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ORIGINAL PAPER

Damselfly females prefer hot males: higher courtship success in males in sunspots

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Abstract Males of some territorial calopterygid damselflies show an elaborate courtship display that involves high-frequency wing-beats directed toward an incoming female. Although it has been suggested that female mate preference is based on some characteristics of male's courtship display, it is unclear whether the courtship display varies between males or is influenced by environmental conditions. We combined two recent technologies, thermographic imaging and high-speed digital videography, to show that the wing-beat frequency during courtship (i.e., courtship intensity) in a damselfly, *Mnais costalis*, is correlated with thorax temperature. Our data indicated that (1) male thorax temperature was associated with solar exposure in his territory, (2) environmentally derived thermal gain enhanced courtship intensity, (3) hotter males were more likely to copulate than others, and (4) female thorax temperature during oviposition within a territory was associated with solar exposure. Males with territories that have longer exposure to sun spots are expected to attain higher thorax temperatures for longer and so are able to successfully court more females. We suggest that females benefit from mating with hot males because they will be on a warmer territory while ovipositing. Hot males might also have greater mate guarding ability, and/or eggs may develop faster in warmer territories.

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Introduction

Flight performance in insects is strongly influenced by body temperature (e.g. Heinrich 1996; Marden et al. 1996; Samejima and Tsubaki 2010), however how flight performance under the influence of body temperature affects fitness is not well known. For example, Davies (1978) showed that male speckled wood butterflies that owned sunspots were more likely to win territorial contests. Stutt and Willmer (1998) subsequently showed that the sunspot owner won because he was hotter than the intruder and so had a thermal advantage over his rival, however other factors have been suggested to be important (Kemp and Wiklund 2004).

Many calopterygid damselflies are territorial (Corbet 1999) with males defending spatially restricted oviposition resources (e.g., particular species of aquatic plants) which females have to use. Males of territorial calopterygids also show an elaborate courtship that involves high frequency wing-beats directed toward an incoming female. Studies have shown that aspects of the display in some calopterygid species convey information about territory quality (Gibbons and Pain 1992; Siva-Jothy et al. 1995). However, there is no empirical work that examines the importance of the high-frequency wing-beats observed during courtship although there is evidence that flying ability in general is linked to condition (Marden and Waage 1990; Plaistow and Siva-Jothy 1996).

Males of the Japanese calopterygid *Mnais costalis* perform a relatively simple courtship. The male flies out from his perch, which is situated next to the oviposition site on his territory, toward an incoming female. He turns towards her and follows her until she alights on vegetation in his territory. If she does not alight in his territory, he returns to his perch: if she lands, he hovers ca. 30 cm in front of her beating his wings alternately, with a reduced wing-stroke amplitude, and at ca. twice the normal frequency (i.e., about 30 Hz instead of approximately 15 Hz; see Rüppel (1985) for details of similar courtship in *Calopteryx splendens*). If she remains motionless during the last phase of his hover approach, he will dart forward, land on the front edge of her wings, form the tandem link (see Corbet 1999), and initiate copulation. Alternatively, she can end the interaction by flying away before the terminal phase of the courtship. A male only courts incoming females and shows no interest in females perching nearby, suggesting that the female's incoming flight indicate her sexual receptivity (e.g., Hooper and Siva-Jothy 1997).

In this study, we examine variation in wing-beat frequency during courtship in *M. costalis* to test if environmentally derived thermal gain enhances the intensity of the courtship display. We combined thermal imaging and high speed digital video recording to remotely, and repeatedly, assess a damselfly's body temperature while recording a high frequency, short-duration behavior in the field. We also tested if the body temperature of *M. costalis* is affected by temporary solar exposure of the male's territory, and if the body temperature is correlated with courtship success of males. We discuss the advantages for a female to mate with a hot male that shows elevated courtship display in sunspots.

