A selective trade-off for territoriality and non-territoriality in the polymorphic damselfly *Mnais costalis*

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Males of the damselfly *Mnais costalis* occur as territorial orange-winged 'fighter' males or non-territorial clear-winged 'sneaker' males. Their morph life histories differ considerably but the estimated lifetime reproductive success is the same for the two morphs. In this study we compared the developmental and reproductive costs associated with the two morphs. Orange-winged male and female reproductive costs resulted in a decline in adult fat reserves with increasing age. In contrast, the fat reserves of clear-winged males remained constant with adult age. Body size was positively correlated with mating success in orange-winged males, but had no influence on the mating success of clear-winged males. The orange-winged male flight muscle ratios (FMRs) were significantly higher than the clear-winged male and female FMRs. However, there was no difference in the size-corrected fat reserves of the two morphs; both had higher fat reserves than females. The gain in mass between eclosion and reproduction in orange-winged males and females was almost double the mass gained by clear-winged males, suggesting that clear-winged male development is less costly. An experiment in which pre-reproductive levels of nutrition were manipulated confirmed this.

Keywords: selective trade-off; polymorphism; damselfly

1. INTRODUCTION

Alternative mating strategies and tactics evolve because ecological and social environments often favour more than one phenotype (Gross 1996). Intrasexual polymorphisms provide extreme examples of the phenotypic diversity that can arise (Crespi 1988; Shuster 1991; Ryan *et al*. 1992; Radwan 1993; Emlen 1994; Lank *et al*. 1995). Most intrasexual polymorphisms result from a genetically monomorphic, conditional strategy in which high-status individuals become the dominant morph and low-status individuals become a subordinate morph with a lower fitness pay-off (Gross 1996). However, polymorphisms may also arise from a genetically polymorphic, condition-independent strategy in which individuals are predetermined to become a particular morph. In this case, the maintenance of the two morphs relies on them having equal fitness at equilibrium since any fitness advantage in one morph would result in the loss of the other (Maynard Smith 1982; Gross 1991).

In the Japanese damselfly *Mnais costalis*, males are either orange-winged, territorial, 'fighter' males or clear-winged, non-territorial, 'sneaker' males. Orange-winged males are larger than clear-winged males and have a higher daily mating rate. However, their reproductive life span and longevity is less than that of clear-winged males (despite being larger). The estimated lifetime reproductive success of the two morphs is the same (Tsubaki *et al*. 1997). Tsubaki *et al*. (1997) proposed that the polymorphism may be genetically determined, the two morphs being maintained by a trade-off between reproduction and longevity which is underpinned by differ-

ences in energetic expenditure. Territorial, orange-winged males fight more than non-territorial, clear-winged males (Nomakuchi *et al*. 1984; Y. Tsubaki, unpublished data). The high energetic costs of fighting (Marden & Waage 1990; Plaistow & Siva-Jothy 1996) and its inhibitory effect on feeding rates (Corbett 1999) provide an obvious explanation for the shorter life span of orange-winged males. However, clear-winged males also lived longer than orange-winged males in the laboratory, where differences in predation, recapture rates and flight activity were absent (Tsubaki *et al*. 1997). This means that reproductive costs alone cannot explain the life-history differences observed between the two morphs. Further costs may be associated with the development and maintenance of morph-specific traits. For example, Hooper *et al*. (1999) found that the pigmentation of territorial, orange-winged males varies over time and may be energetically costly to maintain.

Selective trade-offs occur when selection favours different traits in each morph such that they become specialized for different roles within the same population (Crespi 1988). As a result each morph may be exposed to different developmental and reproductive costs. For example, in 'fighter–flier' polymorphisms fighter males often develop costly weaponry (Hamilton 1979; Crespi 1988). While fighter males often have a higher mating success (Eberhard 1980; Conner 1988; Crespi 1988), the costs of fighting and higher mating rates often result in reduced longevity (Houston 1970) and/or a decreased dispersal capacity (Houston 1970; Hamilton 1979; Crespi 1988).

