ARTICLE

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Seasonal changes in the territorial behaviour of the satyrine butterfly *Lethe diana* are mediated by temperature

Abstract The territorial behaviour of butterflies often changes with temperature. The satyrine butterfly *Lethe diana* has three generations a year, and males display territorial behaviour in the May–June and September–October generations, but not in the July–August generation. This study investigated the relationship between this seasonal change in mate-locating behaviour and thermoregulation. When *L. diana* was able to hold a territory, thoracic temperature ranged from 23.8 to 33.6°C. This temperature was mainly influenced by environmental temperature based on air temperature, solar radiation, and wind, and metabolic heat was estimated to increase thoracic temperature by about 5°C in the May–June generation. When environmental temperature at a territorial site was within this range of the thoracic temperature minus the metabolic heat (approximately 5°C), *L. diana* males held territories. Since territorial sites were selected irrespective of the temperature, *L. diana* could not hold a territory when the temperature of the territorial site exceeded the threshold. In July–August, the temperature of the territorial site was almost always above the suitable range. These results suggest that seasonal change in territoriality of *L. diana* is due to behavioural thermoregulation.

Key words *Lethe diana* · Operative temperature · Seasonal change · Territorial behaviour · Thermoregulation

Introduction

Males of many butterfly species hold territories for mating (Shreeve 1992). Since territories are visited by both females and rival males attempting to take over a territory, contests for territories often occur (e.g. Davies 1978; Alcock and O'Neill 1986; Rosenberg and Enquist 1991; Lederhouse and Scriber 1996; Fischer and Fiedler 2001). To win a contest, males require high flight endurance. Butterflies maintaining high body temperatures are able to fly longer and are more likely to win a territorial bout (Stutt and Willmer 1998). Thus, males maintaining higher body temperatures are advantageous in their territories.

Since butterflies are ectothermic, their body temperature is influenced by air temperature, solar radiation, and wind velocity (Tsuji et al. 1986). To keep their body temperature high, butterflies have to choose sites or time periods with favourable temperature while they are territorial (Ravenscroft 1994; Rutowski et al. 1994; Bitzer and Shaw 1995). However, an adversely high temperature prevents butterflies from holding a territory, leading to changes in their mating tactics (Wickman 1985, 1988; Alcock 1994). Thus, the mating behaviour of ectotherms, such as the territorial behaviour of butterflies, is strongly affected by thermal physiology (see Willmer 1991).

Males of the satyrine butterfly *Lethe diana* (Butler) hold territories around sunlit branch tips that face an open space in the afternoon (Fukuda et al. 1984; Ide 2002). *L. diana* has three generations a year, and territorial behaviour is observed in the generations in May–June and in September–October, but not in July–August (Ide 2002). Since the only time when *L. diana* males do not hold territories is during the summer, it is conceivable that high temperatures prevent the butterflies from doing so; however, mate-locating behaviour has been regarded as an optimal strategy affected by population density, operational sex ratio, or the distribution of each sex (e.g. Scott 1974; Dennis and Shreeve 1988; Rutowski 1991; Sivinski and Petersson 1997; Wickman and Rutowski 1999). In this study, I assess the thermal conditions of territories by measuring *L. diana* body temperature. I then examine whether the seasonal changes in territorial behaviour are caused by thermoregulation.

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Materials and methods

Study site

The field study was carried out at the Kamigamo Experimental Forest Station, Graduate School of Agriculture, Kyoto University, in the north of Kyoto City, Japan (35°04′N, 135°46′E, 140 m above sea level). This area is covered with mixed second-growth forest and a coniferous forest plantation. Bushes of bamboo grass *Sasa veitchii* var. *hirsuta* (Koidzumi), the main food plant of *L. diana* in this area, are scattered on the forest floor. Clearings are also present, providing a mosaic-like environment.

Adults of *L. diana* appear twice a year in Kyoto: from May to mid-June and from mid-July to early October. In the latter period, there are actually two generations (J.-Y. Ide, unpublished data). To separate the two generations, census data were divided into two groups, that is, from July to August and from September to October (Ide 2000a, 2002). In this way, three generations can be distinguished: the May–June, July–August, and September–October generations.

