males at any one flower, but this was not significant (P=0.3345: Table 10.22). There was no significant difference in feeding bout length according to plant species (P=0.2808), although most time was spent on *Centaurea* species.

Oviposition

Oviposition by *M. jurtina* females was observed on 24 occasions. Oviposition occurred on a variety of treatment types and a variety of substrates. Although the sample was not large enough to allow statistical analysis of preferences, sown treatments were utilised for oviposition more than unsown treatments, and treatments which had been cut in the summer were also used more frequently those left uncut. The substrates on which eggs were laid varied greatly. On three occasions, eggs were laid on clods of earth on the recently rotovated sterile strips alongside the managed margins. All other eggs were laid on the margins but in a variety of sward types. Areas of predominantly *Festuca rubra*, *Trisetum flavescens* and *Phleum pratense* subsp *bertolonii* were used most frequently, but often the grass was very dry or even dead. Eggs which were laid on unsown treatments were in swards dominated by *Bromus sterilis*.

P. tithonus females were observed ovipositing on 26 occasions. Again, a variety of treatment types and substrates was used. There was no apparent preference for cut or uncut treatments or sown or unsown treatments although the sample size was very small. Eggs were laid in swards containing *Trisetum flavescens*, *Festuca rubra*, *Bromus sterilis*, *Poa* spp. and *Elymus repens*. Eggs were not necessarily laid in full sunlight; on two occasions eggs were laid in half-shade.

Oviposition was generally during the hottest period of the day. Neither species was observed to oviposit before midday, or after 4pm. Oviposition was usually interspersed with short periods of rest. Females tended to spend the mornings feeding, before oviposition took place.

10.3 Discussion

10.3.1 CONCLUSIONS

Of the habitat zones sampled during the study, significantly more butterflies were captured on the field margin than on any other zone. All of the experimental margins were extended in width, and had a permanent grassy sward from which pesticides and fertilisers were excluded. Although sward-types resulting from some management regimes were preferred over others, all margins were utilised to some extent by both species, indicating their importance as a habitat component on farmland. *P. tithonus* utilised hedges and ditches to a greater extent than *M. jurtina*, which is consistent with their associations with hedgerow and grassland habitats respectively, documented by other authors (e.g. Brakefield 1982, Pollard 1981).

The flight season of both *M. jurtina* and *P. tithonus* in 1991 occurred between the summer and autumn cuts. Half of the treatments had been cut in the week prior to the emergence of *M. jurtina* and so the timing of the 1991 flight period coincided with particularly distinct differences in vegetation structure and composition between some experimental treatments. Consequently, patterns of butterfly distribution were clearly associated with the treatments, and some treatments attracted particularly large aggregations of individuals. The independent estimates of the distributions of *M. jurtina* and *P. tithonus* recorded from the mark-recapture study and from the transect counts (Chapter 9) gave very similar results. However, because records were made much more frequently during the mark-recapture study, some butterfly aggregations around, for example, temporary nectar sources, may have been exaggerated. Dover (unpublished data), for example, found that a single marjoram bush attracted large numbers of *P. tithonus* during the short period in which it was in flower. Such factors may have resulted in recorded butterfly abundances which do not reflect accurately the relative utilisation of the habitats. In the present study, mean abundance of butterflies recorded on the sprayed treatments was higher than was suggested by the transect counts. Close examination of the data showed this to be largely attributable to a short period in late July for which there was no transect count but when there was intense foraging activity on *Cirsium arvensis* flowering on two sprayed plots.

Several factors may have accounted for the responses of *M. jurtina* and *P. tithonus* to the experimental treatments. The treatments with the highest mean number of butterflies were left uncut in the summer; they were either cut in the spring and autumn or received no cutting management at all. These treatments differed from others both in terms of their vegetation height and structure, and in the abundance of nectar sources. *M. jurtina* numbers were higher on sown swards during the study, although not significantly so. *P. tithonus* had a later flight period than *M. jurtina*. Since nectar availability differed with month on the experimental margins (Feber 1993), it was therefore different for the two species. *Leucanthemum vulgare*, the dominant species on the sown swards, flowered early and was the principal nectar source for *M. jurtina* in July. *Cirsium* spp. and *Carduus acanthoides* L. Welted Thistle, by contrast, were heavily utilised as nectar sources by *P. tithonus*; they were less well utilised by *M. jurtina* because the main flowering period did not coincide with the peak flight period of this species. Analyses of data from behavioural observations indicated that later-flying individuals of *M. jurtina*, which had equal access to *Cirsium* spp. and *Carduus acanthoides*, utilised them for nectar to the same extent as *P. tithonus*. Of the plants in the wild flower seed mixture which were utilised for nectar, *L. vulgare*, *Knautia arvensis*, and *Centaurea nigra* and *C. scabiosa* were the most important. *L. vulgare* tended to dominate the sown treatments when it was in flower and was heavily utilised by earlier butterfly species, including *M. jurtina*, although it was not used for foraging at all by some other nectar-feeding insects, including bumblebees (N. Saville, pers. comm.).

Although a range of plants was utilised for foraging, our analyses indicated that both butterfly species were selecting only a limited number of the plant species available on the field margins and of these some were preferred greatly over others. Studies of other nectar-feeding species (e.g. Douwes 1975; Wiklund 1977; Wiklund & Ahberg 1978) and also of *M. jurtina* (Pollard 1981) have shown similar selectivity. Close associations with one or two nectar source plants are well documented for some tropical butterflies (Ehrlich and Gilbert 1973), but not for species of the temperate zones where butterfly emergence and flowering times are weather dependent and frequently not synchronized.

Almost all the plant species utilized for nectar were perennials, although a large number of annuals were also present on the field margins (Chapter 3). Bazzaz (1979) suggests that nectar secretion rates in annuals tend to be low because they are characteristic of early successional stages and have high photosynthetic rates but no accumulated reserves; their daily expenditure of assimilate scarcely exceeds income, and nectar secretion rates are relatively low (Parrish & Bazzaz 1979). In contrast, perennials tend to allocate more biomass to roots, and a positive correlation between root mass and nectar secretion rate has been demonstrated in *Asclepias quadrifolia* (Pleasants & Chaplin 1983). Fussell & Corbet (1991, 1992) showed that perennials are preferred by foraging bumblebees and suggest that they provide high nectar rewards. Although butterflies have lower energy requirements than bumblebees, they would be expected to benefit from this characteristic, making flower-rich, perennial swards desirable foraging areas. On the 2m margins, mowing, sowing and spraying all had significant effects on the annual and perennial components flowering in the sward (Feber 1993). In general, sowing significantly increased the abundance of perennial species in flower while spraying increased the abundance of annual species in flower. Sown plots which were not mown in the summer also had the highest abundances of flowers of nectar sources which were heavily utilised by *M. jurtina* and *P. tithonus*, such as *Centaurea* spp. and *K. arvensis*. Although Dover *et al* (1990) showed that butterfly abundance was higher on conservation headlands recommended by the Game Conservancy's Cereals and Game Birds project than on conventionally managed headlands, our data suggest that the increase in nectar abundance from the predominantly annual flora in selectively sprayed headlands is likely to have a very much smaller impact on butterfly abundance than the provision of permanent perennial swards on the field margin.

M. jurtina and *P. tithonus* both exhibited different behaviour patterns according their sex and the treatment on which they were found. Females of both species spent a greater proportion of their time resting and feeding than males, and spent less time flying. *M. jurtina* females fed for longer periods at flowers than males, implying a greater intake of nectar or a slower rate of feeding. Sexual dimorphism in feeding rates has been demonstrated for several butterfly species (May 1985; Boggs 1988), although the reasons for such a dimorphism are not known.