Material and methods

Study site and study organism

The Japanese damselfly *M. costalis* were observed in an open drainage culvert ca. 3 m deep, 10 m wide, and 150 m long in low mountain woodland in Sigaraki, Shiga Prefecture, Japan (34°56′30″N 136°04′42″E) in June 2008 and June 2009. The culvert contained a sheltered shallow (ca. 10 cm deep) stream environment with ca. 10 cm of silt and mud on which water dropwort *Oenanthe javanica* (oviposition substrate) grows.

In contrast to allopatric *M. costalis* in Ibaraki (Tsubaki et al. 1997), which shows alternative strategies (orange-winged territorial and clear-winged sneaky males) linked to genetic polymorphism (Tsubaki 2003), *M. costalis* in Shiga often coexists with *Mnais pruinosa*. Interestingly, all males of *M. costalis* are orange-winged (male, monomorphic) and females are pale-orange-winged (sexually dimorphic; Fig. 1a). In contrast, all males of *M. pruinosa* are

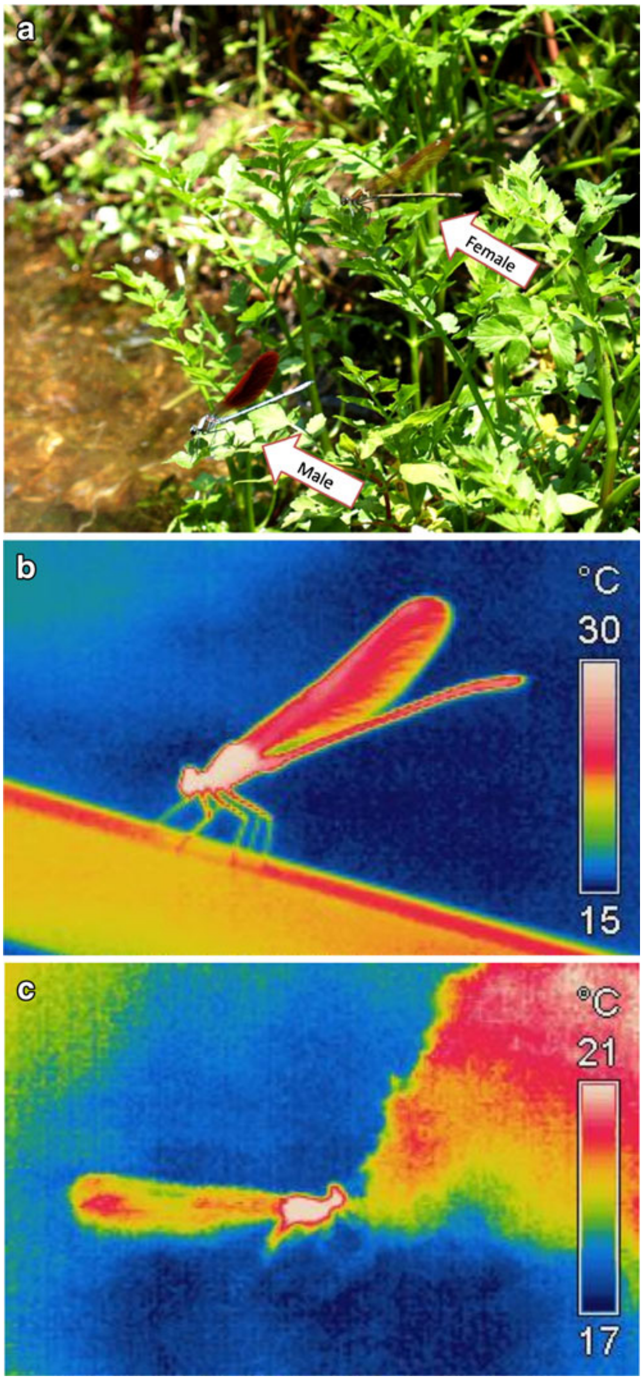

Fig. 1 **a** A male and a female perching on water dropwort in the study site. Males are *orange winged*, while females are *pale orange winged*. **b** Thermogram of a territorial *Mnais costalis* male. The reference bar on the RHS shows the false color coding for the surface temperatures in the thermogram. **c** Thermogram of an ovipositing female. Her abdomen below the first segment is not visible because it is underwater: her ovipositor is at the tip of her abdomen and she uses it to place eggs into vegetation *below the water line*