Thoracic temperature of butterflies in the field

During the flight season of *L. diana* in 2000, I visited the field site on almost every sunny day and measured the thoracic temperature (T_{th}) of butterflies, using a portable digital thermometer (Model 2455, Yokogawa Electric Works Ltd.) with a hypodermic thermocouple probe (0.5 mm diameter). After locating a butterfly and recording its sex and behaviour, I captured it with an insect net. I then quickly held it with its wings closed over its back and inserted the probe into the centre of the thorax from the ventral side. The time from capture to measurement never exceeded 10 s. After measuring T_{th}, the butterfly was released. I also measured air temperature of the site occupied by the butterfly before capture by holding the probe more than 15 cm from the ground with the sunlight blocked off.

Behaviour was categorised into three types upon sighting: flying, resting, or displaying territorial behaviour. A male was regarded as displaying territorial behaviour if (1) he quickly approached any intruders and then returned to his perch site after pursuit, or (2) he perched on the outer branch tip where territorial behaviour (as described above) was often observed in the preliminary investigation. The effects of behaviour, sex, or generation on T_{th} were analysed by ANCOVA.

In addition to T_{th} and behaviour, I recorded the air temperature and light intensity of the location where the butterfly was captured. Light intensity was measured using a portable digital illumination meter (TMS 870, Tasco Japan Co. Ltd.). To test whether air temperature affected the butterfly's choice of light intensity of microhabitats, regression analysis was carried out. To make variance in light intensity independent of the mean, light intensity was ln-transformed.

Diurnal pattern of territorial behaviour

To investigate the diurnal activity patterns of territorial behaviour of *L. diana*, transect censuses were conducted 20 times. I walked along a fixed route, approximately 400 m long, every hour from dawn to dusk, counting the number of male butterflies in the area within 5 m of the centre of the route. The behaviour of each butterfly was recorded and classified into three types as described above. This census was made for 20 days in 1999 and 2000 (9 days for the May–June generation, 10 days for the July–August generation, and 1 day for the September–October generation).

Operative temperature at territories

To estimate the thermal environment of territories during the flight season of each generation, I measured the operative (environmental) temperature (T_e). Thermal environments are influenced not only by air temperature but also by radiation load and convective effects of wind (Chappell 1982; Tsuji et al. 1986). These factors can be integrated into a single measure, T_e (Bakken et al. 1985; Bakken 1992), which can be estimated by mounting a freshly killed insect on a thermocouple probe and placing it in the field environment (Dreisig 1995; Frears et al. 1997; Schultz 1998; Bishop and Armbruster 1999; Stone et al. 1999). I measured T_e at the thorax using a freshly killed male *L. diana* with its wings open every hour from sunrise to sunset at the site often occupied by territorial males in the preliminary investigations. The butterfly for measuring T_e was killed by freezing for 1 day and was thawed 2 h before the beginning of the investigation. In 2000, this measurement was carried out on the same days as transect censuses.

Critical thermal maxima

To estimate the upper critical temperature for *L. diana*, I placed a butterfly in a clear plastic box (1,000 cm^3) and heated the box under an incandescent light. When the butterfly was no longer able to stand and fell down repeatedly, I quickly took it out of the box and measured its thoracic temperature. I repeated this measurement with 15 butterflies (3 males and 12 females) that were caught in September as larvae and were reared indoors at 25°C until eclosion.

Results

Diurnal pattern of territorial behaviour

In both 1999 and 2000, territorial behaviour was observed during every transect census in May–June (Fig. 1). In the territories, males usually perched on the sunlit branch tips that faced an open space with their wings open. When an intruder flew within a 1-m radius of the territory owner, the owner took off and chased the intruder, whether the
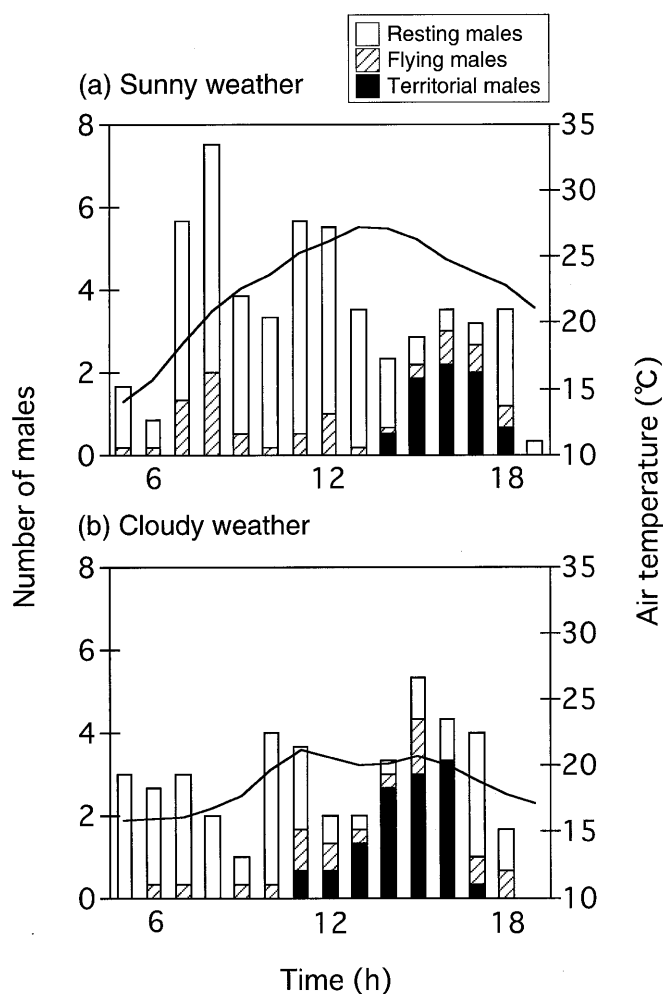
Fig. 1. Diurnal pattern of male *Lethe diana* in the May–June generation on (**a**) sunny weather days (2 days in 1999 and 4 days in 2000) and (**b**) cloudy weather days (1 day in 1999 and 2 days in 2000). *Stack bars* show average number of males in each behavioural category, and *lines* show average air temperature. Details of the behavioural categories are described in the text

