Territorial and mating success of dragonflies that vary in muscle power output and presence of gregarine gut parasites

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Competition for mating territories in libellulid dragonflies involves aerial contests that require high levels of exertion and locomotor performance. Here we test the hypothesis that success of male Libellula pulchella dragonflies in territoriality and mating is affected by muscle contractile performance, and we examine how gregarine gut parasites affect muscle performance, energy reserves and territorial behaviour of their hosts. At a pond where gregarine parasites are rare, long-term territorial and mating success of males showed a significant positive association with muscle power output. At a nearby pond that had a much higher incidence and intensity of gregarine parasitism, there was no relationship between muscle performance and short-term territorial success. Instead, males assorted themselves into aggressive territory holders and submissive satellites, with the large majority of territory holders having no parasites and nearly all of the satellites parasitized. Unparasitized males showed a tight positive relationship between muscle power and fat content, which suggests that they use a known phenotypic adjustment in muscle contractile performance to allow the energy consumption rate of the flight muscles to match the rate at which energy can be mobilized from storage pools. Parasitized dragonflies showed a small decrease in average fat content and a marked change in the relationship between fat content and muscle power output. The apparent loss of the ability to match muscle contractility to the size of the energy storage pool in parasitized dragonflies suggests that gregarines may have systemic effects on signalling pathways and energy homeostasis. By indirectly choosing males that had successfully competed for territories, females consistently mated with physiologically or immunologically superior males despite large between-pond differences in male behaviour and the incidence and intensity of parasitic infection.

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Competition for mates and the resources necessary to obtain mates is a pervasive and well-studied feature of animal behaviour. Much is known regarding the role of externally apparent traits such as ornaments, vocalizations and chemical signals, but sexual competition also commonly involves contests or battles that require high levels of exertion and locomotor performance. In such cases, internal physiological traits are likely to play a strong role in determining success or failure, yet for most types of animals we know little about variability in the physiological features that affect intraspecific competition. Attributes such as high levels of energy reserves (Marden & Waage 1990), ability to up-regulate metabolic flux and produce ATP at a high rate (Harrison & Hall 1993), and contractile performance of muscles (Marden et al. 2001) should enhance success in types of competitive interactions that depend heavily on exertion and locomotion. Knowledge regarding the variability of such traits within populations, the source of the variation, and its consequences for competitive success are important for understanding how selection acts on physiological capacities and how they evolve.

A common source of performance variation in free-living animals is parasitism. The behaviour and success of parasitized animals during competitive interactions with conspecifics often differ markedly from those of non-parasitized animals (Schall & Sarni 1987; Howard & Minchella 1990; Moore & Gotelli 1996), but the physiological mechanisms underlying these differences have seldom been elucidated. Parasites may cause specific lesions or deficiencies that affect performance-related traits (Harrison et al. 2001); they may deprive the host of energy necessary for high levels of exertion (Munger &...
Karosov 1989; Siva-Jothy & Plaistow 1999), and they may cause systemic physiological changes that affect many aspects of host metabolism and locomotion (Schall et al. 1982).

In the particular case of flying animals it has been shown that a high ratio of flight muscle mass to total body weight affects aerial performance and success in competitive interactions (Marden 1989; Coelho & Holliday 2001; Berwaerts et al. 2002). The generality of this result depends on there being fairly little variation in muscle contractile performance (i.e. it requires that the ratio of muscle mass to body weight captures most of the between-individual variation in force or power output relative to total load). However, muscle contractile performance can vary widely between individual conspecific animals (Marden et al. 2001), and contractility is a trait that is likely to be affected by parasites (i.e. perhaps by regulatory responses stimulated by metabolic changes or decreased energy availability). Effects of intramuscular parasites on contractility have been demonstrated (Harwood et al. 1996), but no studies have examined how muscle contractile performance is related to the presence of parasites in nonmuscle tissues.

Here we test the hypothesis that success of male Libellula pulchella dragonflies in territoriality and mating is affected by muscle contractile performance, and we examine how gregarine gut parasites affect muscle performance, energy reserves and territorial behaviour of their hosts.

**METHODS**

We studied *L. pulchella* dragonflies at two ponds in Centre County, Pennsylvania, U.S.A., during June and July in 2000 and 2001. Our main study site in 2000 was Ten Acre Pond (40°48’N, 77°56’W). In 2001, we primarily studied dragonflies at a small unnamed pond (which we called Darlington Pond; 40°51’N, 77°50’W). These two ponds were separated by approximately 12 km.