clear-winged (male, monomorphic) and females are also clear-winged (sexually monomorphic). Males of both male-monomorphic species are potentially territorial. *M. costalis* is usually found relatively lower streams than *M. pruinosa*. Because our study site was located at the lowest end of stream, we saw few *M. pruinosa* during the course of this study.

Hayashi et al. (2004) described more extensive geographic distributions of two *Mnais* species in Japan, while Hooper et al. (1999) reported that the orange color of wings is melanin-based and the expression of sexual ornamentation is correlated with age and condition of individuals.

All adults we saw for the first time were captured and individually numbered on the hind wings with enamel pens. We recorded sex and male morph type, and wing (left hind) was measured with a ruler accurate to 0.5 mm. We marked 215 males and we used stationary damselflies for the body temperature measurements.

Measurement of thorax temperature

We remotely (up to 1 m away) measured the body surface temperature of the thorax of damselflies (Fig. 1b) with an infrared thermographic camera (Chino CPA-1000). The temperature of the lateral surface of the thorax was recorded: thermographic data were stored in the memory of the camera.

Surface temperature may not exactly represent muscle temperature. Therefore, we transformed the surface temperature to the thorax temperature using an equation regressed against core thorax temperature simultaneously measured using micro-thermocouples (diameter of wires 0.05 mm). The relationship between surface thorax temperature measured with the thermal camera (Ts) and the measurement of core thorax temperature with micro-thermocouples (Tb) was almost linear ($Tb=0.836Ts+3.27$, $r^2=0.988$, $P<0.001$) including both sexes (23 males and nine females) within the range between 17°C and 33°C (Samejima and Tsubaki 2010). We estimated core thorax temperature (Tb) using this linear function. Hereafter, we refer to core thorax temperature as Tb, unless it is necessary to distinguish the two measurements.

Measurement of air and water temperatures

We recorded air temperature at the field site on each study day by means of a data logger (Hobo Water temp Pro) and/or a digital thermometer (Sato SK-1250MC). They were placed 1.2 m above the ground in the shade and the record at the time of body temperature measurement was used as "general air temperature". When appropriate, we measured "ambient" air temperature within 10 cm of perching males. We measured ambient air and ambient water temperatures within 10 cm of ovipositing females using the digital thermometer (Sato SK-1250MC).

Inter- and intra-male variation in thorax temperature

We measured the thorax temperature of males to examine the effects of ambient air temperature (Ta), solar exposure, flight activity, and body size on male thorax temperature by (1) comparing the thorax temperature of males and Ta at their perching sites, (2) recording whether the male was perched in a sun spot or in the shade, (3) recording whether the male showed a bout of flight activity prior to the measurement, or perched longer than 3 min (the thorax temperature usually becomes stable within 1 min after a bout of flight), and (4) measuring left hind wing length as a measure of body size.

We also made repeated measurements (1, 2) on four males to examine how thorax temperature changes within a day in relation to solar exposure and air temperature. All measurements were conducted when males perched longer than 3 min.

Thorax temperature of ovipositing female

Soon after a female copulated with a territorial male near an oviposition site, she usually started oviposition after landing on an oviposition substrate (a stem of a water dropwort). When we found ovipositing females, we measured their thorax temperature (Fig. 1c). We also recorded solar exposure at the oviposition site, and measured female left hind wing length, ambient air, and water temperatures.