To the authors' knowledge, no study has previously described a selective trade-off associated with territoriality. However, there is clear evidence that, amongst closely related species, selective pressures vary depending on whether the species is territorial or non-territorial

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(Feinsinger & Chaplin 1975; Anholt *et al*. 1991; Wickman 1992). Anholt *et al*. (1991) found that, in odonates, male mass gain—the increase in mass between eclosion and first reproduction—is higher in species which are territorial compared with species which are non-territorial. The authors proposed that this difference occurs because in territorial species additional mass increases male mating success. Support for this hypothesis comes from several studies of territorial odonates which found that stored fat reserves (Marden & Waage 1990; Plaistow & Siva-Jothy 1996) were correlated with the ability to win escalated fights and that the flight muscle ratio (FMR) (Marden 1989) was correlated with male mating success. If this is the case then we would predict that mass gain and, therefore, developmental costs should be greater in orange-winged males.

In this study we compared the reproductive costs of orange-winged and clear-winged males by measuring the rate at which the size-corrected fat reserves declined with age in orange-winged and clear-winged males and females (see Plaistow & Siva-Jothy 1996). We also compared the relationship between mating success and body size in both orange-winged and clear-winged males, as well as comparing the FMR and stored fat reserves of the two morphs with those of females. The development costs were compared by measuring the mass gain (*sensu* Anholt *et al*. 1991) within natural populations. Since this measure provides no indication of the time over which the mass gain occurs or how differences in the feeding rate affect mass gain, we also compared the flight muscle and fat reserves of newly eclosed males when they were reared in the laboratory where both nutrient availability and the time available for development could be experimentally controlled.

2. METHODS

(a) *Age-related changes in fat reserves*

Males could not be aged from eclosion because during the pre-reproductive period individuals are difficult to observe and mark (Forsyth & Montgomerie 1987). Instead, all adults were recorded as one of three age categories (see also Marden & Waage 1990; Tsubaki *et al*. 1994). Age class 1 individuals had fully pigmented, soft, undamaged wings which were dorso-ventrally flexible along their whole length, slight pruinosity and pink pterostigma. Age class 2 males had red/brown pterostigma, fully pigmented wings which were only flexible from the nodus to the tip and intermediate pruinosity. Finally, age class 3 males had fully pigmented, inflexible, often well-worn wings which were 'papery' to the touch. They showed full pruinosity and dark red/brown pterostigma. All adult age categories were clearly distinguishable from newly eclosed individuals, which had and soft glistening wings, undeveloped wing pigmentation and no pruinosity and 'young' pre-reproductive individuals which had soft wings, pale pigmentation, negligible pruniosity and pink pterostigma.

Fat reserves and FMRs were measured as in Plaistow & Siva-Jothy (1996). Since the fat reserves increase with body size (see Marden & Rollins 1994) and *M. costalis* morphs and sexes differ in size (Tsubaki *et al*. 1997), all measures of fat (mg) were corrected for body size and expressed as residuals from a regression of fat (mg) over dry fatless mass (dry mass following total fat extraction). The FMR was defined as the dry flight muscle mass over dry body mass (head, legs and wings removed).

(b) *Body size and mating success*

The relationship between body size and mating success was determined from 21 h of observations recorded over a period of seven days between 27 May and 3 July 1998. All observations were recorded between 12.00 and 15.00 when reproductive activity is at its peak. The observations were based on all males within a 20 m section of a mountain stream containing ten identical territories in Gozenyama, Ibaraki prefecture, Japan (36°33' N, 140°17' E). Body size was measured as hind wing length (mm) and enamel paint was used to paint a three-digit code on the hind wings of all individuals present so that they could be individually identified.

(c) *Fat reserves and the flight muscle ratio*

The fat reserves and FMRs of adult orange-winged and clear-winged males and females were measured as described above.

(d) *Mass gain*

Newly eclosed (days 0–2 after eclosing), adult, orange-winged and clear-winged males and females were collected every few days between 12 May and 27 June 1997 from the same study site described above. The difference between the newly eclosed and adult dry masses was used to determine the average mass gain (*sensu* Anholt *et al*. 1991).