Females visit territories defended by male *L. pulchella* dragonflies to copulate and deposit their eggs while being guarded by the male (Pezalla 1979). Owing to differences in pond size and terrain, our ability to monitor these events differed at the two ponds, which required us to use different sampling schemes. Ten Acre Pond was too large to monitor the entire pond, so we studied short-term territorial and mating success of focal individuals or pairs of individuals. Our focal observations were made on samples of highly aggressive territorial males and nonterritorial satellite males that were active along the border of one or more established territories. Whenever possible, we collected these samples in a paired fashion so that we could compare a territory holder with a satellite simultaneously present at the same location. Territorial males were identified by their frequent patrolling of a well-defined area, willingness to engage in escalated encounters with neighbours and interlopers, and successful copulation and guarding of females. Satellites were identified by their submissive behaviour (gliding and leaving the area) when confronted by a territorial male, the concentration of their flights along boundaries between territories guarded by aggressive males, and their poor ability to successfully copulate with females or guard the few females with which they copulated.

The focal observations and sampling described above used males that had been marked individually with coloured powder (Day-Glo Color Corp., Cleveland, Ohio, U.S.A.). The powder was applied using a blowgun technique (Marden 1989) that did not require capture or handling of the dragonflies and had no discernable effect on their behaviour. Marked males were observed for at least 1 h before determination of territorial or satellite status. Many of the nonterritorial males that we marked were not site specific; they were primarily feeding and their competitive status could not be determined. We classified as satellites only those nonterritorial males that showed site fidelity, attempts to engage in opportunistic mating, and the submissive behaviours described above.

Darlington Pond measured approximately 300 m² and all of the dragonflies present could be observed simultaneously and across many consecutive days, thereby allowing quantification of long-term mating success of a large population of males. When each male arrived and began to engage in territorial interactions for the first time at Darlington Pond we captured it in an insect net. After netting, we used permanent ink to write a number on one wing and marked the tips of all four wings with a unique combination of coloured spots using the Day-Glo powder described above. The powder rubbed gently onto the wing tips remained visible for up to 3 weeks. Long-lived males were occasionally recaptured to refresh their wing colours. Records were kept of arrival and departure times for each male, and we counted the number of times they copulated with females. We collected a representative sample of males from Darlington Pond near the end of their territorial tenure and tested them for muscle contractile performance. We also used data from this pond to examine the relationship between territorial effort and longevity.

Dragonflies from both ponds were transported to the laboratory to determine their muscle contractile performance (see Marden et al. 2001 for detailed methodology). Briefly, we removed the head, wings and legs and cemented the thorax and abdomen in a controlled temperature chamber. A series of shallow incisions were made around the dorsal attachment point of the mesothoracic basalar muscle to mechanically isolate the muscle and attach it to the lever arm of an ergometer. The lever imposed a sinusoidal oscillation of muscle length in a manner that closely matched the in vivo length oscillation that occurs in this muscle during flight. Electrical stimulation of the muscle was supplied in a manner that corresponded to the in vivo phase relationship between neural stimuli and muscle length. Muscle temperature was regulated at 32–34°C. We recorded the time course of muscle length and tension at integer contraction frequencies ranging from 20 to 45 Hz (which slightly exceeds the range of wingbeat frequencies observed during free flight; Marden et al. 1999) and used those data to compute net work and power output. We used the highest power output observed at any of those
contraction frequencies as our measure of maximal power output. The basalar muscle was removed from the thorax and weighed after each experiment; its fresh mass was used to determine mass specific power output.

To assess gregarine parasite burdens, we made a dorsal incision along the entire length of the abdomen and midgut of all collected dragonflies. Lateral margins of the abdomen were pinned flat and the midgut contents were examined under a stereomicroscope with fibre optic illumination. We removed partially digested food (typically contained within a peritrophic membrane) and counted gregarine trophozoites throughout the midgut, including the recesses surrounding the proventriculus.

We determined levels of energy reserves by extracting lipids from a subsample of dragonflies that were tested for muscle performance. The thorax and abdomen were dried to a constant mass, weighed, placed in refluxing chloroform in a Soxhlet apparatus for 8 h, then dried and weighed again. The difference between dry mass and lean dry mass was used as our measure of lipid content.