Behaviour patterns differed between treatments. Treatments were utilised differently by the two sexes and there was some evidence of spatial separation of habitat for feeding and resting. In *M. jurtina*, more of the individuals encountered on treatments which were cut in the summer than on those left uncut were resting. This pattern could have resulted either from lack of opportunity for feeding on these treatments, or from butterflies preferring to rest on the short turf of the cut treatments because it had a more favourable microclimate for thermoregulation. Although the absolute numbers of butterflies found resting on cut treatments were not significantly greater than on uncut treatments, is still nevertheless possible that they actively preferred the former for resting. It might be expected that, even if butterflies show some tendency to seek short turf for resting following feeding bouts, numbers resting in the best feeding areas may still be high. Undoubtedly, turf height has a major impact on the microclimate at ground level. Thomas (1983a) demonstrated that a 4cm reduction in turf height can increase the temperature at ground level in chalk grassland by 5 °C during the spring larval growing period. However, further data are required to ascertain whether a real preference is exhibited for short turf for resting. The energetic trade-off between possible benefits from resting on short turf and the cost of travelling from feeding sites to find short-turf must depend on the relative disposition of these two resources in a given situation.

M. jurtina fed significantly more on uncut treatments, except for the sprayed treatment where there were no observations of either sex feeding during the study. The sprayed treatment had a greater proportion of flowers of annual species than the other uncut treatments, and the main perennial nectar source on this treatment was *C. vulgare* which was not in flower when *M. jurtina* was on the wing. Flying was equally frequent on all treatments for both *M. jurtina* and *P. tithonus*, but a distinction was not made in the present study between the slow, exploratory flight typical of mate-location, and the characteristic fast, directional flight of a butterfly over unsuitable habitat.

Since activities of both species varied according to sex as well as treatment, utilisation of the treatments may also have varied during the flight season. As the composition of the population changed from being predominantly male to predominantly female, feeding was likely to become an increasingly important activity. The data suggested a trend towards heavier utilisation of flower-rich treatments in the second half of the flight season, although this was not statistically significant. The numbers of males were also higher on flower-rich treatments throughout the flight period. Although foraging was less important for males, such areas would present the highest probability of female encounters and successful matings. Studies have suggested that mate location behaviour in *P. tithonus* is characteristic of "perching" species. It commonly rests on hedgerows or tall vegetation, with wings open displaying the brand of androconial scales on the forewings (Emmet and Heath 1990). The data from our behavioural observations confirmed that this behaviour also occurs on the field margins. Basking in both sexes plays an essential thermoregulatory role. A butterfly is able to regulate its body temperature by positioning itself and its wings with respect to the sun (Clench 1966, Findlay *et al* 1983), and it is the basal regions of the wings which play the important role in thermoregulation by absorbing or reflecting radiation efficiently (Wasserthal 1975, Douglas 1979). However, the frequency of basking behaviour as opposed to resting with the wings closed was not the same for females and males, suggesting an additional function in males related to sexual communication. Basking, particularly in *P. tithonus* males, frequently occurred on prominent vegetation, and the requirement for such structural features of the habitat may further explain the association of this species with the uncut treatments. Some species, such as *Lasiommata megera*, use a combination of both perching and patrolling mate location strategies (Dennis 1982). Our data on *M. jurtina*, for which male basking was a less pronounced activity than for *P. tithonus*, suggest that it falls within this category.

Minor discrepancies in the activity pattern recorded from the mark-recapture and observational data, resulted from the differing data collection methods. In particular, the mark-recapture data was likely to have over-estimated the frequency of flying because flying butterflies were most conspicuous and readily caught. Resting butterflies were less noticeable and may have been overlooked. Butterflies which were feeding on inaccessible hedge or ditch vegetation may also have been under-recorded. However, the overall patterns of behaviour described by both methods were very similar.

There was no significant difference between males and females of either species in the mean distances moved between captures. Females flew less frequently than males, and probably primarily to locate suitable foraging and oviposition sites. Because they are not very mobile it is important for these species to have adult and larval food resources within the same area. Female *M. jurtina* and *P. tithonus* laid eggs on a range of grass species, and indeed other substrates as well. The number of observations of oviposition was small, but suggested that neither species had very exacting requirements in terms of suitable oviposition sites. However, female choice is not always a good indicator of foodplant suitability for the larvae. The foodplant preferences of the larvae are discussed by Feber (1993). Nonetheless, there is a broad requirement for grassy areas associated with nectar sources and this combination is not widely found in arable ecosystems. It seems likely that ovipositing females of both species would tolerate a variety of sward types, but our results suggested a tendency for both species to utilise the more species-rich, sown swards more frequently for oviposition. Such treatments provided abundant nectar and also a range of potentially suitable grass species. Larvae of both *M. jurtina* and *P. tithonus* were, indeed, found in the last two years of the study on the experimental margins (Feber 1993). There were several *a priori* reasons for predicting that the experimental field margins were, in contrast to conventionally managed boundaries, likely to have been successful breeding habitats for these and other butterfly species. Firstly, with the exception of the herbicide treated plots, all agrochemicals were excluded from the experimental field margins from the outset of the project. This would be expected to have beneficial effects on larval populations, primarily by encouraging the development of species rich swards containing suitable larval foodplants, as well as adult nectar sources. Both adult and larval foodplants were abundant in the field margin swards (Feber 1993). Secondly, the extended-width of the margins would considerably reduce or remove the risks to larvae from insecticide drift (see Feber & Smith 1993). Thirdly, and perhaps most importantly, the field margins were permanent, providing undisturbed overwintering habitat for all developmental stages. Thus there are no reasons to believe that habitat quality on the field margins would result in lower larval survival than on more semi-natural grassy swards, although over a period of years the probability of chance extinctions may be higher than in semi-natural habitats because of the high perimeter/area ratio of the field margins, together with the possibility of agricultural 'accidents'.

Both *M. jurtina* nor *P. tithonus* showed low mobility. Not only were mean distances between captures low, but there was a high recapture rate, particularly associated with some treatment types. These measurements, together with the synchrony of appearance of large numbers of butterflies in fresh condition at the beginning of the season, suggest strongly that the majority of individuals present on the field margins also hatched there. Although mark-recapture experiments invariably under-estimate longer distance movements, the estimates of adult mobility of *M. jurtina* were of a similar order to those of Brakefield (1982) for butterflies in semi-natural grassland habitats. However, they were considerably lower than those of Dover *et al* (1992), who studied movements of *M. jurtina* and *P. tithonus* on an arable site where nectar availability was generally low, indicating that mobility may differ with habitat quality.

Although both species, and particularly *P. tithonus*, moved, on average, very short distances, the distribution of distances moved between captures, and the numbers of individuals captured for the first time in a worn condition, suggested a degree of immigration into the study area. The experimental margins were linked not only to other hedgerows, but also to different habitat types including woodland and pasture. This network may have facilitated immigration and emigration of these and other some species. Although data to support the proposal that hedgerows act as wildlife corridors linking isolated habitats are limited (eg Johnson & Adkisson 1985; Van Dorp & Opdam 1987; Baudry 1988; Maelfait & De Keer 1990), it is possible that field margins may act as corridors for some species. Many species do not readily cross unsuitable habitats; roads, woodland or agricultural fields may act as barriers to interchange between already fragmented populations, particularly of rarer species (Thomas 1983a; Warren 1987; Munguira & Thomas 1992). As well as facilitating the movement of individual butterflies within arable systems, field margin corridors which provide continuity of breeding habitat could also facilitate a gradual distribution in the extent of populations.

Establishment of populations of these relatively immobile species within arable systems thus depends both on ability to colonise from source populations and on provision of suitable and sufficient nectar sources and of larval foodplants within a confined area. Other species may have more exacting habitat requirements. Colonisation either of similar habitat patches by less mobile species, or of more isolalated habitat patches, may require active introductions but the probability of extinctions in such circumstances must remain relatively high. Provision for more mobile species by management of arable field margins is likely to be less exacting because the different types of functional habitats required can be more widely dispersed.