(e) *Controlled rearing experiment*

In order to compare the relative time taken to accumulate 'mass', 20 newly eclosed, orange-winged and clear-winged males and 20 newly eclosed females were collected from the field and housed in separate plastic pots (20 cm diameter and 10 cm depth) containing a perch and a source of water. The pots were maintained under a 16 L:8 D photoperiod at 20 °C, at which temperature *M. costalis* do not fly (S. J. Plaistow, unpublished data). Orange-winged males, clear-winged males and females were each randomly allocated to a 'high-' or a 'low-' nutrition treatment. High-nutrition animals were hand fed *Chironomus yoshimatsu* (Diptera: Chironomidae) (average dry weight 0.695 ± 0.092 mg and $n = 20$) until they were satiated or had consumed a total of six flies. In contrast, low-nutrition animals were fed just two flies. Feeding was carried out twice a day at 8.00 and 18.00. After seven days we measured the stored fat reserves and flight muscle mass of all surviving experimental animals (see Plaistow & Siva-Jothy 1996). We compared these with the flight muscle masses and fat reserves of 'young' males and females which were collected from the field seven days after collecting the newly eclosed individuals. These measurements enabled us to compare the development of our laboratory-reared animals with normal development in the field. The skewed distribution of the stored fat reserves meant that fat data for all types had to be log transformed in order to meet the requirements of parametric statistics.

(f) *Statistical analysis*

Deviations from normality were tested using Kolmogorov–Smirnov (Liliefors test) and homogeneity of variance was tested using F_{max} tests (Sokal & Rohlf 1997). In cases where the data deviated from normality and would not fit a normal distribution following transformation, non-parametric statistics were used. In all cases the tests were two-tailed and where multiple tests
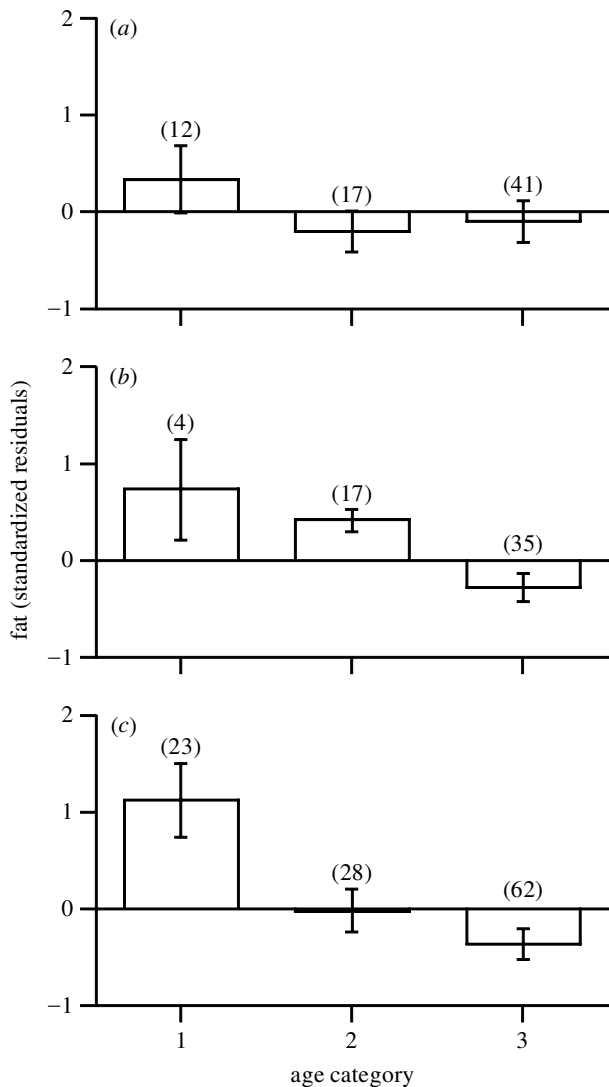
Figure 1. The mean fat content ($\pm$ s.e.) for (*a*) clear-winged males, (*b*) females and (*c*) orange-winged males in different age categories. The numbers above the bars refer to the sample sizes. In order to correct for size bias, the fat content is expressed as the standardized residual from a regression of the fat content (mg) over the dry fatless mass (mg) (clear-winged males, $r^2 = 0.13$, $F_{1,77} = 1.327$ and $p = 0.0012$; females, $r^2 = 0.37$, $F_{1,55} = 31.244$ and $p < 0.0001$; and orange-winged males, $r^2 = 0.076$, $F_{1,115} = 9.320$ and $p = 0.0028$).

were necessary a Bonferroni correction was used to eliminate the possibility of type 1 statistical errors (Sokal & Rohlf 1997). All statistical analyses were carried out using Statview 5.0 (1998).