**RESULTS**

We measured muscle power output for 15 of the 21 individuals collected from Ten Acre Pond for which we had determined territorial versus satellite behavioural status. There was no difference in the mean or variance of power output of territorial and satellite males. This was true for both our entire sample ($X \pm SE$; territorial males: $104 \pm 8$ W/kg, $N = 9$; satellite males: $107 \pm 11$ W/kg, $N = 6$; $t_{13} = -0.2$, $P = 0.86$) and for 10 males that were collected in a paired fashion (mean difference $= 3 \pm 21$ W/kg; one-tailed $t$ test of the hypothesis that territory holders have greater muscle power output than satellites: $t_9 = 0.2$, $P = 0.44$). Thus, in the population at Ten Acre Pond, there was no support for the hypothesis that a high muscle power output enhanced success in short-term competition for mating territories.

Territorial and satellite males at Ten Acre Pond differed markedly in their incidence and level of infection by gregarine gut parasites (protists; Fig. 1). Only three of the 13 territory holders were infected, whereas seven of the eight satellites were infected (chi-square test: $\chi^2 = 9.0$, $P = 0.003$). All infections appeared to be a single species of gregarine (Hoplorhynchus sp., family Actinocephalidae: subfamily Menosporinae; Clopton 2002). The infected territorial males had an average of 11 trophozoites ($SE = 2$; $N = 3$) compared with an average of 30 ($SE = 11$; $N = 7$) for satellite males. A crude measure of age, a four-level ranking based on wing wear, was not significantly associated with territorial/satellite status (chi-square test: $\chi^2 = 4.7$, $P = 0.09$), presence or absence of gregarine parasites ($\chi^2 = 3.8$, $P = 0.15$) or the mean number of parasites (ANOVA: $F_{2,24} = 1.0$, $P = 0.40$). Because wing wear is dependent in part on behaviour and perhaps also on the ability of the insect to maintain itself, the apparent lack of age effects must be interpreted with some scepticism. Note, however, that *L. pulchella* frequently contain large numbers of gregarines even when they are newly mature, and none of the satellite males in our sample showed extensive wing wear.

Of the 174 mature males that we marked at Darlington Pond, 46 spent time defending territories over a time interval as great as 25 days after their initial arrival at the pond (Fig. 2). We collected a representative sample of these dragonflies to determine how muscle power and parasitism were related to long-term mating success. Collections were timed in such a way that the dragonflies had already accomplished most of the mating that they were likely to have achieved had we not collected them. Specifically, we collected two dragonflies (Males 4 and 21) after 15 days of observation when their early-emerging cohort was disappearing (Fig. 2) and they showed considerable wing wear. We collected another group (Males 37, 41, 59, 63, 127, 135, 161) 43 days after the start of the experiment, by which time the arrival rate of ovipositing females had dropped to such a low level that little mating was occurring. A final group of freshly mature males (Males 180, 181 and 182) were collected late in the season shortly after our behavioural observations had ended. Two additional males (Males 112 and 136) were collected and

![Figure 1](image_url)  
**Figure 1.** (a) Distribution of parasitized and unparasitized males among territory holders and satellites. (b) A *L. pulchella* midgut containing parasitic gregarine trophozoites (oblong white objects) and a small number of newly formed gamontocysts (spherical white objects). (c) Close-up of a single gregarine trophozoite (Hoplorhynchus sp., family Actinocephalidae: subfamily Menosporinae).
Figure 2. Territorial and mating activity of 174 individual male *L. pulchella* dragonflies at Darlington Pond during the summer of 2001. The experiment began on 12 June, which is Day 1 on the horizontal axis. Bar width represents time spent defending a territory relative to the total observation time that day. Bar height above the minimum height, which represents only presence, is proportional to the number of copulations obtained that day. The smallest bars include males that were present at the pond only momentarily; their width and height do not represent relative measures of territoriality or mating. The letter ‘C’ indicates the day of capture for dragonflies collected for muscle performance analyses. Vertical grey bars represent rainy days (single-day width) or weekends (2-day width) when we did not collect data.
checked for parasites after they were injured when we netted them at the time of their initial arrival at the pond.