10.3.2 IMPLICATIONS FOR MANAGEMENT

The results of the detailed study described in this chapter support those of Chapter 9 and have several additional implications for habitat management for butterflies on arable field margins. The results show clearly that, of the habitat available to butterflies in arable ecosystems, perennial grassy strips on the field margin are much the most important. They further confirm that mowing substantial areas of field margin in summer is likely to be very deleterious to both of these species. Uncut vegetation provides both foraging and mate location habitat. It is possible that areas of short grass may have additional benefits for these species but further data are needed to confirm this.

Only a small number of the plant species likely to occur on field margins are suitable as nectar sources. Most of these are thistles and are likely to be the targets of weed control measures. Our data nevertheless show that attractive and agriculturally benign composites, such as *Leucanthemum vulgare*, *Centaurea* species and *Knautia arvensis*, can provide effective substitutes.

Although both species moved over short distances between patches of preferred habitat there was evidence of immigration into the population. The relatively close proximity of larger patches of semi-natural grassland and the network of extended field margins was likely to have facilitated such immigration. The creation of suitable habitat for these species in areas which lack suitable source populations, or migration routes, may not result in colonisation. Consideration should be given to the desirability of short-distance introductions of such relatively common species as part of habitat re-creation schemes in arable farmland.

10.4 Summary

We have shown that appropriately managed arable field margins can support large breeding populations of *M. jurtina* and *P. tithonus*. Most activities of these butterflies were concentrated on the grassy field margins with relatively little use made of crops, sterile strips and boundary features, although *P. tithonus* used boundary features more than *M. jurtina*.

The way in which field margins were managed influenced profoundly the distribution of butterflies. Butterflies were concentrated on swards that were not mown in summer (both uncut and cut in spring and autumn). Sown swards had a similar but smaller effect on the distribution of *M. jurtina* but did not affect significantly the distribution of *P. tithonus*. Butterflies tended to move between treatments of these types and avoid treatments of other types. The butterflies also behaved differently on different sward types. On uncut treatments a lower proportion of *M. jurtina* was found feeding and a higher proportion resting than on treatments cut in summer. Although the numbers of butterflies resting on cut treatments was not significantly higher than on uncut treatments, we could not ascertain reliably whether short swards were preferred for resting or simply offered limited opportunity for feeding. We suggest that the warmer microclimate on cut swards may have advantages for resting butterflies. The behaviour of *P. tithonus* was less influenced by sward type. Treatments left uncut in summer were preferred for feeding but there was no evidence of a preference for sown swards for feeding or for cut swards for resting.

Male and female butterflies of both species differed in their behaviour patterns with males spending less time resting and feeding than females, and more time flying and interacting with other butterflies. There were no significant differences in the treatments utilised by the sexes; although mate location and display were more important activities for males, they were concentrated in the areas where the females were feeding.

The adults of both species fed on a very restricted range of plant species flowering on the field margins. Of the species used *Cirsium arvense, C. vulgare* and *Carduus acanthoides* were the most frequented but *Leucanthemum vulgare, Knautia arvensis* and *Centuarea nigra* in the wild flower-seeded swards were also popular. *P. tithonus* made more use of hedge and ditch species, such as *Rubus fruticosus* sens. lat. Bramble and *Pulicaria dysenterica*, than did *M. jurtina*.

Both species were protandrous with sex ratios differing substantially for much of the flight season. This did not result in any significant variation in preferred sward type during the season.

In both species, but particularly in *P. tithonus*, more of the time spent resting involved basking behaviour in males than in females. Prominent vegetational structures were preferred for basking, suggesting that it was a means of sexual signalling.

Oviposition was rather indiscriminate for both *M. jurtina* and *P. tithonus*. Eggs were laid predominantly, but not exclusively, on grasses. There was some preference for laying on sown plots but eggs were laid on both live and dead grasses.

Both species were relatively immobile. Over 80% of *P. tithonus* were recaptured within 150m and over 70% of *M. jurtina* within 200m. However, there was some evidence of immigration into the site.

Table 10.1 Frequency of capture of *M. jurtina* and *P. tithonus* in each habitat zone. Data for location of initial captures only.

	Species			
	Maniola jurtina		*Pyronia tithonus*	
	n	percent	n	percent
margin	530.0	80.8	601.0	76.6
hedge	0.0	0.0	31.0	3.9
ditch	43.0	6.6	134.0	17.1
sterile strip	44.0	6.7	3.0	0.4
crop	28.0	4.3	7.0	0.9
track	11.0	1.7	9.0	1.1

Table 10.2 The distribution of *M. jurtina* captures on the experimental treatments (data are block means).

Treatment	**Mean no. captures**[1]
sown, cut spring & autumn	22.69 (3.16)
sown, no cut	15.73 (2.82)
unsown, cut, spring & autumn	12.83 (2.63)
unsown, no cut	10.11 (2.41)
sown, cut, spring & summer	6.28 (1.99)
unsown, sprayed	5.55 (1.88)
unsown, cut, spring & summer	4.31 (1.67)
sown, cut, summer only	3.64 (1.54)
unsown, cut, spring & summer, leave hay	3.22 (1.46)
unsown, cut, summer only	2.73 (1.32)

[1] Means presented are back-transformed. Analyses were performed on log-transformed means (shown in parentheses). Minimum Significant Difference = 1.287.

2-Way Analysis of Variance (all treatments)

Main Effects	df	F value	P	Sig. level
Block	4	1.86	0.1388	n s
Treat	9	5.49	0.0001	***
Planned comparisons				
Spray vs uncut in summer	1	0.21	0.6481	ns
Spray vs cut in summer	1	1.04	0.3144	ns

3-Way Factorial Analysis of Variance

Main Effects	df	F value	P	Sig. level
Sowing	1	4.01	0.0551	ns
Cutting	3	13.51	0.0001	***
Sow*cut	3	0.13	0.9388	ns
Planned comparisons				
Cutting vs not cutting	1	6.92	0.0137	*
Cut in summer vs not cut in summer	1	37.03	0.0001	***
Cut spring & autumn vs no cut	1	1.17	0.2887	ns

Table 10.3 The distribution of *P. tithonus* captures on the experimental treatments

Treatment	**Mean no. captures**[1]
unsown, no cut	16.59 (2.87)
sown, no cut	15.04 (2.78)
unsown, cut, spring & autumn	13.47 (2.67)
sown, cut, spring & autumn	9.88 (2.39)
unsown, cut, spring & summer	6.79 (2.05)
unsown, cut, spring & summer leave hay	6.41 (2.00)
unsown, sprayed	5.87 (1.93)
sown, cut, spring & summer	5.47 (1.87)
unsown, cut, summer only	4.53 (1.71)
sown, cut, summer only	4.12 (1.63)

[1] Means presented are back-transformed. Analyses were performed on log-transformed means (shown in parentheses). Minimum Significant Difference = 1.287.

2-Way Analysis of Variance (all treatments)

Main Effects	df	F value	P	Sig. level
Block	4	3.51	0.0161	*
Treat	9	2.73	0.0155	*
Planned comparisons				
Spray vs uncut in summer	1	1.09	0.3032	ns
Spray vs cut in summer	1	0.81	0.3745	ns

3-Way Factorial Analysis of Variance

Main Effects	df	F value	P	Sig. level
Sowing	1	0.71	0.4082	ns
Cutting	3	7.52	0.0008	***
Sow*cut	3	0.06	0.9786	ns
Planned comparisons				
Cutting vs not cutting	1	12.12	0.017	*
Cut in summer vs not cut in summer	1	20.26	0.0001	***
Cut spring & autumn vs no cut	1	1.17	0.2892	ns

Table 10.4 The distribution of *M. jurtina* on recapture for each initial capture category tested for adherance to random expectation. Cut or uncut refers to summer cut only. Expected values shown in parentheses.