3. RESULTS

(a) *Age-related changes in fat reserves*

The size-corrected, stored fat reserves declined with increasing age in females (Kruskal–Wallis test, d.f. = 2, $H = 12.97$ and $p = 0.0015$) (figure 1) and also in orange-winged males (Kruskal–Wallis test, d.f. = 2, $H = 11.90$ and $p = 0.0026$) (figure 1). However, in clear-winged males the size-corrected stored fat reserves of the males were statistically indistinguishable across all three age classes (Kruskal–Wallis test, d.f. = 2, $H = 1.692$ and $p = 0.4291$) (figure 1).
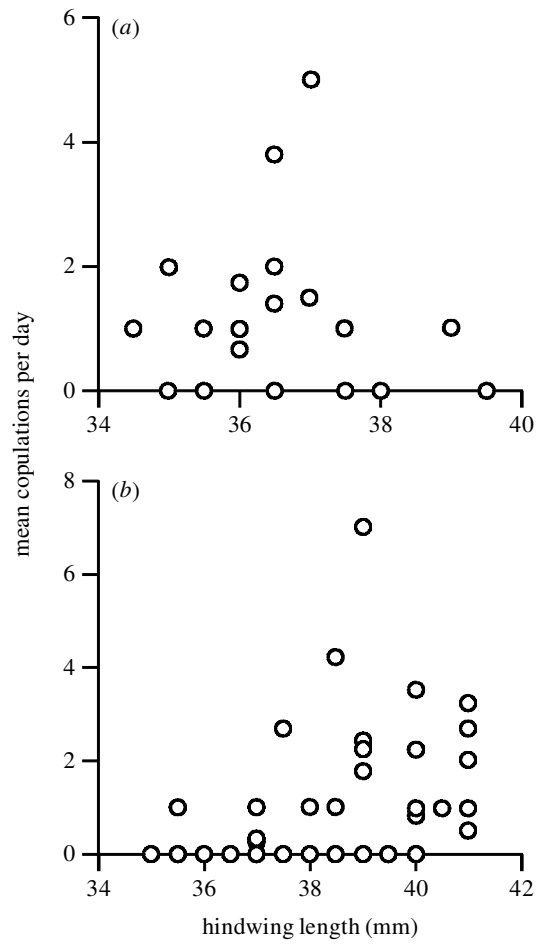

Figure 2. The relationship between body size measured as hindwing length (mm) and average daily copulatory success in (*a*) clear-winged males and (*b*) orange-winged males.

(b) *Body size and mating success*

Body size had no influence on the mating success of clear-winged males (Kendall's rank order correlation, $\rho = 0.091$, $z = 0.429$ and $p = 0.668$) (figure 2*a*) but it was positively correlated with the mating success of orange-winged males (Kendall's rank order correlation, $\rho = 0.430$, $z = 2.617$ and $p = 0.009$) (figure 2*b*).

(c) *Fat reserves and the flight muscle ratio*

The fat reserves (mg) were positively correlated with the dry fatless mass (mg) in orange-winged males ($r^2 = 0.076$, $F_{1,115} = 9.320$ and $p = 0.0028$), clear-winged males ($r^2 = 0.13$, $F_{1,77} = 1.327$ and $p = 0.0012$) and females ($r^2 = 0.37$, $F_{1,55} = 31.244$ and $p < 0.0001$). There was no difference in the homogeneity of the slopes in any of the three types (ANCOVA, dry fatless mass × type interaction $F_{2,244} = 1.200$ and $p = 0.303$). Consequently, all fat measurements were expressed as the residuals of a pooled regression of fat (mg) over dry fatless mass (mg) ($r^2 = 0.142$, $F_{1,248} = 41.038$ and $p < 0.0001$). The size-corrected fat reserves varied significantly (ANCOVA, type $F_{2,246} = 9.883$ and $p < 0.0001$) (figure 3). Females had significantly less fat than both orange-winged males (Fisher's protected least significant difference (PLSD), $p < 0.0001$) and clear-winged males (Fisher's PLSD, $p = 0.009$) (figure 3). However, there was no difference in
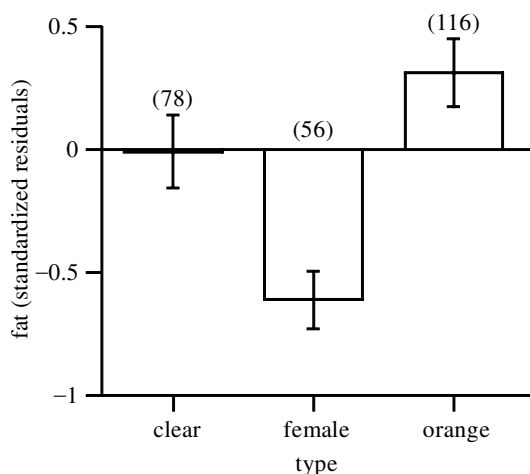
Figure 3. The mean fat content (s.e.) in clear-winged males, females and orange-winged males. The numbers above the bars refer to the sample sizes. In order to correct for size bias, the fat content is expressed as the standardized residual from a pooled regression of the fat content (mg) over the dry fatless mass (mg) for all individuals ($r^2 = 0.142$, $F_{1,248} = 41.038$ and $p < 0.0001$).
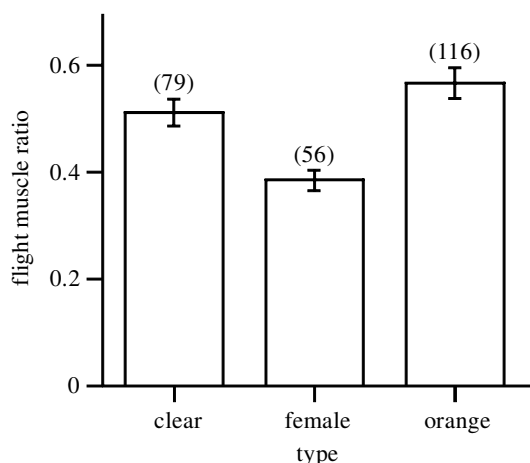