Among the nine males at Darlington Pond for which we obtained data for both long-term mating success and muscle contractile performance, there was a significant positive relationship between muscle power output and total time spent defending a territory (Fig. 3; $F_{1,7} = 4.1$, one-tailed $P = 0.04$) and total number of copulations (Fig. 4; ANOVA: $F_{1,7} = 8.8$, one-tailed $P = 0.01$; all of these variables were log transformed to achieve normality). In a multivariate model, only the total time defending a territory had a significant effect on the number of copulations ($F_{1,6} = 15.4$, one-tailed $P = 0.004$), although the effect of muscle power approached significance ($F_{1,6} = 3.0$, one-tailed $P = 0.07$). There was no effect of body size (measured by thorax mass) in any of these analyses. These results suggest that the primary effect of high muscle performance was on the ability to establish and maintain a territory, after which there was no significant additional effect on the ability to obtain copulations.

One of the males at Darlington Pond (Male 41) obtained approximately twice the number of copulations and spent twice as much time at the pond as the next best competitor (Fig. 5). He also had the highest muscle power output (184 W/kg) among all of the males that we have sampled from this species (Fig. 6; $N = 51$, which includes data from Marden et al. 2001 and represents dragonflies at Darlington Pond. In each plot the darkened bar represents Male 41, which was by far the most successful male in that population.

**Figure 3.** The relationship between a male’s mass specific muscle power output and the total time he spent defending a territory. Data were log transformed to achieve normality.

**Figure 4.** The relationship between a male’s mass specific muscle power output and the total number of copulations he obtained. Data were log transformed to achieve normality.

**Figure 5.** Frequency distributions of time spent defending a territory, number of copulations and mass specific muscle power output for dragonflies at Darlington Pond. In each plot the darkened bar represents Male 41, which was by far the most successful male in that population.

**Figure 6.** Frequency distribution of mass specific muscle power output from 51 mature *L. pulchella* males. The darkened bar represents Male 41, which was by far the most successful male in our study of long-term mating success at Darlington Pond.
from a number of ponds over 4 years). The sample sizes in our study of mating success (174 dragonflies) and our survey of muscle performance (51 dragonflies) makes it highly unlikely that, based on chance, an individual would be an outlier for both of these measures.

Only three of the 14 dragonflies collected from Darlington Pond were infected with gregarines (Males 127, 136 and 180), and all three had relatively low levels of infection (N = 1, 10 and 3 trophozoites, respectively). This contrasts sharply with what we found at Ten Acre Pond, where 18 of the 36 dragonflies collected during 2000 and 2001 were infected with gregarines. The mean number of gregarines among all individuals (i.e. both infected and uninfected) at the two ponds differed by a factor of 30 (1.0 ± 0.7, N = 14 at Darlington Pond versus 30.0 ± 9.9 at Ten Acre Pond; Wilcoxon chi-square approximation: $\chi^2 = 5.7$, $P = 0.02$). None of the males at Darlington Pond was observed to consistently behave as a satellite, nor did any of them consistently retreat from territorial encounters by gliding. This is quite different from what we observed at Ten Acre pond, where submissive satellite behaviour was common, especially among males that were infected with gregarines.

Among the three infected dragonflies at Darlington Pond, only Male 127 was represented in our long-term observational data (Male 136 was injured at initial capture and Male 180 arrived after we had concluded the behavioural survey). During the 20-day span from his first appearance at the pond until he was collected, Male 127 defended a territory for a total of only 35 min. This is the second lowest total among the 46 dragonflies in our sample that spent any time defending a territory, and he never copulated.

In the 2001 study at Darlington Pond we sought to determine whether there was a negative relationship between male longevity and territorial intensity. If true, this might provide an incentive for gregarine parasites to manipulate their hosts in order to make them less aggressive and thereby extend host survival, allowing more time for trophozoites to mature and reach the gamontocyst stage of their life cycle (Fig. 1). We tested for such a trade-off by comparing the number of copulations per minute of territorial defence to the total time spent defending a territory, and the total time spent defending a territory with the maximum known age (days between initial marking and last sighting; this is an underestimate of chronological age because it does not include the teneral period of early adult maturation). Contrary to our expectation of a trade-off, both of these relationships showed significant positive slopes (ANOVA: $F_{1,44} = 6.7$, $P = 0.01$ and $F_{1,44} = 12.9$, $P = 0.001$, respectively). Thus, there is either no trade-off between these life history traits, or more likely, a large amount of between-individual variation in male performance and longevity obscures the presence or absence of trade-offs within individuals (van Noordwijk & de Jong 1986; Stearns 1992). Thus, it remains an open question whether there exists an opportunity for gregarine parasites to beneficially manipulate the behaviour of their dragonfly hosts.