	INITIAL CAPTURE			
FIRST RECAPTURE	sown uncut[1]	sown cut[2]	unsown uncut[3]	unsown cut[4]
sown,uncut	32(14)	7(3.75)	10(7.25)	5(4.25)
sown,cut	4(14)	4(3.75)	4(7.25)	4(4.25)
unsown,uncut	13(14)	2(3.75)	15(7.25)	5(4.25)
unsown,cut	7(14)	2(3.75)	0(7.25)	3(4.25)

[1] $\chi^2_{(3)}=33.85$, $P<0.001$.

[2] Expected values less than five, therefore treatments grouped as follows: first recapture on sown (cut and uncut) vs. unsown (cut and uncut) treatments: $\chi^2_{(1)}=3.267$, $P=0.07$. First recapture on cut (sown and unsown) vs. uncut (sown and unsown) treatments: $\chi^2_{(1)}=0.6$, $P=0.44$.

[3] $\chi^2_{(3)}=18.03$, $P<0.001$.

[4] Expected values less than five, therefore treatments grouped as follows: first recapture on sown (cut and uncut) vs. unsown (cut and uncut) treatments: $\chi^2_{(1)}=0.059$, $P=0.81$. First recapture on cut (sown and unsown) vs. uncut (sown and unsown) treatments: $\chi^2_{(1)}=0.529$, $P=0.47$.

Table 10.5 The distribution of *P. tithonus* on recapture for each initial capture category tested for adherance to random expectation. Cut or uncut refers to summer cut only. Expected values shown in parentheses.

	INITIAL CAPTURE			
FIRST RECAPTURE	sown, uncut[1]	sown, cut[2]	unsown, uncut[3]	unsown, cut[4]
sown, uncut	32(175)	2(4.75)	12(20)	6(6.75)
sown, cut	7(16.75)	8(4.75)	8(20)	2(6.75)
unsown, uncut	21(16.75)	7(4.75)	50(20)	14(6.75)
unsown, cut	7(16.75)	2(4.75)	10(20)	5(6.75)

[1] $\chi^2_{(3)}=26.31$, $P<0.001$.

[2] Expected values less than five, therefore treatments grouped as follows: first recapture on sown (cut and uncut) vs. unsown (cut and uncut) treatments: $\chi^2_{(1)}=0.053$, $P=0.819$. First recapture on cut (sown and unsown) vs. uncut (sown and unsown) treatments: $\chi^2_{(1)}=0.053$, $P=0.819$.

[3] $\chi^2_{(3)}=60.4$, $P<0.001$.

[4] $\chi^2_{(3)}=11.66$, $P<0.01$.

Table 10.6 The distribution of *M. jurtina* on recapture for each initial capture category tested for adherance to random expectation. Cut or uncut refers to summer cut only. Expected values shown in parentheses. Sample does not include butterflies which remained on the same plot.

	INITIAL CAPTURE			
FIRST RECAPTURE	sown uncut[1]	sown cut[2]	unsown uncut[3]	unsown cut[4]
sown,uncut	15(8.25)	5(2.25)	5(2.25)	4(3.0)
sown,cut	2(8.25)	1(2.25)	0(2.25)	3(3.0)
unsown,uncut	11(8.25)	2(2.25)	0(2.25)	5(3.0)
unsown,cut	5(8.25)	1(2.25)	0(2.25)	0(3.0)

[1] $\chi^2_{(3)}=12.46$, $P=0.006$.

[2] Expected values less than five, therefore treatments grouped as follows: first recapture on sown (cut and uncut) vs. unsown (cut and uncut) treatments: $\chi^2_{(1)}=1.000$, $P=0.317$. First recapture on cut (sown and unsown) vs. uncut (sown and unsown) treatments: $\chi^2_{(1)}=2.78$, $P=0.956$.

[3] Expected values less than five, therefore treatments grouped as follows: first recapture on sown (cut and uncut) vs. unsown (cut and uncut) treatments: $\chi^2_{(1)}=0.11$, $P=0.739$. First recapture on cut (sown and unsown) vs. uncut (sown and unsown) treatments: $\chi^2_{(1)}=9.000$, $P=0.002$.

[4] First recapture on sown vs unsown treatments: $\chi^2_{(1)}=0.33$, $P=0.584$. First recapture on cut vs uncut treatments: $\chi^2_{(1)}=3.000$, $P=0.083$.

Table 10.7 The distribution of *P. tithonus* on recapture for each initial capture category tested for adherance to random expectation. Cut or uncut refers to summer cut only. Expected values shown in parentheses. Sample does not include butterflies which remained on the same plot.

	INITIAL CAPTURE			
FIRST RECAPTURE	sown, uncut[1]	sown, cut[2]	unsown, uncut[3]	unsown, cut[4]
sown, uncut	13(9.25)	1(0.75)	8(7.0)	3(3.75)
sown, cut	3(9.25)	0(0.75)	7(7.0)	1(3.75)
unsown, uncut	15(9.25)	2(0.75)	5(7.0)	10(3.75)
unsown, cut	6(9.25)	0(0.75)	8(7.0)	1(3.75)

[1] $\chi^2_{(3)}=10.46$, $P=0.015$.

[2] Expected values too low for analysis.

[3] $\chi^2_{(3)}=0.857$, $P=0.836$.

[4] Expected values less than five, therefore treatments grouped as follows: first recapture on sown (cut and uncut) vs. unsown (cut and uncut) treatments: $\chi^2_{(1)}=3.267$, $P=0.071$. First recapture on cut (sown and unsown) vs. uncut (sown and unsown) treatments: $\chi^2_{(1)}=8.067$, $P=0.0045$.

Table 10.8 Distances between consecutive capture locations for *M. jurtina* and *P. tithonus*

	M. jurtina		*P. tithonus*	
Distance between capture locations (m)	n	percent	n	percent
0	56	22.9	132	34.0
1-50	31	12.7	82	21.0
51-100	61	25.0	72	18.5
101-150	22	9.0	29	7.0
151-200	10	4.0	16	2.5
201-250	10	4.0	7	1.7
251-300	18	7.0	10	2.5
301-350	14	5.7	10	2.5
351-400	10	4.0	9	2.3
401-450	4	1.6	2	0.05
451-500	4	1.6	12	4.0
>501	4	1.6	8	2.2

Table 10.9 Distances between capture and first recapture locations of *M. jurtina* and *P. tithonus*.

i) *Maniola jurtina*

Interval between captures	Mean distance (m) 1 day	 2 days	 3 days
Sex			
Female	186.1	138.8	191.6
Male	148.1	142.9	143.1
Probability[1]	0.956	0.629	0.767

[1] Wilcoxon 2-sample test for differences in mean distance between capture locations between males and females.

ii) *Pyronia tithonus*

Interval between captures	Mean distance (m) 1 day	 2 days	 3 days
Sex			
Female	89.75	60.96	102.1
Male	109.03	96.39	102.5
Probability[1]	0.4140	0.9632	0.431

[1] Wilcoxon 2-sample test for differences in mean distance between capture locations between males and females.

iii) *M. jurtina* and *P. tithonus*, sexes combined

Interval between captures	Mean distance (m) 1 day	 2 days	 3 days
Species			
M. jurtina	168.6	127.6	174.5
P. tithonus	96.7	76.6	102.3
Probability[1]	0.0069	0.038	0.029

[1] Wilcoxon 2-sample test for differences in mean distance between capture locations between species.