Recording of courtship flight data

We recorded courtship flights with a high-speed video camera (Fastec Imaging, SportsCam500CS). The camera records continuously onto a hard disk, enabling us to stop recording once we have captured target behavior. We used a video frame rate of 250-frames/s, which allowed us to quantify wing-beat frequencies during natural courtship flights. We could also experimentally solicit courtship flights by presenting tethered females (see Siva-Jothy and Tsubaki 1989) to territorial males. By soliciting courtship flights, we were able to measure the thorax temperature of the same male immediately before (within 10 s) and immediately after (within 10 s) each courtship flight. The change in the thorax temperature within 10 s is negligible (Samejima, unpublished data). At the beginning of the study, we attempted to record the courtship display of every male; however, we abandoned this sampling regime for logistic reasons. We measured the hind wing length and abdomen length of all males.

Courtship success and thorax temperature

Every time we found males showing a natural courtship flight toward an incoming female, we recorded whether his

Table 1 ANCOVA of the factors associated with for the thorax temperature of perching males

Term	Estimate	SE	*t*	*P*
Ambient temperature	0.817	0.081	10.10	<0.0001
Solar exposure (sunny/shade)	1.981	0.182	10.88	<0.0001
Flight activity (flight/perch)	−0.061	0.206	−0.30	0.769
Hind wing length	0.025	0.084	0.30	0.766

courtship display resulted in copula formation (successful courtship), or not (unsuccessful courtship). Then, we measured the surface thorax temperature of the male and the female within 10 s of the end of the natural courtship flight.

Duration of sunspots

We recorded the onset and end of direct solar illumination for each of the 20 territories in our field site throughout a day (June 1, 2008). Territorial males fly into territorial sites usually within 10 min after the site is exposed to direct sunlight. They leave soon after the site becomes completely shaded. Therefore, the duration of sunspots is almost equivalent to the maximum duration of male reproductive activity at each territorial site (Tsubaki, unpublished data).

We also measured body size of the territorial male on each territory.

Statistical analysis

We used four-factor analysis of covariance (ANCOVA) to evaluate how male thorax temperature was affected by general air temperature, flight activity (flight/perch), solar exposure (sunny/shade), and hind wing length. We measured the thorax temperature of four males repeatedly and used two-factor ANCOVA to test the effects of solar exposure (sunny/shade) and general air temperature on the thorax temperature of individual males. The individuals were put into the analysis as random effect. We used four-factor ANCOVA to evaluate how ovipositing female's thorax temperature was affected by ambient air temperature, ambient water temperature, solar exposure (sunny/shade) and hind wing length. We used three-factor ANCOVA to evaluate how wing-beat frequency of courtship display was affected by male thorax temperature, hind wing length, and type of courtship display (natural/solicited). We used multiple regressions to evaluate how male thorax temperature changes during courtship display and how it is affected by the air temperature, wing-beat frequency, and male body size. We used logistic nominal regressions to test the effects of the air temperature, male thorax temperature, female thorax temperature, and solar exposure on the male courtship success. Analyses were performed using R 2.10.1 or JMP v.6.1, SAS.

Our initial models always included main effects and all possible interactions of the tested variables, but when interactions were non-significant, they were excluded from the model and the analyses were run again.

Results

Inter- and intra-male variation in thorax temperature

ANCOVA showed that Ta and solar exposure were significant predictors of male Tb (Table 1). Territorial males in sunspots were on average 7°C hotter than males on shady sites (Fig. 2). Flight activity, hind wing length, and abdomen length were not correlated with the Tb.