To determine whether gregarine parasitism causes satellite behaviour, we fed portions of gregarine-infected midgut from dragonflies collected at Ten Acre Pond to four of the marked males at Darlington Pond (Males 70, 81, 86 and 105) on day 16 of our territorial observations during the summer of 2001. Preliminary experiments showed that this technique results in many intact trophozoites becoming established in the midgut. As a control, three other males (Males 50, 80 and 98) were fed uninfected midgut. The sample size of this pilot experiment proved too small to clearly determine the effect of experimental gregarine infection on territorial behaviour, and it would not be mentioned here except for an incident that involved one of the experimentally infected males (Male 86). Although he continued to be one of the more successful males during the 2 days immediately following infection with trophozoites, at 9 days post-infection he was observed acting in a highly submissive manner at the pond, so much so that he was apparently mistaken for a female and grasped in a precopulatory position by a territorial male. In 15 years of experience with this species, the senior author (J.H.M.) has never previously observed a homosexual pairing of L. pulchella males, so it is noteworthy that this event corresponded with experimental gregarine infection and a sharp change from the earlier aggressive behaviour of this individual.

Gregarine parasites may affect the behaviour of their dragonfly hosts by a mechanism that involves some combination of changes in neural, hormonal, muscle contractile and metabolic traits. We initiated an exploration of these possibilities by comparing muscle contractile performance and lipid content between parasitized and unparasitized dragonflies. We found no significant effect of parasitism on power output ($N = 32$ males sampled for both power output and parasitism; $F_{1,30} = 0.3$, $P = 0.6$), but there was a significant decrease in the fat content of parasitized dragonflies ($F_{1,38} = 4.2$, one-tailed $P = 0.024$; Fig. 7). There was also a marked change in the relationship between fat content and muscle power output (Fig. 8).

Gregarine parasites may cause satellitism in nonhuman animals. The result is quite clear: in the absence of parasites, long-term territorial and mating success has a significant positive association with muscle power output in L. pulchella (Figs 3–5). Given such strong sexual selection favouring high muscle performance, why do all dragonfly males not possess high-power flight muscles? The tight positive relationship between muscle power and fat content in healthy dragonflies (Fig. 8) provides a probable answer. Males with different levels of fat appear to make a phenotypic adjustment in their muscle contractile performance that presumably allows the maximum energy consumption rate of their muscles to match the rate at which energy can...
be mobilized from storage pools. The ability to phenotypically adjust muscle power output and ATP consumption to match nutritional state has been suggested previously for mammals (Russell et al. 1984) and is an intuitively appealing extension of other known forms of cellular and organismal energy homeostasis.

An alternative hypothesis for the correlation between muscle performance and fat content is that more powerful flight muscles allow for greater foraging success. We think that this is unlikely because most L. pulchella foraging flights appear to involve a much lower level of exertion than the flights used to obtain and defend territories and mates. These large dragonflies appear to capture their much smaller prey with ease, and therefore, there seems little reason to believe that differences in muscle performance could cause large differences in foraging success and accumulation of fat reserves.

Our previous work with L. pulchella dragonflies has revealed the mechanism that allows for phenotypic adjustment of muscle power output (Marden et al. 2001). Alternative splicing of mRNA that encodes the muscle regulatory protein troponin-t creates isoform diversity that affects how the muscle responds to activation by calcium, which in turn affects force, work and power output during cyclical contraction. The relationship between power and fat that we have found in the present study makes a significant advance in this line of work because it implies that there is a signalling pathway that communicates information about global energy reserves to the intracellular mechanisms that control alternative splicing. Knowledge of the mechanisms that control alternative splicing (Maniatis & Tasic 2002) and their connection with extracellular signalling pathways (van der Houven van Oordt et al. 2000) is rudimentary; however, this is an important topic, because it is likely to be one of the primary mechanisms by which organisms accomplish proteomic diversity and adaptive phenotypic plasticity.