Table 10.10 Behavioural activities of male (M) and female (F) *M. jurtina* and *P. tithonus* immediately prior to capture
(Percentage of total sample on each treatment in parentheses)

i) *M. jurtina*

	Activity							
Treatment	Resting		Flying		Feeding		Interacting	
	M	F	M	F	M	F	M	F
U/Su	6(55)	9(64)	5(45)	5(36)	.	.	.	.
U/SpSu	6(38)	9(64)	9(56)	4(29)	.	1(7)	1(6)	.
U/SpAu	18(27)	20(30)	33(49)	20(30)	12(18)	33(49)	4(6)	.
U/SpSu/L	7(47)	14(79)	7(47)	2(11)	.	1(5)	.	1(5)
U/NC	6(19)	11(21)	13(42)	14(27)	8(26)	25(48)	4(3)	2(4)
U/Spray	10(40)	11(41)	5(20)	6(22)	5(20)	9(33)	5(20)	1(4)
S/Su	5(42)	11(52)	6(50)	8(38)	1(8)	2(10)	.	.
S/SpSu	5(29)	23(67)	9(53)	6(18)	.	5(15)	3(18)	.
S/SpAu	12(12)	15(19)	26(26)	14(18)	58(58)	48(62)	4(4)	1(1)
S/NC	11(22)	11(41)	5(20)	17(25)	24(49)	32(47)	1(2)	.

i) *P. tithonus*

	Activity							
Treatment	Resting		Flying		Feeding		Interacting	
	M	F	M	F	M	F	M	F
U/Su	6(24)	11(39)	13(52)	10(36)	3(12)	6(21)	3(12)	1(4)
U/SpSu	9(27)	12(63)	22(67)	6(32)	2(6)	1(5)	.	.
U/SpAu	21(18)	24(24)	66(55)	33(33)	31(26)	43(43)	1(1)	.
U/SpSu/L	4(17)	10(37)	16(70)	7(26)	2(9)	9(33)	1(4)	1(4)
U/NC	13(17)	43(48)	36(46)	36(41)	27(35)	36(41)	2(2)	.
U/Spray	7(30)	19(56)	12(53)	7(21)	3(13)	8(23)	1(4)	.
S/Su	3(25)	6(25)	8(67)	7(29)	1(8)	10(42)	.	1(4)
S/SpSu	4(25)	12(43)	10(63)	6(21)	2(13)	10(36)	.	.
S/SpAu	12(23)	16(36)	34(64)	9(20)	7(13)	19(42)	.	1(2)
S/NC	9(16)	16(25)	35(63)	23(36)	10(18)	25(39)	2(3)	.

Table 10.11 The effects of treatment and sex on resting activity by *M. jurtina*

Treatment	**Mean % butterflies**[1]
unsown, cut, spring and summer, leave hay	75.5 (0.93)
unsown, cut, summer only	70.1 (0.88)
unsown, cut, spring & summer	59.2 (0.79)
sown, cut, spring & summer	55.1 (0.76)
sown, cut, summer only	53.9 (0.75)
unsown, sprayed	45.8 (0.69)
sown, no cut	27.0 (0.52)
unsown, cut, spring & autumnm	25.8 (0.51)
unsown, no cut	21.3 (0.46)
sown, cut, spring & autumn	16.1 (0.40)

[1] Means presented are back-transformed. Analyses were performed on square root arcsine transformed means (shown in parentheses). Minimum Significant Difference = 1.287.

2-Way Analysis of Variance (all treatments)

Main Effects	df	F value	P	Sig. level
Sex	1	7.73	0.0214	*
Treat	9	6.01	0.0067	**
Planned comparisons				
Spray vs uncut in summer	1	0.17	0.6937	ns
Spray vs cut in summer	1	0.02	0.9040	ns

3-Way Factorial Analysis of Variance

Main Effects	df	F value	P	Sig. level
Sowing	1	1.06	0.3385	ns
Cutting	3	13.89	0.0025	**
Sow*cut	3	0.70	0.5798	ns
Planned comparisons				
Cutting vs not cutting	1	10.80	0.017	*
Cut in summer vs not cut in summer	1	41.12	0.0001	***
Cut spring & autumn vs no cut	1	0.26	0.626	ns

Table 10.12 The effect of treatment on the abundance of resting *M. jurtina*

Treatment	**Mean abundance butterflies**[1]
sown, no cut	6.00
sown, cut, spring & summer	5.60
sown, cut spring & autumn	5.40
unsown, cut, spring & autumn	4.20
unsown, sprayed	4.20
unsown, cut, spring & summer, leave hay	4.00
unsown, no cut	3.40
sown, cut, summer only	3.20
unsown, cut, spring & summer	3.00
unsown, cut, summer only	3.00

[1] Minimum Significant Difference = 0.3872

2-Way Analysis of Variance (all treatments)

Main Effects	df	F value	P	Sig. level
Treatment	9	0.85	0.5724	ns
Block	4	0.76	0.5609	ns

Table 10.13 The effects of treatment and sex on feeding activity by *M. jurtina*

Treatment	**Mean % butterflies**[1]
sown, cut, spring & autumn	70.7 (0.88)
sown, no cut	55.3 (0.77)
unsown, no cut	41.0 (0.65)
unsown, cut, spring & autumn	35.9 (0.61)
unsown, sprayed	28.5 (0.54)
sown, cut, summer only	9.2 (0.30)
sown, cut, spring & summer	3.9 (0.19)
unsown, cut, spring & summer	1.8 (0.13)
unsown, cut, spring & summer leave hay	1.2 (0.11)
unsown, cut, summer only	0 (0.00)

[1] Means presented are back-transformed. Analyses were performed on square root arcsine transformed means (shown in parentheses). Minimum Significant Difference = 0.4238

2-Way Analysis of Variance (all treatments)

Main Effects	df	F value	P	Sig. level
Sex	1	12.67	0.0061	**
Treat	9	17.38	0.0001	***
Planned comparisons				
Spray vs uncut in summer	1	1.71	0.2240	ns
Spray vs cut in summer	1	3.44	0.0965	ns

3-Way Factorial Analysis of Variance

Main Effects	df	F value	P	Sig. level
Sowing	1	10.62	0.0139	*
Cutting	3	31.39	0.0002	***
Sow*cut	3	1.03	0.4372	ns
Planned comparisons				
Cutting vs not cutting	1	27.19	0.0012	**
Cut in summer vs not cut in summer	1	93.92	0.0001	***
Cut spring & autumn vs no cut	1	0.22	0.6550	ns

Table 10.14 The effects of treatment and sex on feeding activity by *P. tithonus*

Treatment	**Mean % butterflies**[1]
unsown, no cut	42.7 (0.66)
unsown, cut, spring & autumn	38.1 (0.63)
sown, no cut	30.5 (0.56)
sown, cut, spring & autumn	28.4 (0.54)
sown, cut, spring & summer	25.3 (0.51)
sown, cut, summer only	24.3 (0.49)
unsown, cut, spring & summer leave hay	20.9 (0.46)
unsown, sprayed	18.8 (0.43)
unsown, cut, summer only	17.1 (0.42)
unsown, cut, spring & summer	5.6 (0.24)

[1] Means presented are back-transformed. Analyses were performed on square root arcsine transformed means (shown in parentheses). Minimum Significant Difference = 0.3872

2-Way Analysis of Variance (all treatments)

Main Effects	df	F value	P	Sig. level
Sex	1	23.00	0.0010	***
Treat	9	3.16	0.0510	ns
Planned comparisons				
Spray vs uncut in summer	1	1.70	0.2251	ns
Spray vs cut in summer	1	0.27	0.6187	ns

3-Way Factorial Analysis of Variance

Main Effects	df	F value	P	Sig. level
Sowing	1	0.57	0.4757	ns
Cutting	3	4.69	0.0423	*
Sow*cut	3	2.92	0.1095	ns
Planned comparisons				
Cutting vs not cutting	1	5.64	0.0493	*
Cut in summer vs not cut in summer	1	12.58	0.0094	**
Cut spring & autumn vs no cut	1	0.16	0.7007	ns