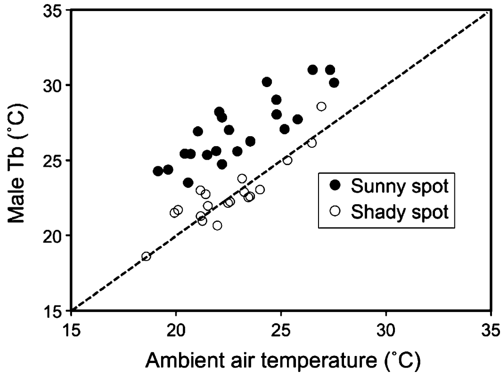

Fig. 2 Variation in male thorax temperature in relation to ambient temperature. The *broken line* shows where two temperatures are equal

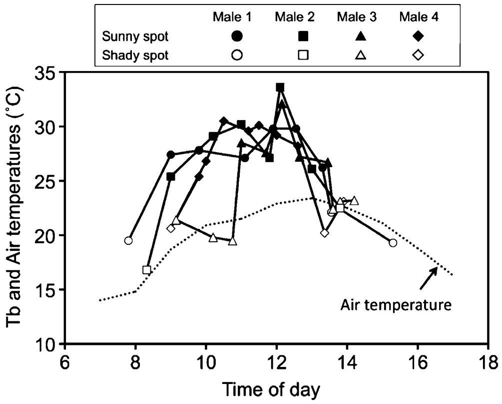

Fig. 3 Diurnal change in the body temperature of four individual males. Solid symbols indicate that the male was perching in a sunspot, while open symbols indicate his perch was in the shade. The broken line shows ambient air temperature

Table 2 ANCOVA of the factors associated with the thorax temperature of four males measured repeatedly

Term	Estimate	SE	*t*	*P*
General air temperature	0.431	0.126	3.43	<0.0001
Solar exposure (sunny/shade)	5.62	0.528	10.65	<0.0001

The individuals were put into the analysis as random effect

The Tb of individual males varied diurnally as shown in Fig. 3. The time between two consecutive measurements (ca. 30 min) was much longer than, and long enough compared to, the response time to thermal condition (shorter than 3 min). Results of ANCOVA suggested that thorax temperature changes dramatically within individuals under the influence of solar exposure and ambient temperature (Table 2).

Female thorax temperature at the oviposition site

Females ovipositing in sunny spots showed higher Tb than other females in shady spots (Fig. 4). ANCOVA showed that solar exposure and ambient air temperature were the significant predictors of Tb in ovipositing females (Table 3).

Male thorax temperature and courtship flight

Male Tb did not change much during the courtship flight (Fig. 5a): but it slightly increased or decreased (ranging between −1.8 and 2.5°C). There was no indication of Tb increasing significantly as a function of wing-beat frequency (Table 4). However, the direction of change was dependent on air temperature (Table 4): this result indicates that flight activity increased Tb when air temperature was high, but it decreased Tb when air temperature was relatively low (Fig. 5c). The effect of wing-beat frequency on Tb was not significant (Fig. 5d).

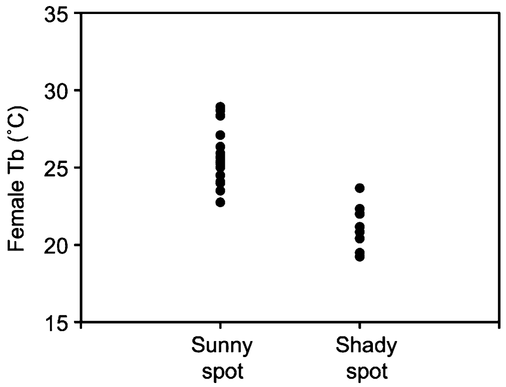

Fig. 4 Thorax temperature of females ovipositing at sunny and shady oviposition sites

We were not able to measure the Tb immediately before natural courtship flights, hence we regressed post-courtship flight Tb with wing-beat frequency. It revealed that courtship wing-beat frequency was positively correlated with Tb (Fig. 5b). There was no significant effect of experimental solicitation of courtship flights on the relationship between wing-beat frequency and post courtship Tb (Table 5). Body size (measured as wing length) had no significant effects on wing-beat frequency (Table 5).