Figure 4. The mean FMRs ($\pm$ s.e.) in clear-winged males, females and orange-winged males. The numbers above the bars refer to the sample sizes.

the size-corrected fat reserves of orange-winged and clear-winged males (Fisher's PLSD, $p = 0.378$) (figure 3).

The orange-winged male FMR was significantly greater than that of clear-winged males (Mann–Whitney U-test, $Z = -6.931$ and $p \leqslant 0.0001$) (figure 4). Moreover, both the orange-winged and clear-winged male FMRs were greater than that of females (Mann–Whitney U-test, orange-winged males $Z = -10.426$ and $p \leqslant 0.0001$ and clear-winged males $Z = -9.111$ and $p \leqslant 0.0001$) (figure 4).

(d) Mass gain

There was no difference in the dry mass (mg) of newly eclosed, orange-winged males, clear-winged males and females (ANOVA, $F_{2,78} = 1.942$ and $p = 0.1503$) (figure 5), but at sexual maturity clear-winged males were significantly lighter than orange-winged males (Mann–Whitney U-test, $Z = -6.931$ and $p \leqslant 0.0001$) (figure 5) and females (Mann–Whitney U-test, $Z = -8.595$ and
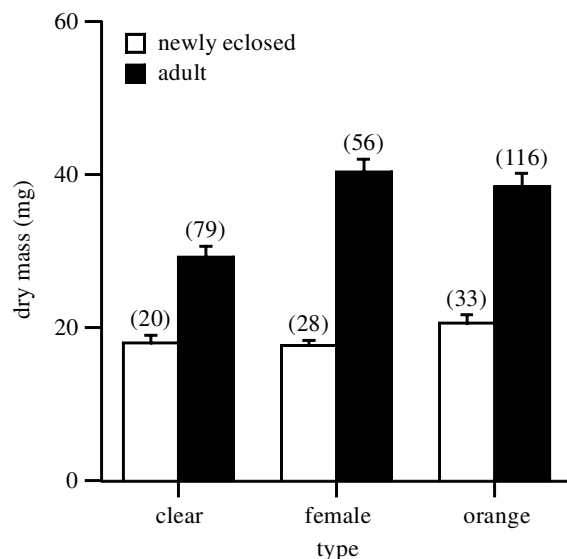

Figure 5. The mean dry mass ($\pm$ s.e.) of newly eclosed (days 0–2 after eclosion), clear-winged males, females and orange-winged males (open bars) and sexually mature adults (closed bars). The numbers above the bars refer to the sample sizes. The difference between the dry mass at eclosion and adulthood represents the average mass gain in each type (see § 2(d)).

$p < 0.0001$) (figure 5). There was no difference between the dry mass (mg) of sexually mature, orange-winged males and females (Mann–Whitney U-test, $Z = -1.461$ and $p = 0.1441$) (figure 5). The average mass gain in females (22.474 mg) and orange-winged males (17.68 mg) was approximately double that of clear-winged males (10.994 mg). Expressed as a percentage, females gained an average of 56.243% of their body mass during the immature feeding period compared to 46.421% for orange-winged males and 37.997% for clear-winged males.

