Behav Ecol Sociobiol (2010) 64:685–692
DOI 10.1007/s00265-009-0886-3

ORIGINAL PAPER

Body temperature and body size affect flight performance in a damselfly

Yuka Samejima · Yoshitaka Tsubaki

Received: 12 August 2009 / Revised: 10 November 2009 / Accepted: 11 November 2009 / Published online: 5 December 2009

Abstract Flight performance is undoubtedly an important factor for behavioral success in flying insects. Though it is well-known that the flight performance is influenced by body temperature and body size, the relative importance of these factors is not well-understood. We performed laboratory experiments using the male-polymorphic damselfly *Mnais costalis* with larger territorial males and smaller non-territorial males in a population. We analyzed the effects of body temperature and body size, measured as the thoracic temperature and left hind-wing length, respectively, on two indices of flight performance: maximum lifting force and size-corrected lifting force. The latter is an index of acceleration that is related to aerial agility. The results showed that higher body temperature produced both larger maximum lifting force and larger size-corrected lifting force. In contrast, while larger size produced a larger maximum lifting force, it produced a lower size-corrected lifting force. The results of field measurements showed that territorial males had variable thoracic temperatures depending on the insolation in their territories. In contrast, non-territorial males had less variable and generally higher thoracic temperatures than territorial males as they are mostly found in sunny spots. Until now, the influence of body temperature on behavioral performance has remained unclear although considerable studies have suggested such influence. We showed, here, for the first time, combined effects of body size and body temperature on flight performance. We also showed that body temperature was influenced by the mating strategies of a damselfly. These findings provide new insights into the cost and benefits of territorial behavior in ectothermic animals.

Keywords Body temperature · Lifting force · Alternative mating strategies · Thermoregulation · Wing-color polymorphism · *Mnais costalis*

In many winged insects, flight performance is known to affect individual fitness by way of feeding, predation avoidance (Chai and Srygley 1990; Almbro and Kullberg 2008), inter-male fighting outcome, mate acquisition (Marden 1989a; Coelho and Holliday 2001; Marden and Cobb 2004), etc. Flight performance will be largely influenced by changes in an individual's body temperature (hereafter, written as Tb; Heinrich 1993; Berwaerts and Van Dyck 2004). Although the importance of Tb for mating success and individual fitness has been suggested (Willmer 1991; Kemp 2000), only a few studies have examined how Tb of insects influences reproductive success and individual fitness (Larsson and Tengo 1989; Larsson and Kustvall 1990; Stutt and Willmer 1998; Van Dyck and Matthysen 1998). One reason for this is supposed that the Tb of an individual insect fluctuates. Insects are ectothermic and what factors affect their Tb is well-understood (Heinrich 1993; Dreisig 1995; May 1995). These factors include body size, behavior (moving or not), and some environmental factors (May 1976; Stevenson 1985a; Casey 1992; Heinrich 1993) with ambient temperature and solar exposure playing major roles in most insects (Stevenson 1985b; Heinrich 1993). Whenever insects move from one site to another, their Tb can change which makes it hard to assess the effect of Tb on behavioral performance.

Communicated by M. Siva-Jothy

Y. Samejima (✉) · Y. Tsubaki
Center for Ecological Research, Kyoto University,
2-509-3 Hirano,
Otsu, Shiga, Japan
e-mail: samejima@ecology.kyoto-u.ac.jp

Y. Tsubaki
e-mail: tsubaki@ecology.kyoto-u.ac.jp

In addition to body temperature, body size has also been reported to influence flight performance in insects (Carchini et al. 2000; Coelho and Holliday 2001; Alcock and Kemp 2006; Serrano-Meneses et al. 2007). Marden (1989a, b) reported that flight muscle ratio (FMR), which increased with body size, positively affected aerial agility. In contrast, some other studies suggested an advantage of small body size for flight agility and behavioral performance of flying insects. These confusing finding about the effect of body size indicate that body size is not necessarily a good index of fitness (Zamudio and Crill 1995; Stoks 2000; Carchini et al. 2001) despite being a commonly used one. Thus, although both body temperature and body size have previously been suggested to explain between-individual variations in flight performance, the relative importance of these factors has not been evaluated simultaneously.