Table 1. Starting and ending time of territorial behaviour of *Lethe diana* in May–June (mean ± SE). Both starting and ending time differed significantly depending on weather (Mann–Whitney U test)

	Sunny days ($n = 6$)	Cloudy days ($n = 3$)	U	P
Starting time (h)	14.83 ± 0.31	12.67 ± 0.88	1.00	<0.05
Ending time (h)	17.33 ± 0.21	16.33 ± 0.33	2.00	<0.05

intruder was conspecific or not. When the intruder was heterospecific, the owner immediately came back to the site where he had been. For conspecific males, the owner chased the intruders until they left the territory, and then the owner came back and perched. I did not observe females flying into a territory. However, a copulating pair was observed in the territorial site. These territorial behaviours were never observed in July–August (Fig. 2). In September–October, territorial behaviour was observed in one transect census in 2000.
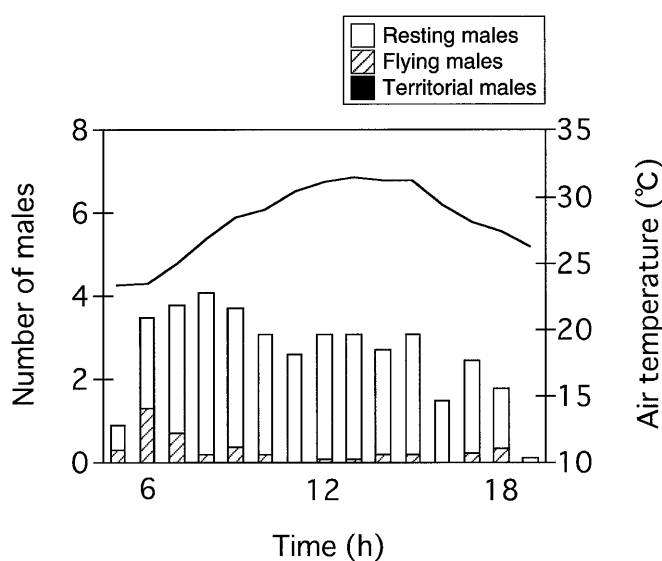

Fig. 2. Diurnal pattern of male *L. diana* in the July–August generation (3 days in 1999 and 7 days in 2000). *Stack bars* show average number of males in each behavioural category, and the *line* shows average air temperature

The diurnal activity of males of the May–June generation is shown in Fig. 1. Territorial behaviour was usually observed from 1100 hours onwards. The times when territories were settled depended on the weather. On sunny and warm days, butterflies started territorial behaviour later than on cloudy and cool days (Table 1). Butterflies also ended territorial behaviour later on warm sunny days than on cool cloudy days (Table 1).

Thoracic temperature of butterflies in the field

T_{th} varied between 18.1 and 34.4°C with air temperature (Fig. 3), indicating that *L. diana* is not able to regulate body temperature physiologically. Although the lower limits of T_{th} differed among generations and behaviours, the upper limits were consistent (Table 2). There were no significant differences in T_{th} between generations (Table 3). T_{th} also did not differ between sexes, but it did differ significantly among behaviours, except in May–June females (Table 3). T_{th} of territorial and flying individuals was higher than that of resting ones.