(e) Controlled rearing experiment

After seven days the flight muscle mass of laboratory-reared, clear-winged males was not significantly different from the flight muscle mass of individuals caught in the field and was unaffected by the nutrition treatment (ANOVA, treatment $F_{2,36} = 0.962$ and $p = 0.3917$) (figure 6). However, the nutrition treatment did have a significant effect on the female flight muscle mass (ANOVA, treatment $F_{2,45} = 3.347$ and $p = 0.0442$) (figure 6) and showed a trend within orange-winged males although the result was not significant (ANOVA, treatment $F_{2,50} = 2.659$ and $p = 0.0799$) (figure 6). Females in the high-nutrition treatment had more flight muscle than individuals in the low-nutrition treatment (Fisher's PLSD, $p = 0.0456$) (figure 6), as well as females caught in the field (Fisher's PLSD, $p = 0.0163$) (figure 6). Low-nutrition females had the same flight muscle mass as field-caught females (Fisher's PLSD, $p = 0.9996$) (figure 6). For orange-winged males, the flight muscle mass of field-caught males and high-nutrition males was not significantly different (Fisher's PLSD, $p = 0.7975$) (figure 6); field-caught males had a significantly greater flight muscle mass than low-nutrition males (Fisher's PLSD, field collected $p = 0.0349$), as did
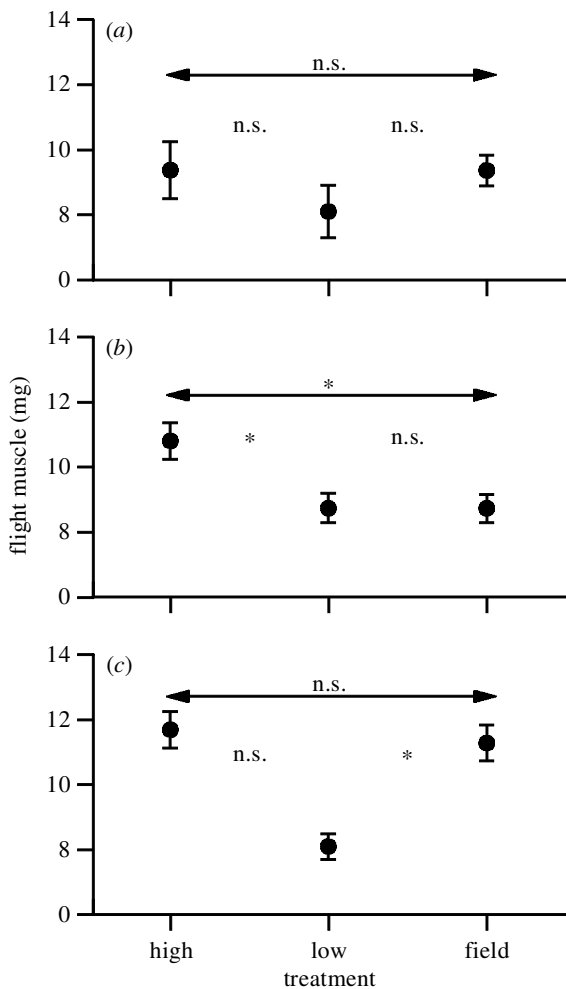
Figure 6. The mean flight muscle mass ($\pm$ s.e.) (mg) for (*a*) clear-winged males, (*b*) females and (*c*) orange-winged males after seven days in either the high-nutrition treatment, the low-nutrition treatment or the field.

Figure 7. The mean fat content (mg) for (*a*) clear-winged males, (*b*) females and (*c*) orange-winged males after seven days in either the high-nutrition treatment or the field. All data were log transformed for analysis. The error bars represent antilogs of the (log) 95% confidence limits.

males from the high-nutrition treatment, although this effect was not significant (Fisher's PLSD, $p = 0.0557$) (figure 6).