The Japanese damselfly *Mnais costalis* (Odonata: Calopterygidae) provides a unique opportunity to study the interaction between Tb and body size, and their effects on flight performance. In this species, the males of a population show distinct microhabitat selection and body size in association with wing color. Their fitness characteristics associated with flight performance may be affected by complex interplays between Tb and body size. The wing-color polymorphism (orange- and clear-winged males) of *M. costalis* is genetically controlled (Tsubaki et al. 1997) and associated with alternative mating strategies (Tsubaki 2003). Orange-winged males are larger than clear-winged males, and hold territories around an oviposition substrate such as wet, dead wood, or semi-submerged or emerging plants in low mountain streams. In contrast, clear-winged males do not hold territories, and try to sneak copulations with females ovipositing in orange-winged males' territories. Territorial orange-winged males perch near oviposition substrates. The degree of insolation in each territory will depend on the condition of the forest canopy at the site. Therefore, differences in Tb among territorial males may occur. What impact variation in Tb has on male flight performance in *M. costalis* is currently unknown. In addition, larger male size typically favors mating behaviors in insects (Thompson and Fincke 2002; Alcock and Kemp 2006), although these species also maintain small males. Investigating the effect of body size on flight performance in this damselfly might provide a morph-dynamic explanation of this species' mating behavior.

In this study, we examined the effects of Tb and body size on flight performance in the laboratory. We also measured the Tb variation of both orange and clear-winged males in the field. Lifting force is defined as Newton, and is used as a general measure of flight performance. In still air, flying animals require that lifting force exceeds their body mass in order to control aerial movement. Hence, maximum lifting force is a functionally important component of flight performance (Marden 1987). We analyzed the relative impact of Tb and body size on vertical maximum lifting force in *M. costalis*, and compared the vertical maximum lifting force between the two morphs.

Materials and methods

Study site and species

Field observations and the collection of animals for lab experiments were carried out at a mountain stream in Gozenyama, Ibaraki Prefecture, northeast Japan (36°33′N 140°17′E; elevation, about 100 m) in mid-June, 2005. The study site was a narrow and shallow stream that was surrounded by trees and bushes, which created sunny and shady spots. Adult emergence of *M. costalis* occurs in early May at this study site. After eclosion, there is a teneral feeding period that lasts for approximately a week. During this time, individuals develop the majority of their flight muscles (Plaistow and Tsubaki 2000). At this study site, the ratio of orange to clear-winged males is approximately 50:50. Orange-winged males are significantly larger than clear-winged males (Tsubaki et al. 1997; Plaistow and Tsubaki 2000).

Measurement of body temperature

As a measure of body temperature, we measured the thoracic surface temperature of damselflies non-invasively using an infrared thermographic camera (Chino CPA-1000). Surface temperature may not exactly represent the temperature of internal flight muscles. Therefore, we estimated the core thorax temperature using a regression equation of thoracic surface temperature against core thorax temperature simultaneously measured using micro-thermocouples (diameter of wires 0.05). For these measurements, we used males separately collected at the study site.

Measurement of maximum lifting force

For the experiments, *M. costalis* males were caught at our study site and brought to the laboratory. All individuals were tested within 24 h of being captured. Prior to lifting force measurements, we controlled Tb of males by keeping them in a constant temperature room at 15, 20, or 25°C, or by warming them with a halogen lamp. In this way, we could prepare males with variable thorax temperatures ranging from 15°C to 35°C, roughly equivalent to the range of field measurements (see below). Then, the experiment was conducted. We used 0.3-mm fishing line tied between the fore and hind wings of individuals to create tethers for each test subject. At the other end of the fishing line, twenty 0.25-g weights were attached at 10-mm intervals. The beaded weights were placed at the bottom of a 2,000 ml measuring cylinder. The length between the damselfly and the first weight was 500 mm over the height of measuring cylinder. Treated damselflies were put at the edge for a time to acclimatize to their surroundings. Subjects were encouraged to fly by touching their legs with a pair of forceps. Once subject were flying, maximum lifting force was recorded as the maximum number of weights lifted within a 10-s time interval. Unlike the methods used in previous studies, which required various weights and repeated trials (Marden 1987), our method enabled us to measure maximum lifting force at a particular body temperature within a single trial.

Measurements of body size and flight muscle mass

After the experiment, all specimens used were measured for abdomen length (abl) and left hind wing length (hwl); then, dried in an 80°C oven for a day, and dry body mass was measured. Flight muscle mass was obtained using the following procedure. Heads, legs, wings, and abdomens of specimens were removed and the thorax part was soaked in chloroform to elute fat. After weighing, the fatless thoraxes were soaked in 0.35 $\text{mol}\cdot\text{l}^{-1}$ NaOH for a day before being re-weighed. Dry flight muscle mass was estimated by subtracting this mass from the dry fatless mass. These methods were based on that of Marden (1987, 1989a) and Plaistow and Siva-Jothy (1996).