Table 10.15 Nectar source utilisation by *M. jurtina* and *P. tithonus* in 1991

Plant species	Rank abundance of flowers[2]		Percentage of visits[1] by:	
	July	August	*M. jurtina*[3]	*P. tithonus*[4]
Cirsium/Carduus spp.	13	10	37.0	46.7
Centaurea spp.	45	11	12.0	2.8
Knautia arvensis	19	18	7.7	2.3
Tripleurospermum inodorum	6	2	4.3	2.4
Leucanthemum vulgare	4	5	33.0	10.0
Trifolium spp.	12	44	2.0	0.3
Convolvulus spp.	24	1	1.3	2.3
Pulicaria dysenterica	-	37	0.0	20.5
Ranunculus spp.	25	52.5	0.7	0.0
Rubus spp.	23	39	0.3	7.7
Senecio jacobaea	59	50.5	0.3	2.6
Umbelliferae	10	6	0.3	1.7
Hypericum spp.	17	31	0.0	0.3
Achillea millefolium	62	42	0.0	0.3
Dipsacus fullonum	-	40	0.0	0.3

[1] Data are percentages of total observations of feeding butterflies (300 systematic observations of *M. jurtina* and 351 of *P. tithonus*)

[2] All broad-leaved plant species were ranked in order of the mean abundance of their flowers during summer 1991. Species included in the July list are those on which *M. jurtina* were observed feeding and in the August list those on which *P. tithonus* were feeding. - indicates species not in flower.

[3] Null hypothesis that *M. jurtina* visited flowers at random based on their abundance in the sward: $\chi^2_{(9)} = 718.2$, $P<0.001$ (lowest values grouped to increase expected frequencies to a value > 5).

[4] Null hypothesis that *P. tithonus* visited flowers at random based on their abundance in the sward: $\chi^2_{(7)} = 2631.9$, $P<0.001$ (lowest values grouped to increase expected frequencies to a value > 5).

Table 10.16 Sex ratios, and wing wear ratings of adult *M. jurtina* and *P. tithonus* in relation to progress of the flight season

i) *M. jurtina*

Dates	Sample size[a]	male: female	$\chi^2_{(1)}{}^{b}$	Sig. level[c]	average wing wear[d]: male	female
2-8 July	51(3)	1:0.21	21.35	***	1.9	1.7
9-15 July	147(4)	1:0.21	64.01	**	2.6	2.1
16-22 July	181(4)	1:0.35	41.82	***	3.5	2.5
22-29 July	154(5)	1:1.52	6.65	**	4.1	2.7
30 July-5 Aug	193(4)	1:7.39	111.90	***	4.4	3.4
6-12 Aug	105(3)	1:14	78.86	***	4.7	3.5
13-19 Aug	64(6)	1:9.7	42.25	***	4.5	3.9
20-22 Aug	11(3)	1:4.5	4.46	*	5.0	3.9

ii) *P. tithonus*

Dates	Sample size[a]	male: female	$\chi^2_{(1)}{}^{b}$	Sig. level[c]	average wing wear[d]: male	female
22-28 July	111(4)	1:0.11	71.36	***	2.1	1.9
29 July-4 Aug	186(5)	1:0.51	30.89	***	2.7	2.3
5-11 Aug	192(4)	1:1.18	1.33	ns	2.8	2.5
12-18 Aug	331(6)	1:1.88	30.82	***	3.5	3.1
19-25 Aug	253(4)	1:2.4	41.95	***	3.6	2.9
26 Aug-2 Sept	12(2)	1:2	1.33	ns	4.3	3.6

[a] Number of sampling rounds in parentheses.

[b] For 1:1 male:female capture ratio.

[c] Significance levels indicated by asterisks. *** = $P \leq 0.001$, ** = $P \leq 0.01$, and * = $P \leq 0.05$.

[d] For wing wear categories see text.

Table 10.17 Frequency of first time captures of *M. jurtina* and *P. tithonus* according to their sex and wing condition (for description of wing wear categories see text)

	Wing wear category				
	1	2	3	4	5
M. jurtina (F)	4	126	116	121	12
M. jurtina (M)	4	115	41	62	61
P. tithonus (F)	3	221	127	41	3
P. tithonus (M)	1	203	109	65	4

Table 10.18 Total time (in seconds) spent in different categories of behaviour by male and female *M. jurtina* and *P. tithonus* from butterfly observations (percentage shown in parentheses)

i) *M. jurtina*

	Female		Male	
Feeding	10691	(45%)	7666	(34.5%)
Flying	1151	(5%)	6071	(27.3%)
Resting (wings closed)	8381	(35%)	5217	(23.5%)
Basking (wings open)	3264	(13.7%)	3283	(14.7%)
Ovipositing	320	(1.3%)	--	--

ii) *P. tithonus*

	Female		Male	
Feeding	11475	(49.3%)	1043	(44.3%)
Flying	1580	(6.8%)	1090	(46.2%)
Resting (wings closed)	6640	(28.5%)	24	(1%)
Basking (wings open)	2787	(12%)	200	(8.5%)
Ovipositing	788	(3.4%)	--	--

Table 10.19 Mean lengths of resting and basking periods of *M. jurtina* and *P. tithonus*. Time shown in seconds

i) *M. jurtina*

Activity	**Sex**			
	Male	Female	T	P[1]
Resting (wings closed)	58.96	98.79	1.64	0.114
Basking (wings open)	51.42	78.56	0.96	0.347

ii) *P. tithonus*

Activity	**Sex**			
	Male	Female	T	P[1]
Resting (wings closed)	23.25	92.44	2.66	0.031
Basking (wings open)	14.83	84.84	2.09	0.074

[1] Probability derived from T test (unequal variances).

Table 10.20 Nectar source use by *M. jurtina* and *P. tithonus*; frequency of observed feeding bouts

Species	*M. jurtina*	*P. tithonus*
Leucanthemum vulgare	166	27
Centaurea spp.	52	5
Ranunculus spp.	10	.
Cirsium spp. and *Carduus* spp.	107	111
Tripleurospermum inodorum	14	2
Knautia arvensis	28	4
Crepis spp.	9	.
Veronica spp.	3	.
Rubus spp.	11	9
Pulicaria dysenterica	.	43

Table 10.21 Effect of sex and plant species on mean feeding bout length by *M. jurtina*

Sex	**Mean feeding bout length**	**Grouping**
Female	58.324	A
Male	27.467	B

Species	**Mean feeding bout length**	**Grouping**
Cirsium spp. & *Carduus* spp.	62.40	A
Centaurea nigra	61.96	A
Ranunculus spp.	33.39	A
Triplerospermum inodorum	31.78	A
Knautia arvensis	23.03	A
Leucanthemum vulgare	19.96	A
Rubus spp.	17.28	A
Crepis spp.	14.39	A
Veronica spp.	3.00	A

2-way Analysis of variance

Main effects	d.f.	F value	P
Sex	1	7.56	0.0095
Species	8	2.00	0.0696
Sex*species	7	1.65	0.1731

Table 10.22 Effect of sex and plant species on mean feeding bout length in *P. tithonus*