There was no difference in the stored fat reserves of clear-winged males caught in the field and clear-winged males reared in either of the two nutrition treatments (ANOVA, treatment $F_{2,36} = 1.260$ and $p = 0.2958$) (figure 7). However, there were significant effects in both females (ANOVA, treatment $F_{2,45} = 3.347$ and $p = 0.0442$) (figure 7) and orange-winged males (ANOVA, treatment $F_{2,45} = 3.347$ and $p = 0.0442$) (figure 7). The fat content of field-collected females and high-nutrition females was not significantly different (Fisher's PLSD, $p = 0.2513$) (figure 7). Field-collected females and high-nutrition females had more fat reserves than low-nutrition females (Fisher's PLSD field collected $p = 0.0368$ and high nutri- tion $p = 0.0090$) (figure 7). In orange-winged males, individuals reared in both nutrition treatments had significantly less fat than field-collected, orange-winged males (Fisher's PLSD, high nutrition $p = 0.0022$, and low nutrition $p < 0.0001$) (figure 7). There was no difference in the fat content of males reared within the high- and low-nutrition treatments (Fisher's PLSD, $p = 0.2187$) (figure 7).
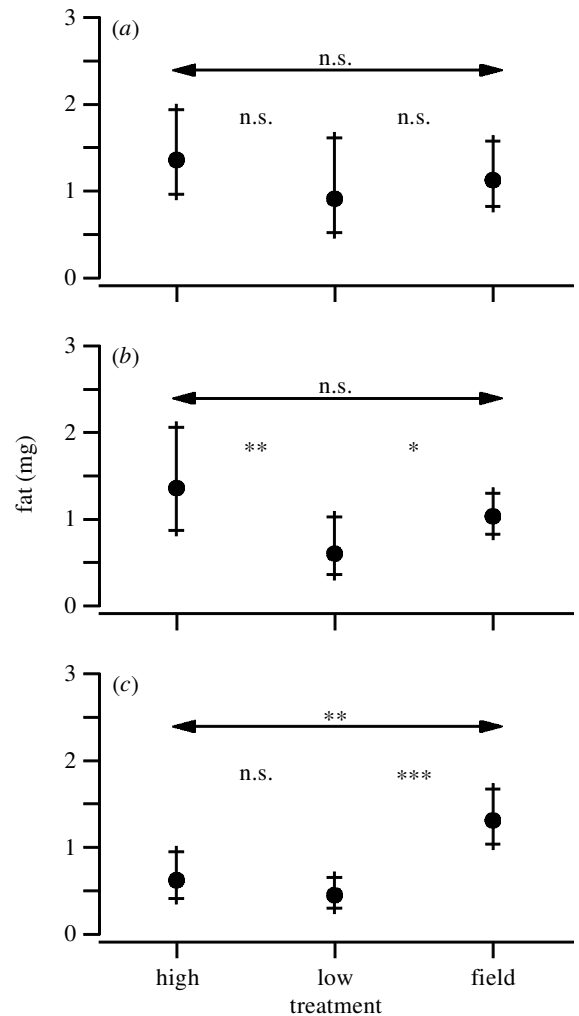
4. DISCUSSION

The size-corrected fat reserves of orange-winged, male and female *M. costalis* declined as individuals increased in age. In contrast, the size-corrected fat reserves of clear-winged males remained at a constant level throughout their lives suggesting that clear-winged males are able to balance their energy expenditure with their energy intake. Presumably female fat stores decline with age because of the cost of continuously developing clutches of eggs. Females will become more energetically constrained as they get older. This idea ties in well with previous studies which have shown that odonate interclutch inter- vals increase with age while clutch sizes often decrease with age (see Corbert 1999). In the case of orange-winged and clear-winged males, the difference is almost certainly associated with the higher mating rate of orange-winged males (Tsubaki *et al.* 1997) and the fact that they tend to fight more (Nomakuchi *et al.* 1984; Y. Tsubaki, unpub- lished data). However, the results of this study suggest

that further differences in energy expenditure may arise from differences in the development costs as well the cost of maintaining morph-specific traits.

Orange-winged males are larger than clear-winged males. In insects, eclosing at a larger size increases the time required to develop (Roff 1992). If reproduction is seasonal, delaying development can have considerable fitness costs (Ludwig & Rowe 1990; Rowe & Ludwig 1991; Rowe *et al.* 1994; Johansson & Rowe 1999; Plaistow & Siva-Jothy 1999). A trade-off therefore exists between body size and development time (Roff 1992; Johansson & Rowe 1999; Plaistow & Siva-Jothy 1999), with selection favouring an optimal body size which maximizes fitness (Werner 1986; Rowe & Ludwig 1991; Plaistow & Siva-Jothy 1999). This will depend on the relative influence that body size has on reproductive success (Plaistow & Siva-Jothy 1999), as well as the time and nutrition available for development (Rowe & Ludwig 1991; Johansson & Rowe 1999; Plaistow & Siva-Jothy 1999).