Field measurement of Tb

Field observations were made between 11:00 and 16:00 on fine days when *M. costalis* were reproductively active. All observed damselflies were captured in a net and their thoracic temperature was measured as their Tb using the same non-invasive thermovision camera technique described above. In odonates, thoracic temperature is particularly important because flight muscle within the thorax is largely responsible for defining patterns of activity and energy expenditure (May 1976; Marden 1989a). All field measurements of thoracic temperature were made within 10 s from the time of capture. We were careful not to touch the bodies of subjects with our hands, instead handling the wings of captured individuals. If the time from capture to measurement exceeded 10 s or if we accidentally touched the thorax or abdomen, the data were discarded. We also recorded the degree of shade or sunlight on subjects' perch sites prior to capture. Following measurement of Tb, individuals were uniquely numbered on the hind wing using enamel pens and released to avoid repeated measurements on the same individuals. Ambient temperature was successively recorded by a thermometer data logger at a shaded point 1.5 m above the water.

Analysis

Prior to the analysis, the value of maximum lifting force was log-transformed to improve normality. Left hind wing length was used as a measure of body size. A general linear mixed model was used to analyze the effects of Tb and body size on lifting force. Male morph was included as a fixed factor to analyze the relationship between Tb and flight performance. The individuals were put into the analysis as random effect because of repeated measurement of maximum lifting force. All analyses were performed using R 2.5.1 free software.

Results

The relationship between surface thorax temperature measured with a thermal camera (Ts) and core thorax temperature measured with micro-thermocouples (Tb) was almost linear ($\text{Tb}=0.836\text{Ts}+3.27$, $r^2=0.988$, $P<0.0001$) within the range between 17 and 33°C. We estimated core thorax temperature (Tb) using this linear function. Hereafter, we use the core thorax temperature as Tb in this study.

Body size and morphological traits of males

Table 1 summarizes the morphological traits of males. All traits of orange-winged males were significantly larger than those of clear-winged males. Flight muscle mass was significantly correlated with the body mass (Pearson's correlation, $r=0.97$, $n=29$, $P<0.01$, Fig. 3a). Hind wing length was also significantly correlated with the body mass

Table 1 Morphological traits of *Mnais costalis* males

	Orange-winged males ($n=17$)			Clear-winged males ($n=13$)		
	Mean	SE	CV (%)	Mean	SE	CV (%)
Dry body mass (mg)	55.06	1.80	13.05	43.57	1.31	10.43
Hind-wing length (mm)	38.03	0.40	4.22	35.00	0.40	3.92
Abdomen length (mm)	45.91	0.42	3.66	42.85	0.38	3.05
Muscle mass (mg)	19.24	0.77	16.10	13.38	0.56	14.63

(Pearson's correlation, $r=0.65$, $n=29$, $P<0.01$, Fig. 3b). There was no significant difference in the relationship between orange-winged and clear-winged morphs (analysis of covariance, hwl $df=1$, $F_{1,376.2}=53.07$, $P<0.01$, male morph $df=1$, $F_{50.02}=1.93$, $P=0.18$, hwl×male morph $df=1$, $F_{17.6}=0.68$, $P=0.42$), suggesting that the same allometric relationship can be applied to both morphs.

Maximum lifting force

We used two indices of the flight performance of males: the maximum lifting force and the size-corrected maximum lifting force. The size-corrected maximum lifting force is an index of acceleration (force is the product of mass and acceleration). Tb had significant positive effects on both the maximum lifting force ($r^2=0.497$, Fig. 1a) and the size-corrected lifting force ($r^2=0.226$, Fig. 2a) while body size had a positive effect on the maximum lifting force ($r^2=0.096$, Fig. 1b) and a negative effect on the size-corrected lifting force ($r^2=0.44$, Fig. 2b). The results of general linear mixed model (GLM) for the maximum lifting force and the size-corrected lifting force are shown in Tables 2 and 3, respectively. Both results of GLM included individuals as random effect. While Tb and body size had significant effects on the maximum lifting force and the size-corrected maximum lifting force, male morph was not a significant predictor of them.

Body temperature in the field

The Tb of *M. costalis* males measured in the field is shown in Fig. 4. The Tb of males in shady spots was, on average, almost equal to ambient temperature. The Tb of males in