Male thorax temperature and courtship success

We recorded the courtship displays of 42 males without replication. Fig. 6 shows the relationship between courtship success and male Tb, and the curve fitted by a logistic regression ($\chi^2=12.8$, DF=1, $P<0.001$) suggests that a male with higher thorax temperature had a greater probability of successful courtship (50% threshold around 27°C). In 25 cases, we could record both male and female thorax temperatures. GLM test for courtship success of males (with courtship success as a dependent variable, air temperature, male Tb, and female Tb as independent variables) showed that the male's Tb was the only significant predictor of courtship success (Table 6).

Duration of sunspots

Sunrise and sunset times at the field site was 04.43 and 19.05 h (JST), respectively on June 1, 2008. However, the duration of sunspot on territories (*D*) was only 5.8±0.46 h (Mean ± SD, $n=20$) because of the shading effects of the slopes, forests, and vegetation in the surrounding habitat. Male body size measured as left hind wing length (*L*) was positively correlated with the duration of direct sunlight on his territory ($D=0.373\ L–8.73$, $r^2=0.540$, $P=0.0002$).

Table 3 ANCOVA of the factors associated with the thorax temperature of ovipositing females

Term	Estimate	SE	*t*	*P*
Ambient air temperature	0.498	0.325	1.53	0.143
Ambient water temperature	0.252	0.283	0.89	0.387
Solar exposure (sunny/shade)	1.705	0.387	4.40	<0.001
Hind wing length	0.171	1.415	0.41	0.685

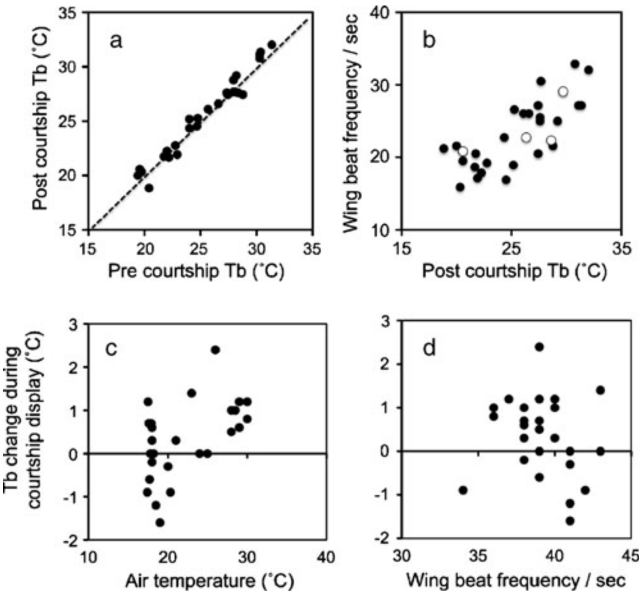

Fig. 5 **a** Relationship between the thorax temperatures of a male measured before and after the single courtship display. The *broken line* shows where two temperatures are equal. **b** Wing beat frequency in relation to the thorax temperature of males. *Solid circles* indicate solicited courtship flights while *open circles* are natural courtship flights (see text). **c** Tb change during a single courtship display (post-courtship Tb minus pre-courtship Tb) in relation to air temperature. **d** Tb change during a single courtship display in relation to wing-beat frequency

Discussion

We have shown that females prefer hot males in sunspots, and males in sunspots show more intensive courtship display than others. It was suggested, though indirectly, that characteristic high frequency wing-beat might have a signaling function that females can detect and base mate choice on.