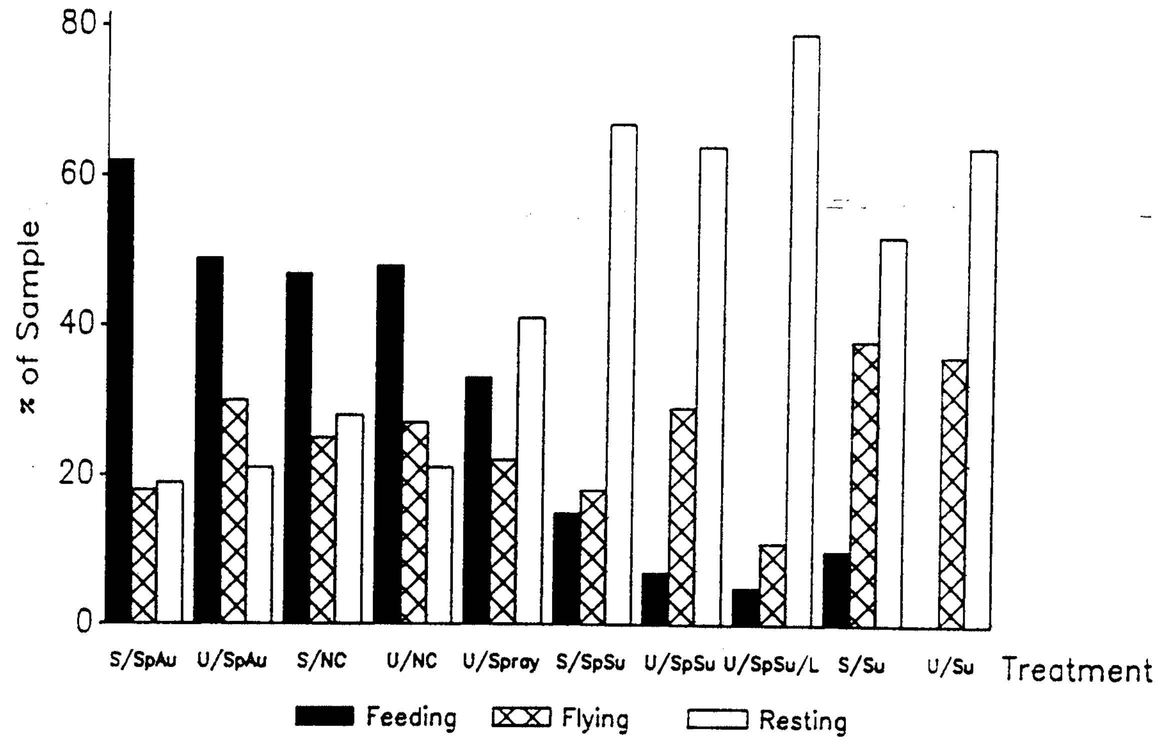
Sex	**Mean feeding bout length**	**Grouping**
Female	67.24	A
Male	34.23	A

Species	**Mean feeding bout length**	**Grouping**
Centaurea spp.	157.0	A
Cirsium spp. & *Carduus* spp.	69.68	A
Leucanthemum vulgare	47.09	A
Pulicaria dysenterica	43.67	A
K. arvensis	33.50	A
T. inodorum	14.00	A
Rubus spp.	11.85	A

2-way Analysis of variance

Main effects	d.f.	F value	P
Sex	1	1.01	0.3345
Species	6	1.43	0.2808
Sex*species	5	0.41	0.7977