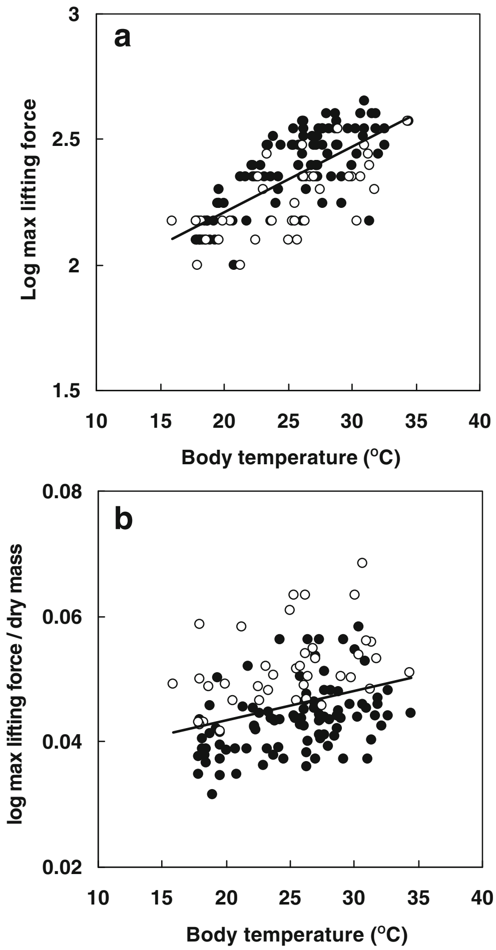

Fig. 1 Linear regression curves showing **a** maximum lifting force as a function of Tb in two male morphs $y=0.026x+1.692$, $r^2=0.497$ and **b** size-corrected maximum lifting force as a function of Tb in two male morphs $y=0.0005x+0.034$, $r^2=0.096$. *Open circles* clear-winged males, *closed circles* orange-winged males, $n=134$

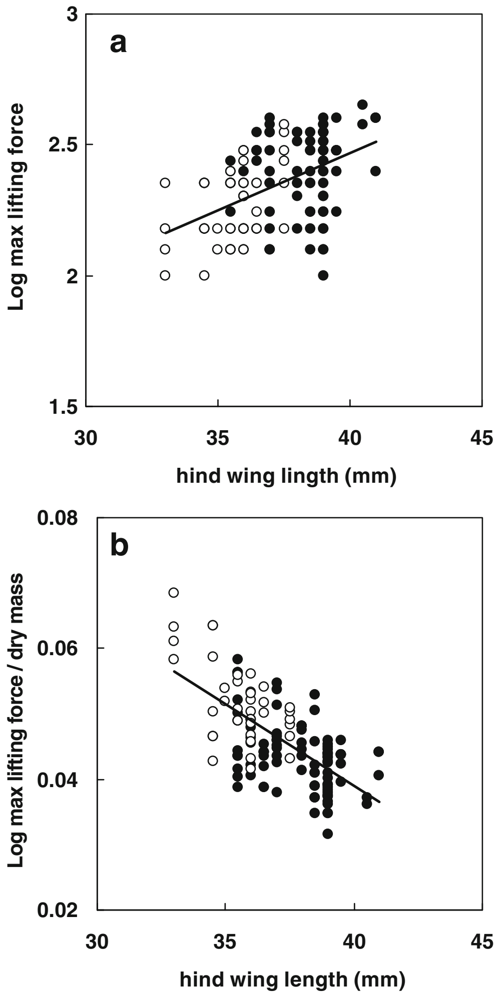

Fig. 2 Linear regression curves showing **a** maximum lifting force as a function of hind-wing length in two male morphs, $y=0.0434x+0.7334$, $r^2=0.226$ and **b** size-corrected maximum lifting force as a function of hind wing length in two male morphs, $y=-0.0025x+0.1388$, $r^2=0.4396$. *Open circles* clear-winged males, *closed circles* orange-winged males, $n=134$

Table 2 Results of GLM test for maximum lifting force

	Estimated value	SE	t	P
Log maximum lifting force				
Intercept	366.30×10^{-3}	319.82×10^{-3}	1.1	0.255
Tb	25.20×10^{-3}	1.61×10^{-3}	15.64	<0.001
Hind wing length	35.40×10^{-3}	9.00×10^{-3}	3.93	0.001
Male morph	31.20×10^{-3}	35.44×10^{-3}	0.88	0.387

sunny spots was significantly higher than that of males in shady spots, and clear-winged morph had, on average, higher Tb than orange-winged (two-way ANOVA, Table 4; orange-winged males Fig. 4a; sunlit=27.46±1.90°C, shade=23.15±2.30°C, clear-winged males Fig. 4b; sunlit=28.38±2.48°C, shade=24.69±1.76°C, shown as mean±SD). The difference in Tb of males in sunlight and in shade was larger in orange winged males.