One of our study ponds had a much higher incidence and intensity of gregarine parasitism. At that pond we found no relationship between muscle performance and short-term territorial success. Instead, males assorted themselves into aggressive territory holders and submissive satellites, with the large majority of territory holders having no parasites and nearly all of the satellites parasitized. Together with the changed relationship between fat and muscle power in parasitized dragonflies, these results support the hypothesis that gregarine parasites alter the physiology and behaviour of their dragonfly hosts, thereby changing the processes and mechanisms that determine the outcome of intermale competition. However, we cannot be confident that the effect of gregarine parasites on the dynamics of male territorial competition is generally true because our study involved just two ponds that differed greatly in size (i.e. we have no replication of the effect of different levels of parasitism between ponds). Crowding of males into highly overlapping territories at the small pond also may have played

Figure 7. Fat content (% of dry mass of the abdomen and thorax) of dragonflies with and without gregarine gut parasites.

Figure 8. Relationship between fat content and muscle power output for dragonflies with and without gregarine gut parasites.
a role in the importance of muscle power and in the absence of males acting as satellites.

Although we detected no difference in the average muscle power output of parasitized and unparasitized dragonflies, our data reveal subtle physiological changes associated with parasitism. There was a small decrease in the average fat content of parasitized dragonflies (Fig. 7) and a marked change in the relationship between fat content and muscle power output (Fig. 8). Gregarines have previously been shown to reduce the fat content of parasitized male odonates (Siva-Jothy & Plaistow 1999), and differences in fat content among competing pairs of males have been shown to strongly affect the outcome of territorial battles (Marden & Waage 1990; Marden & Rollins 1994; Plaistow & Siva-Jothy 1996). However, it is unlikely that reduced fat content was the cause of the poor territorial success of parasitized males at Ten Acre Pond because the distribution of fat content was broadly overlapping between healthy and parasitized males (Fig. 7). For this reason, it is unlikely that parasite-induced differences in fat reserves were the mechanism that led to the strong association between infection and territorial/satellite status (we did not measure the fat content of most of the paired males in the 2000 study, so we cannot evaluate the relative fat content of territory holders and satellites). Rather, we are more impressed by the change in the relationship between lipid content and muscle power output (Fig. 8). In parasitized dragonflies, the apparent loss of the ability to match muscle contractility to the size of the energy storage pool suggests that gregarines may cause physiological changes that affect signalling pathways and energy homeostasis. Indeed, dragonflies with gregarine trophozoites in their midgut have chronically activated p38 map kinase in their flight muscles (R. J. Schilder & J. H. Marden, unpublished data). This molecule is involved in pathways that control a wide variety of cellular functions and gene expression (Cowan & Storey 2003), which in mammals includes insulin signalling, glucose transport, and the function of fat storage cells (Carlson et al. 2003; Fujishiro et al. 2003). Chronic and systemic changes in p38 MAPK signalling are likely to have strong effects on internal physiology that could affect behaviour and flight performance in ways that we did not detect with our measure of short-duration muscle power output. We are presently performing additional analyses of cellular physiology and signalling in this species to gain a more detailed understanding of this interesting host–parasite interaction.

Dragonflies are a classic example of resource defence polygyny, with males defending territories that contain sites that females use for oviposition (Fincke 1997). Libellulid females are clearly choosy about where they oviposit, and males appear to assess which sites are favoured by females (Pezalla 1979; Koenig & Albano 1985). At Darlington Pond, where gregarine parasites were rare, the outcome of territorial competition between males was correlated with differences in muscle contractile performance and presumably flight ability, and females mated most frequently with the most powerful males. At Ten Acre Pond, which was larger, less crowded, and had a much higher incidence of gregarine parasitism, infected males were unlikely to defend a territory and females mated predominately with noninfected territory holders of widely varying muscle performance. Thus, there was a marked difference between these two ponds in the male characteristics that were sorted by territorial interactions, but the difference did not appear to involve any change in female behaviour. Rather, it appears that the strong tendency of females to favour certain oviposition sites served as a consistent filter for mating with males that were in peak condition and/or were free of parasites. Libellula pulchella females often make rigorous evasive flights when approached by males, which provokes a chase that may constitute an additional test of male flight performance. By being choosy about oviposition sites and sometimes evasive, females consistently avoid mating with physiologically or immunologically inferior males despite large between-pond differences in male behaviour and the incidence and intensity of parasitic infection. This mating system, in which males largely sort themselves prior to female arrival, appears to be a quick and effective way for females to choose high-quality mates indirectly (Wiley & Poston 1996) in an environment where male condition varies quite widely between individuals and between ponds.

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References