a) Females



b) Males

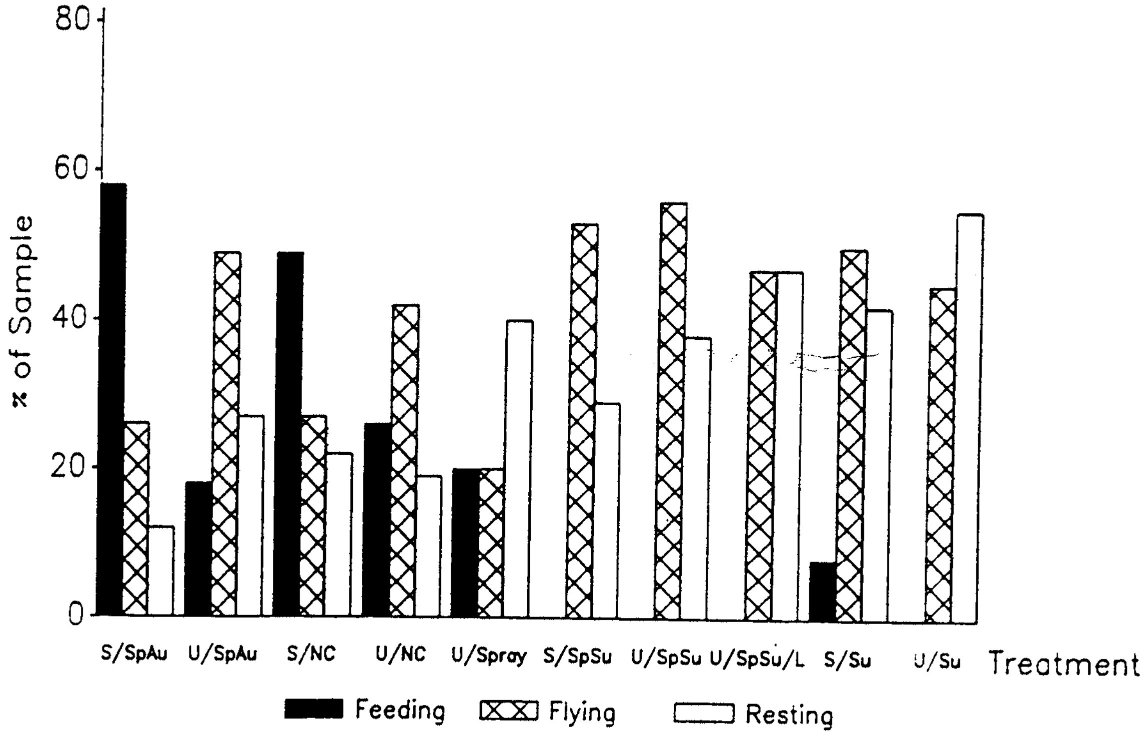


Figure 10.1 Behaviour of *M. jurtina* individuals immediately prior to capture

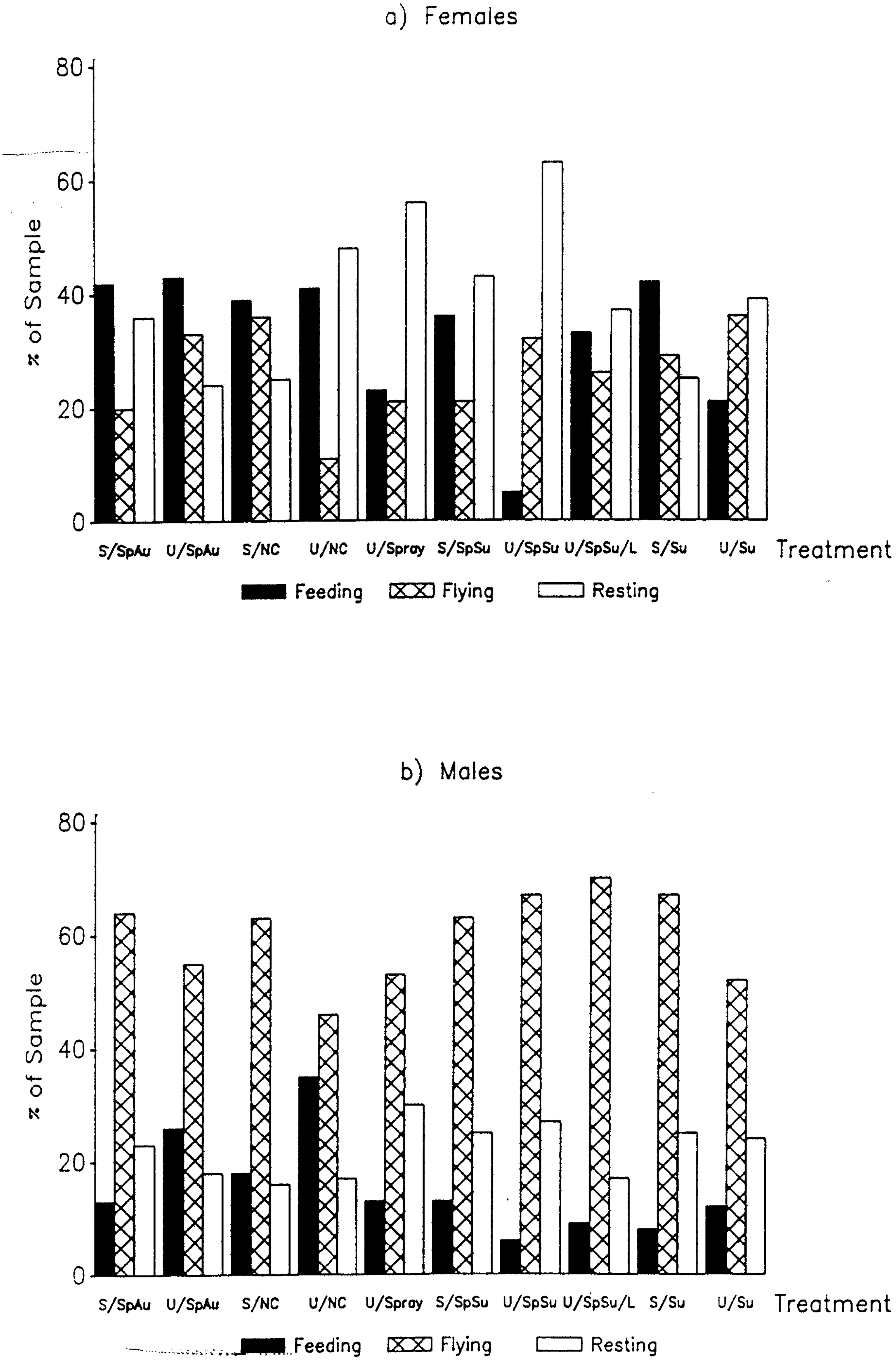


Figure 10.2 Behaviour of *P. tithonus* individuals immediately prior to capture

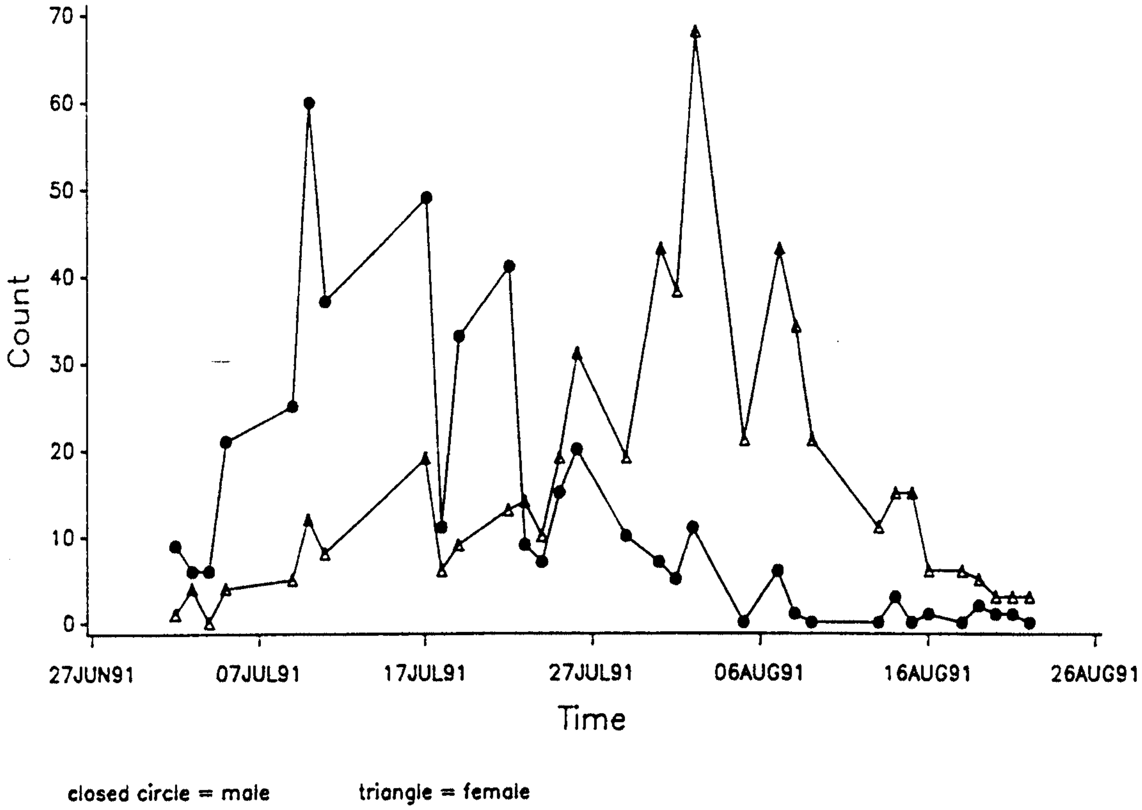


Figure 10.3 Abundance of first-time captures of *M. jurtina* (all treatments) in 1991

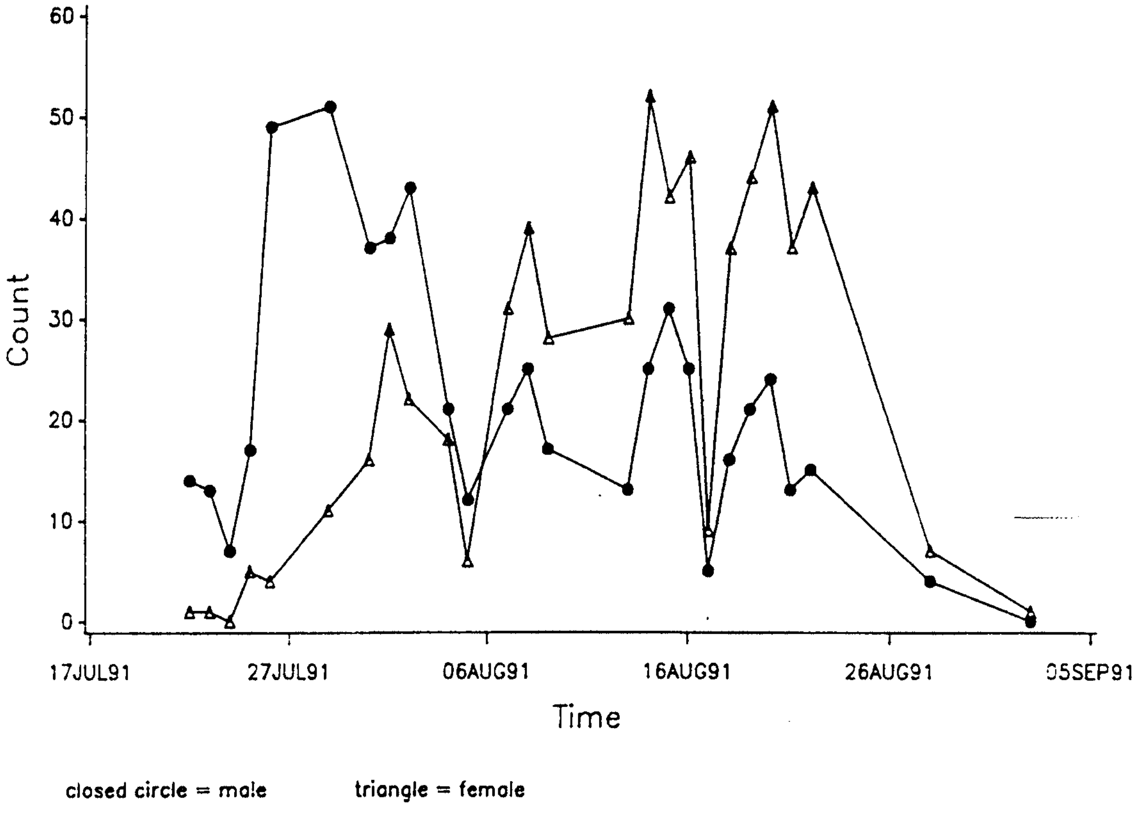


Figure 10.4 Abundance of first-time captures of *P. tithonus* (all treatments) in 1991