Discussion

In this study, we showed that Tb had a significant positive effect on the maximum lifting force and the size-corrected lifting force of *M. costalis* males (Figs. 1a and 2a). This is not surprising because the power output of insect flight muscle increases with temperature (Stevenson and Josephson 1990), and wing-stroke frequency is increased at elevated flight muscle temperature (May 1981). Body size had also a positive effect on the maximum lifting force (Table 2, Fig. 1a) probably because the flight muscle mass increases with body size (Fig. 3a). In contrast, size-corrected lifting force (a measure of acceleration) decreased with the increase of body size (Fig. 2b). That is, size-corrected lifting force decreased with increased FMR (flight muscle/body mass), which increased with body size (Fig. 3a). This result suggests that increased FMR is not necessarily linked to an increase of flight agility. Our result apparently contradicted a previous study by Marden (1989a, b), which showed an increase of agility with a substantial increase of FMR. In the case of *M. costalis*, however, the rate of increase of FMR with the increase of body size might be too small to increase the flight agility. Consequently, orange-winged males might have larger maximum lifting force but smaller size-corrected lifting force than clear-winged males (Table 3, Figs. 1 and 2).

Maximum lifting force is likely to be correlated with female lift for tandem formation and inter-male competition, especially aerial direct strike. Orange-winged males, which have larger body size than clear-winged males, may have higher ability to perform these. In contrast, size-correlated lifting force should be associated with aerial agility such as maneuverability and aerial acceleration, which may be causes of advantages of small body size in mating success by way of sneaking, mate acquisition in air, and predation avoidance. Smaller clear-winged males may have such advantages.

The results of our field study showed that Tb of males in sunlight was significantly higher than that of males in shade in both male morphs (Table 4, Fig. 4). In *M. costalis*, the Tb of males in the shade was almost equal to standard ambient temperature, while Tb in sunlight was higher than Tb in shade because of solar radiation. Like many other insects, *Mnais* damselflies accomplish thermoregulation by changing perch sites.

There was a significant difference in Tb between orange and clear-winged males (Table 4). This was mainly because orange-winged males had lower Tb than clear-winged males in shade (Fig. 4), rather than the because of a difference between morphs in sunny spots. This is probably because orange-winged males are territorial and cannot leave their territories. The Tb of orange-winged males will depend upon how much sunlight falls on their territory. Most territories are only sunny for limited periods throughout the day. Orange-winged males that had lower Tb than ambient temperature (Fig. 4a) were probably positioned at, or near, the water surface in shaded territories where the temperature was below the ambient temperature. Thus, the opportunity of orange-winged males to thermoregulate is constrained because territorial males need to be site-fixed to protect their territories. Limitation of solar input and constraints on thermoregulation may explain the lower Tb

Table 3 Results of GLM test for size-corrected maximum lifting force

	Estimated value	SE	t	P
Size-corrected log maximum lifting force				
Intercept	114.66×10^{-3}	20.19×10^{-3}	5.68	<0.001
Tb	0.50×10^{-3}	0.03×10^{-3}	16.53	<0.001
Hind wing length	-2.11×10^{-3}	0.57×10^{-3}	−3.72	0.001
Male morph	-3.31×10^{-3}	2.26×10^{-3}	−1.46	0.156

Table 4 Results of two-way ANOVA for Tb of males in the field

	df	*F*	*P*
Tb in the field			
Male morph	1	18.48	<0.001
Solar exposure	1	133.98	<0.001
Solar exposure × male morph	1	0.79	0.370

of orange-winged male in the shade. This might be a disadvantage of being territorial. Orange-pigmented wings are not likely to affect the damselfly's thoracic temperature because the hemolymph vessels of the wing are so fine that they cannot efficiently conduct heat from the wing to the thorax (May 1976). In contrast, many clear-winged males caught in the shade had higher Tb than orange-winged males in the shade. They had probably been at sunny site until a short time before. The thorax temperature usually became stable within 3 min when a male changed its perch from a sunny site to a shaded site, or vice versa (Samejima and Tsubaki, unpublished data). Clear-winged males can thermoregulate by changing perch sites and their thermoregulation is not constrained by having to defend a territory. In fact, most clear-winged males usually perch above the trees where it is sunny and only fly down to near the water surface (where the temperature is low) if they are trying to find females. This difference in behavior may explain why clear-winged males with Tb lower than standard ambient temperatures were rarely observed (Fig. 4b).