In *M. costalis*, body size had no influence on clear-winged male mating success (figure 2*a*) but was positively correlated with orange-winged male mating success (figure 2*b*) suggesting that selection on body size differs between the two morphs. We argue that this difference is the result of selection for increased FMRs in orange-winged males which, despite orange-winged males having double the body mass, was still significantly higher than that of clear-winged males. This means that the orange-winged male flight muscle weight is almost double the mass of clear-winged males (orange-winged 21.65 ± 0.39 mg and clear-winged 14.81 ± 0.31 mg). Since the FMR determines all aspects of flight performance (Marden 1987, 1989; Wickman 1992) and was highest in territorial, orange-winged males, our results add weight to previous studies (Marden 1989; Marden & Chai 1991; Wickman 1992) that have concluded that high FMRs are the result of selection for increased flight performance. The size-corrected fat reserves did not differ between orange-winged and clear-winged males. However, this may be because no age correction was applied to our sample. Clear-winged males maintain constant levels of fat reserves whereas orange-winged males' fat reserves are either higher than clear-winged males or lower than clear-winged males according to their age (see figure 1). Consequently, if age is not controlled for, orange-winged and clear-winged males may appear to have similar size-corrected fat reserves. A fairer test of the initial investment in stored fat reserves would be to repeat the comparison at the point at which they begin reproduction when the fat reserves should be maximal (see Plaistow & Siva-Jothy 1996).

Correlations between mating systems and the morphological aspects of flight performance have been previously documented in birds (Feinsinger & Chaplin 1975) and other insects (Anholt *et al.* 1991; Wickman 1992). However, it has not always been possible to remove alternative explanations for the differences, such as phylogenetic explanations or the influence of different habitats (see Wickman 1992). In *M. costalis*, the two morphs are the same species and they occur in the same environment and yet they still demonstrate morphological specializations which are correlated with the mating tactic that they adopt. This result clearly demonstrates that such

differences are the result of varying selection pressures rather than the product of phylogeny or different habitats. The different selection pressures operating on females and the two male morphs result in different development costs. Orange-winged males, clear-winged males and females had similar masses at eclosion, yet females and orange-winged male pre-reproductive mass gain was almost double that of clear-winged males, supporting Anholt *et al.*'s (1991) hypothesis that mass gain is an adaptation to territoriality. These conclusions were further supported by the results of the laboratory rearing experiment; after seven days in the laboratory, clear-winged males were able to develop normal (the same as field-collected animals) levels of flight muscle and fat independent of nutrition. However, in orange-winged males and females, flight muscle and fat development was strongly influenced by the nutrition treatment (see figures 6 and 7). The increased costs of development were most obviously demonstrated in orange-winged males; both their flight muscle and fat content were considerably lower than normal when reared under conditions of low nutrition. In the case of fat, even the high-nutrition conditions were not sufficient to develop fat contents comparable to field-collected animals.

How the different developmental costs of the two male morphs translate into differences in energy expenditure or longevity is at present unclear. It may be that the increased pre-reproductive feeding of orange-winged males increases their exposure to gregarine gut parasites, resulting in reduced feeding efficiency (Abro 1990; S. J. Plaistow, unpublished data) and a reduced capacity to accumulate fat reserves (Siva-Jothy & Plaistow 1999) which may then influence their longevity. Alternatively, there is some evidence that higher FMRs increase the cost of flying (Marden 1987; Wickman 1992). The maintenance of larger and potentially more dynamic flight muscles may further increase the rate of energy expenditure. In the polymorphic cricket *Gryllus firmus*, recent studies have shown that the flight muscle in each of the two morphs is in itself polymorphic. Flight muscle in 'flightless' females was smaller with a reduced number of muscle fibres, lower *in vitro* enzyme activities and lower respiration rates compared with the flight muscles of flight-capable females (Zera *et al.* 1997). Since selection on flight ability appears to differ between orange-winged and clear-winged males, it may be that the flight muscle characteristics or the activity of the flight muscles differs between the two morphs, resulting in different rates of energy expenditure. Work is in progress to test this hypothesis.

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