Thermal condition at territories

T_e at territorial sites varied with air temperature in May–June (Fig. 4) and was generally slightly higher than air temperature, possibly due to solar radiation. The regression of T_{th} of territorial males on air temperature had a slope not different from that for T_e at territorial sites [ANCOVA: $F(1, 124) = 2.72, P = 0.1019$] but had a higher elevation for T_{th} of territorial males than for T_e at territorial sites [ANCOVA: $F(1, 125) = 83.48, P < 0.0001$]. In the range of air temperatures at which territorial behaviour was observed, T_{th} was
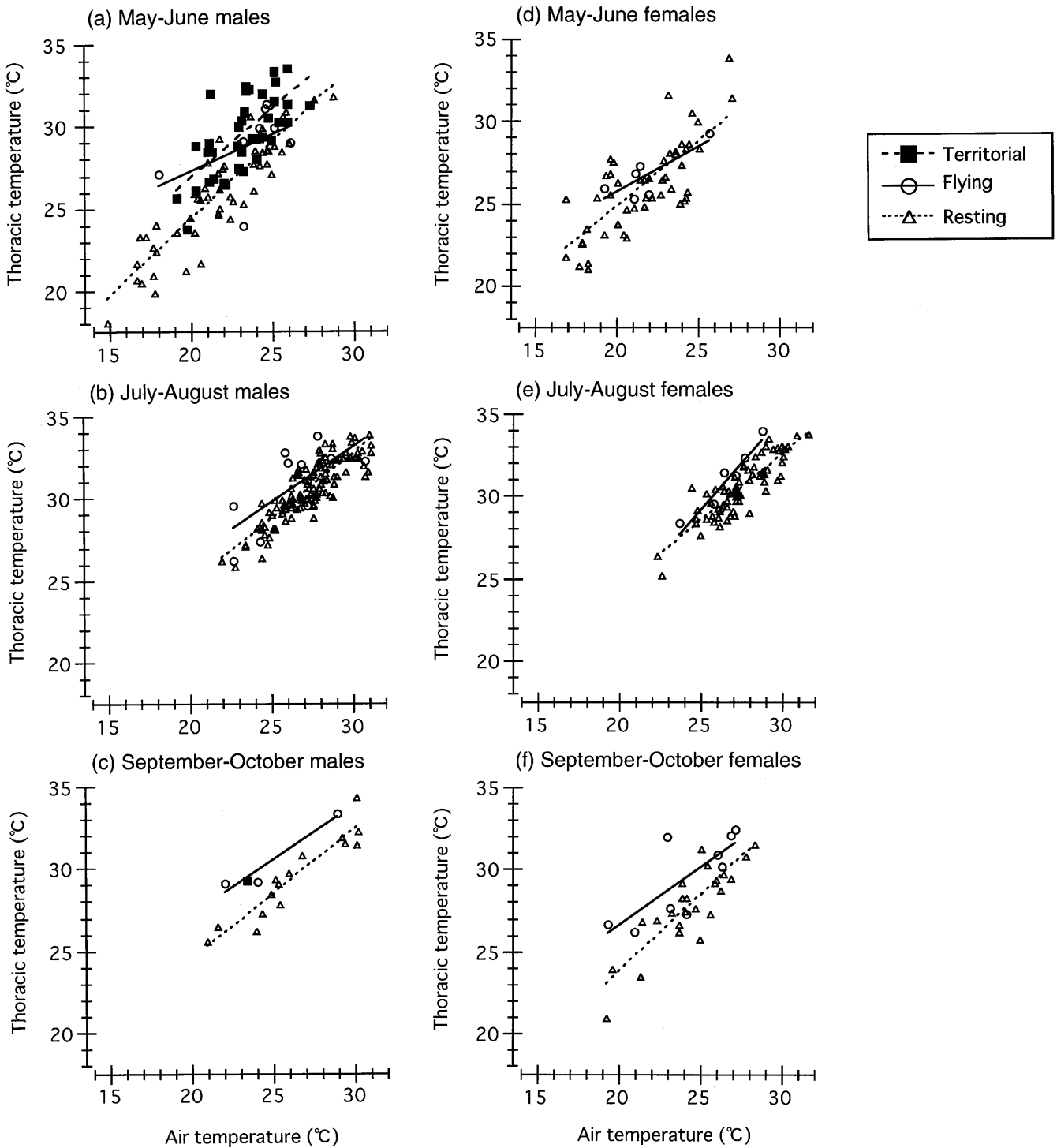
Fig. 3a–f. Thoracic temperature (T_{th}) of *L. diana* in the field in relation to air temperature. **a** May–June males; **b** July–August males; **c** September–October males; **d** May–June females; **e** July–August females; **f** September–October females

about 5°C higher than T_e. This difference may be due to metabolic heat.