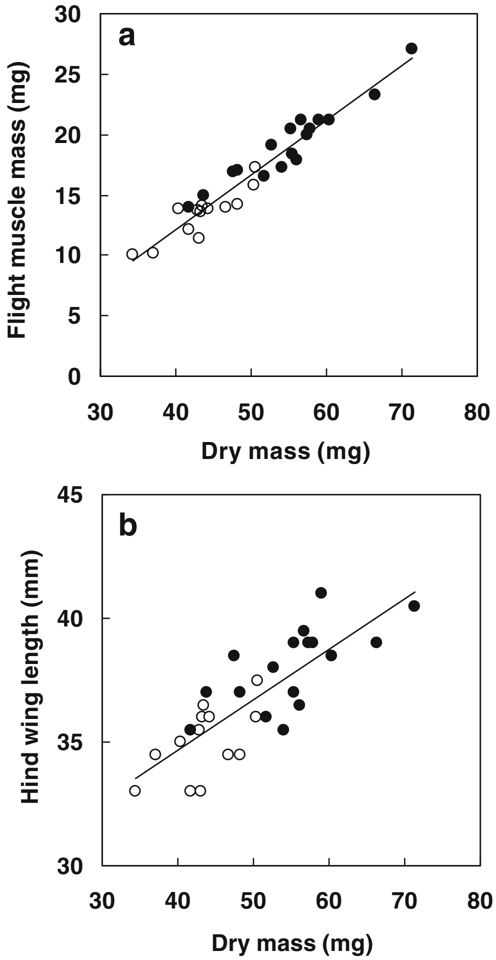

Fig. 3 Graphic analysis of the correlation **a** between flight muscle mass and dry body mass, $y=0.4527x-5.9711$, $r^2=0.932$, $n=29$ and **b** between left hind wing length and dry body mass, $y=0.2041x+26.4939$, $r^2=0.6498$, $n=29$. *Open circles* clear-winged males, *closed circles* orange-winged males

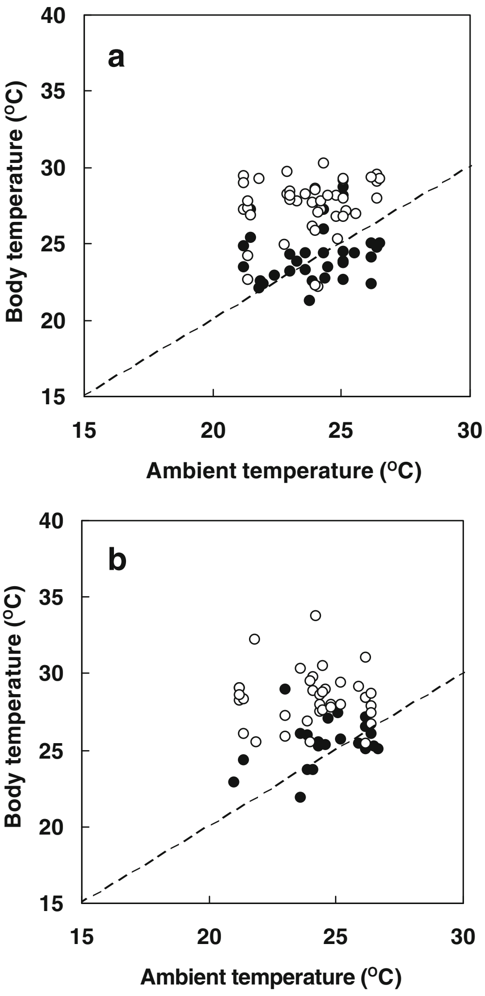

Fig. 4 The Tb of *M. costalis* males in the field **a** orange-winged males, $n=87$ and **b** clear-winged males, $n=63$. *Open circles* the Tb of males in sunlight, *closed circles* the Tb of males in shade; the discontinuous line is drawn through the points at which the body temperature and ambient temperature are same

The limited thermoregulation and different environmental conditions of each territory in orange-winged males could result in a large variation in orange-winged male flight performance. Males with territories that are exposed to direct sunlight for longer during the day may maintain higher flight ability than males with more shaded territories. Flight performance is important for male mating success (Neems et al. 1998; Serrano-Meneses et al. 2007) through male-male competition (Marden and Cobb 2004; Moya-Larano et al. 2007), and courtship behavior (Marden 1989b), and evasion of predation risk during mating (Almbro and Kullberg 2009). At our study site, territorial males with territories in direct sunlight appeared to have much higher reproductive success than other males (Tsubaki and Samejima, unpublished data). This could be because these males had better flight performance (Tsubaki et al. unpublished data) or, alternatively, it could be that females prefer to oviposit in warm territory sites where their egg developmental rates are higher (Corbet 1999).

Large male size has often been suggested to be advantageous for longevity and stamina for flight time, etc. (Neems et al. 1998; Serrano-Meneses et al. 2007). However, in *M. costalis*, orange-winged males have been suggested to have shorter longevity and rapid fat decrease during their lifetime compared with clear-winged males (Tsubaki et al. 1997; Plaistow and Tsubaki 2000). Territorial males at sunny spots may enjoy a higher mating rate. However, at the same time, they are forced to keep a high Tb during the time of solar exposure. This constraint may partly explain why territorial behavior is more energetically costly than sneaking behavior (Plaistow and Siva-Jothy 1996). To confirm this effect, we would need to compare the duration of solar exposure time between the two male morphs.