We have shown that (1) male thorax temperature, Tb, is influenced by direct solar radiation on his territory (Figs. 2 and 3, Tables 1 and 2), (2) Tb of ovipositing females in sunspots is higher than that at shady spots (Fig. 4, Table 3), (3) that courtship flight wing-beat frequency was positively correlated with the male Tb (Table 5), (4) that females prefer males whose Tb exceeds about 27°C (Fig. 6, Table 6),

Table 4 Multiple regression analysis of the factors associated with the change in male thorax temperature during courtship display (post-courtship Tb minus pre-courtship Tb)

Term	Estimate	SE	*t*	*P*
Ambient air temp	0.133	0.036	3.69	0.0013
Wing beat frequency	−0.058	0.038	−1.53	0.140
Hind wing length	−0.083	0.072	−1.21	0.241

Table 5 ANCOVA for the wing-beat frequency of courtship display

Term	Estimate	SE	*t*	*P*
Male Tb	1.024	0.152	6.75	<0.001
Hind wing length	−0.243	0.279	−0.87	0.391
Solicited/natural	−0.142	0.828	−0.17	0.865

Tb may not only increase because of solar exposure but also because of flight activity; however, our results suggest that the influence of flight activity is trivial (Figs. 2, 3, and 5a). The negative changes in Tb (Fig. 5c) during courtship probably occurred because it decreased due to evaporative cooling (since Tb is generally higher than Ta (Fig. 2)). For small insects like *M. costalis*, an increase in Tb will be canceled out when Ta is much lower than Tb, because the cooling rate is a function of the difference between Ta and Tb (Bartholomew 1981).

The influence of wing pigmentation on Tb was not tested in this study. However, it is clear from Fig. 1 that Tb is higher than wing temperature, which suggests that net heat transfer does not occur from wings to thorax: wings may be too thin to store heat energy and the veins may be too narrow to enable blood circulation that increase Tb quickly (May 1976). Consequently, it is unlikely that wing pigmentation influences the regulation of Tb during the activity that we measured.

Calopterygid courtship behavior has been extensively studied (Pajunen 1966; Waage 1973, 1988; Kumar and Prasad 1977; Higashi 1981; Miyakawa 1982; Nomakuchi et al. 1984; Conrad and Herman 1987; Plaistow 1997; Tsubaki et al. 1997; Plaistow and Tsubaki 2000; Thompson 2000; Raihani et al. 2008) and we know that female preference may be partially based on (a) the size of the oviposition site (Meek and Herman 1990, but see Waage 1987), or aspects of the courtship which reveal (b) the rate of water flow through the territory (Gibbons and Pain 1992;

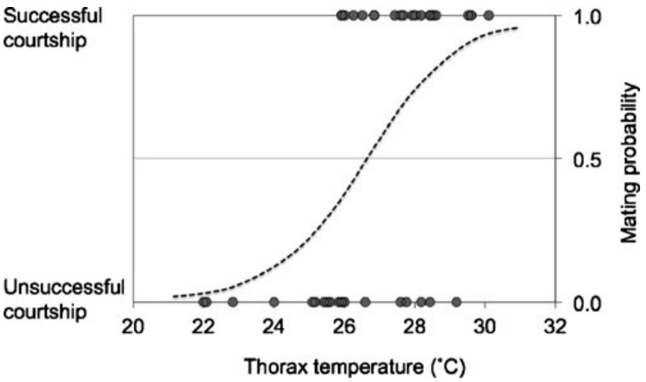

Fig. 6 Courtship success in relation to the male thorax temperature. A curve was fitted using a logistic regression equation

Table 6 Logistic regression analysis of the factors associated with the courtship success of males

Term	df	χ^2	*P*
Air temperature	1	1.354	0.245
Male Tb	1	5.480	0.019
Female Tb	1	0.875	0.349
Solar exposure (sunny/shade)	1	0.799	0.371

Siva-Jothy et al. 1995), and (c) the male's wing pigment traits (Grether 1996; Siva-Jothy 1999). Among these suggested bases for female preference, it is unlikely that female preference is based on the size of the oviposition site as there were dropworts everywhere in the stream of our study site and they are almost evenly distributed among territories. In support of this speculation, Córdoba-Aguilar (2002) showed that, in *Calopteryx haemorrhoidalis*, mating success of territorial males did not change when oviposition site was controlled. Information about water flow rate is unlikely to be transmitted during *M. costalis* courtship because males never show the display that is associated with this parameter (males dive onto the water's surface then float down stream). While it is possible that female preference is based on male wing pigment traits, our results show that courtship success varied within the same male in association with solar exposure. It is important to note that our study does not exclude other aspects/functions of courtship, and it is still open to question whether females responded directly to male wing-beat frequency.