Clear-winged males are likely to have higher aerial agility. Our results suggested two reasons for this. First, they can thermoregulate by moving around because they are not site-fixed. That would enable them to increase Tb only if they need high flight activity. Second, they have higher size-corrected lifting force (Fig. 2b) because they are smaller than orange-winged males. In fact, they appear to fly faster than orange-winged males. When territorial orange males chase intruding clear-winged males, we have never seen orange-winged males catching up with fleeing clear-winged males, whereas it is often the case that they catch fleeing orange-winged males in the field. Although this could also be because the clear-winged intruders are less visible and the orange-winged intruders are often young or fat-depleted old males (Plaistow and Tsubaki 2000), difference in flight performance seems to be an additional cause of the asymmetrical fighting. Higher average flight ability of clear-winged males caused by these factors may lead to smaller variation of lifetime reproductive success than that of orange-winged males. Several empirical studies have also suggested the advantage of small male size for flight activity and consequently increased male mating success (McLachlan and Allen 1987), e.g., in damselflies *Ischnura elegans* and *Lestes viridis* (Carchini et al. 2000; De Block and Stoks 2007) and the beetle *Stator limbatus* (Moya-Larano et al. 2007). Small male size may be advantageous for non-territoriality (Carchini et al. 2000).The present study suggests that the ability to thermoregulate is another advantage favoring non-territoriality.

In *M. costalis*, Tsubaki et al. (1997) demonstrated a different distribution pattern of lifetime reproductive success (LRS) among male morphs. In orange-winged males, a few males have a very high LRS, while the majority of orange-winged males have a low LRS, whereas in clear-winged males, there is much less variation in LRS. Our results suggest that the cause of this different pattern of LRS is the result of behavioral variation in alternative mating strategies associated with the different constraints of thermoregulation. The alternative mating strategies of *M. costalis* are associated with the males' color polymorphism. Therefore, in addition to the effect of negative density dependent selection, such constraints on thermoregulation may also contribute to the maintenance of the intraspecific polymorphism. Our preliminary field survey suggested that the proportion of orange-winged males was higher in sunny-site populations, whereas clear-winged males dominated in shady-site populations (Tsubaki, unpublished data), although several other factors also seem to influence the local variation of the morph proportions.

Acknowledgments We would like to thank Stewart Plaistow for reading and providing many valuable comments on an earlier version of this paper and Elizabeth Nakajima for critical reading of the manuscript. This research was financially supported in part by Global COE Program A06 to Kyoto University and Japan Ministry of Education, Science and Culture (No. 19201047 to YT).

References

Alcock J, Kemp D (2006) The behavioral significance of male body size in the tarantula hawk wasp *Hemipepsis ustulata* (Hymenoptera: Pompilidae). Ethology 112:691–698

Almbro M, Kullberg C (2008) Impaired escape flight ability in butterflies due to low flight muscle ratio prior to hibernation. J Exp Biol 211:24–28

Almbro M, Kullberg C (2009) The downfall of mating: the effect of mate-carrying and flight muscle ratio on the escape ability of a pierid butterfly. Behav Ecol Sociobiol 63:413–420

Berwaerts K, Van Dyck H (2004) Take-off performance under optimal and suboptimal thermal conditions in the butterfly *Pararge aegeria*. Oecologia 141:536–545

Carchini G, Chiarotti F, Di Domenico M, Paganotti G (2000) Fluctuating asymmetry, size and mating success in males of *Ischnura elegans* (Vander Linden) (Odonata: Coenagrionidae). Anim Behav 59:177–182

Carchini G, Chiarotti F, Di Domenico M, Mattoccia M, Paganotti G (2001) Fluctuating asymmetry, mating success, body size and heterozygosity in *Coenagrion scitulum* (Rambur) (Odonata: Coenagrionidae). Anim Behav 61:661–669

Casey TM (1992) Biophysical ecology and heat-exchange in insects. Am Zool 32:225–237

Chai P, Srygley R (1990) Predation and the flight, morphology, and temperature of neotropical rain-forest butterflies. Am Nat 135:748–765

Coelho J, Holliday C (2001) Effects of size and flight performance on intermale mate competition in the cicada killer, *Sphecius speciosus* Drury (Hymenoptera: Sphecidae). J Insect Behav 14:345–351

Corbet PS (1999) Dragonflies: behavior and ecology of odonata. Comstock Pub Assoc, New York

De Block M, Stoks R (2007) Flight-related body morphology shapes mating success in a damselfly. Anim Behav 74:1093–1098

Dreisig H (1995) Thermoregulation and flight activity in territorial male graylings, *Hipparchia semele* (Satyridae), and large skippers, *Ochlodes venata* (Hesperiidae). Oecologia 101:169–176

Heinrich B (1993) The hot-blooded insects: strategies and mechanisms of thermoregulation. Harvard University Press, Cambridge

Kemp D (2000) Contest behavior in territorial male butterflies: does size matter? Behav Ecol 11:591–596

Larsson F, Kustvall V (1990) Temperature reverses size-dependent male mating success of a cerambycid beetle. Funct Ecol 4:85–90

Larsson FK, Tengo J (1989) The effects of temperature and body size on the mating pattern of a gregariously nesting bee, *Colletes-Cunicularius* (Hymenoptera, Colletidae). Ecol Entomol 14:279–286

Marden JH (1987) Maximum lift production during takeoff in flying animals. J Exp Biol 130:235–258

Marden JH (1989a) Bodybuilding dragonflies: costs and benefits of maximizing flight muscle. Physiol Zool 62:505–521

Marden JH (1989b) Effects of load-lifting constraints on the mating system of a dance fly. Ecology 70:496–502

Marden J, Cobb J (2004) Territorial and mating success of dragonflies that vary in muscle power output and presence of gregarine gut parasites. Anim Behav 68:857–865

May ML (1976) Thermoregulation and adaptaion to temperature in dragonflies (Odonata:Anisoptera). Ecol Monogr 46:1–32

May M (1981) Wingstroke frequency of dragonflies (Odonata: Anisoptera) in relation of temperature and body size. J Comp Physiol 144:229–240

May ML (1995) Dependence of flight behavior and heat production on air temperature in the green garner dragonfly *Anax junius* (Odonata: Aeshnidae). J Exp Biol 198:2385–2392

McLachlan AJ, Allen DF (1987) Male mating success in Diptera—advantages of small size. Oikos 48:11–14

Moya-Larano J, El-Sayyid MET, Fox CW (2007) Smaller beetles are better scramble competitors at cooler temperatures. Biol Let 3:475–478

Neems RM, Lazarus J, McLachlan AJ (1998) Lifetime reproductive success in a swarming midge: trade-offs and stabilizing selection for male body size. Behav Ecol 9:279–286

Plaistow S, Siva-Jothy M (1996) Energetic constraints and male mate-securing tactics in the damselfly *Calopteryx splendens xanthostoma* (Charpentier). Proc R Soc Lond B Biol Sci 263:1233–1239

Plaistow S, Tsubaki Y (2000) A selective trade-off for territoriality and non-territoriality in the polymorphic damselfly *Mnais costalis*. Proc R Soc Lond B Biol Sci 267:969–975

Serrano-Meneses MA, Cordoba-Aguilar A, Mendez V, Layen SJ, Szekely T (2007) Sexual size dimorphism in the American rubyspot: male body size predicts male competition and mating success. Anim Behav 73:987–997

Stevenson R (1985a) Body size and limits to the dairy range of body temperature in terrestrial ectotherms. Am Nat 125:102–117

Stevenson RD (1985b) The relative importance of behavioral and physiological adjustments controlling body temperature in terrestrial ectotherms. Am Nat 126:362–386

Stevenson R, Josephson R (1990) Efects of operating frequency and temperature on mechanical power output from moth flight muscle. J Exp Biol 149:61–78

Stoks R (2000) Components of lifetime mating success and body size in males of a scrambling damselfly. Anim Behav 59:339–348

Stutt A, Willmer P (1998) Territorial defence in speckled wood butterflies: do the hottest males always win? Anim Behav 55:1341–1347

Thompson DJ, Fincke OM (2002) Body size and fitness in Odonata, stabilising selection and a meta-analysis too far? Ecol Entomol 27:378–384

Tsubaki Y (2003) The genetic polymorphism linked to mate-securing strategies in the male damselfly *Mnais costalis Selys* (Odonata: Calopterygidae). Popul Ecol 45:263–266

Tsubaki Y, Hooper R, Siva-Jothy M (1997) Differences in adult and reproductive lifespan in the two male forms of *Mnais pruinosa costalis Selys* (Odonata: Calopterygidae). Res Popul Ecol 39:149–155

Van Dyck H, Matthysen E (1998) Thermoregulatory differences between phenotypes in the speckled wood butterfly: hot perchers and cold patrollers? Oecologia 114:326–334

Willmer P (1991) Thermal biology and mate acquisition in ectotherms. Trends Ecol Evol 6:396–399

Zamudio KRRBH, Crill WD (1995) Bigger isn't always better: body size, developmental and parental temperature and male territorial success in *Drosophila melanogaster*. Anim Behav 49:671–677