Our study shows that courtship wing-beat frequency is correlated with male Tb, which in turn is dependent on the ambient temperature and solar exposure on the male's territory. It is important to point out that it is unclear what information is conveyed by the courtship flight (i.e., females may be focused on unmeasured traits correlated with wing-beat frequency such as maneuverability, or conspicuousness). However, it is unlikely that courtship wing-beat frequency in *M. costalis* correlates directly with male "quality", since preference for individual males changed according to their Tb (Fig. 6) and changes from time to time (Fig. 3). However, it may represent a summary measure of a portfolio of quality variables leading up to a male's success in gaining a sunny territory; thus indirectly indicating male phenotypic and/or genetic quality.

Our study shows that larger males tended to hold high quality (longer solar gain) territories. However, we did not find any indication suggesting that larger size is advantageous in the courtship display. Moreover, we could not find any clear relationship between wing-beat frequency and male body size (Table 5). These observations suggest that larger males are probably better able to acquire high-quality territories and enjoy higher mating success than smaller males. However, at each male-female encounter, the courtship success may be largely influenced by thermal conditions rather than male body size. Our data suggest that females acquire information about the direct benefits available on a particular oviposition site via the courtship display of the male: in particular, the likelihood that there is direct sunlight on the areas of the site with oviposition sites (i.e., next to the place where the male perches). Although most of the female's abdomen is under water when she oviposits (into submerged aquatic macrophytes), her thorax is always above the water surface (Fig. 1b) and remains at a relatively high temperature, especially if she lays her eggs in direct sunlight (Fig. 3, Table 5). Therefore, there are several potential benefits for females of choosing sunlight territories. Being partially submerged in a cold stream will affect a female's probability of escaping from aquatic predators or male harassment, maintaining a higher body temperature while ovipositing should therefore improve reaction times even when a female has no time for reheating.

If egg development rate is under the control of water temperature (Corbet 1999), and if faster development results in higher survival rate of larvae, laying eggs in sunny territories may also be advantageous to females.

In this study, we have shown that the courtship success of males is correlated with male Tb (Table 6), which is under influence of his exposure to direct sunlight while on his territory (Tables 1 and 2). By showing intensive courtship display toward females, we propose that males transmit information about the solar input at the oviposition site and thereby signal the direct fitness benefits of their territory to females. The fact that individual males were unattractive when they were at lower temperatures but attractive at higher temperatures (Fig. 6), strongly suggests an important choice criterion for females centers on the direct benefit of thermal gain on the male's territory. Clearly this function does not exclude the possibility that other information is also transmitted by the display or by other aspects of the male's phenotype. For example, wing beating under direct sunlight might be more attractive to females than the wing beating in shade (i.e., conspicuousness of a male might be different between sunny and shady sites). To separate the effects of solar light and body temperature on courtship success, we need further experiments controlling these factors independently.

Another reason that female mate preference should be based on male's wing beating may come from the sympatric distribution of two *Mnais* species and the males' ability for species recognition. We sometimes observed heterospecific copulations between two *Mnais* species at other study sites where both species were abundant. Although it is probably not so hard for *M. costalis* females to detect sunny oviposition sites, females that oviposit without mate guarding may be subject to frequent reproductive interference from other male *M. pruinosa*. We suggest that female fitness will be greatest when they lay eggs under conspecific male guard in a sunspot, rather than a weak guard by a male in shade. If this is the case, there should be some geographical variation in the mate preference in association with the distributional overlap of the two species.

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