T_{th} of territorial males ranged between 23.8 and 33.6°C (Table 2). T_e at which *L. diana* can hold a territory is estimated to range between 18.8 and 28.6°C by subtracting temperature rise due to metabolic heat (5°C) from T_{th} of territorial males. This range of temperatures represents the "suitable T_e range for holding a territory".

In the May–June generation, territorial behaviour was observed in the afternoon, when T_e was in the suitable range for holding a territory (Fig. 5). T_e at the same site in the July–August generation was higher than that in May–June.

Table 2. Range of thoracic temperature T_{th} of *L. diana* in the field. Upper limits of T_{th} were roughly the same irrespective of behaviour or generation

	Behaviour					
	Territorial		Flying		Resting	
	n	Range of T_{th} (°C)	*n*	Range of T_{th} (°C)	*n*	Range of T_{th} (°C)
May–June males	38	23.8–33.6	8	24.0–31.4	56	18.1–31.8
July–August males	0		12	26.2–33.8	114	25.9–33.9
September–October males	1	29.3	3	29.1–33.4	15	25.6–34.4
May–June females	0		6	25.3–29.3	49	21.1–33.9
July–August females	0		7	28.4–34.0	75	25.2–33.8
September–October females	0		9	26.2–32.5	24	21.0–31.6

Table 3. Summary of results of ANCOVA on T_{th} of *L. diana*. The slopes of regression lines were not different in every analysis. T_{th} did not differ among generations or sexes but did differ among behaviours
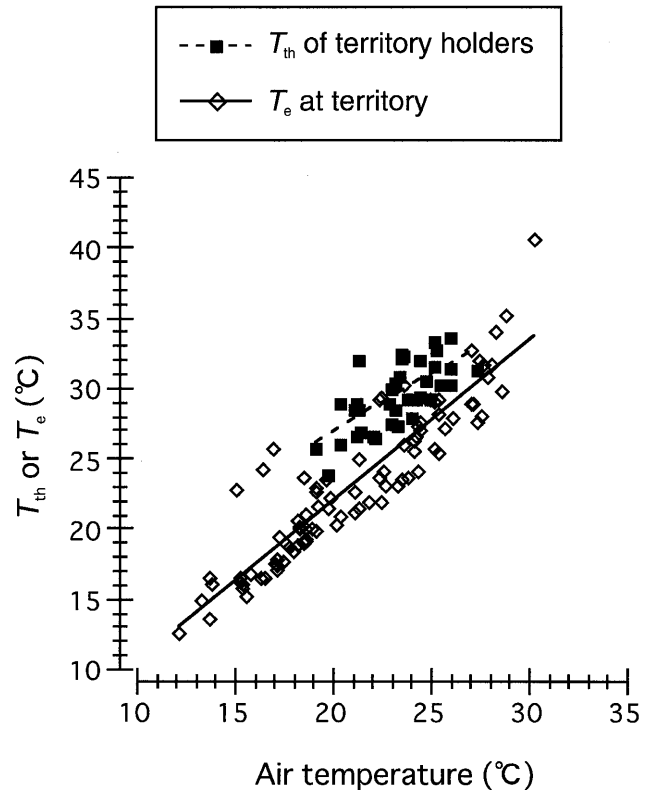
Factor	*df*	*F*	*P*
Generation			
Flying males	2, 19	0.213	0.8097
Resting males	2, 181	0.456	0.6348
Flying females	2, 18	0.962	0.4009
Resting females	2, 144	1.307	0.2738
Sex			
Flying in May–June	1, 11	1.440	0.2553
Resting in May–June	1, 102	0.633	0.4281
Flying in July–August	1, 16	0.020	0.8885
Resting in July–August	1, 186	0.568	0.4520
Flying in September–October	1, 9	0.162	0.6969
Resting in September–October	1, 36	0.017	0.8959
Behaviour			
May–June males	2, 98	20.026	<0.0001***
May–June females	1, 52	0.424	0.5180
July–August males	1, 123	7.600	0.0067**
July–August females	1, 79	10.893	0.0015***
September–October males	1, 15	12.083	0.0034***
September–October females	1, 30	11.344	0.0021***

**P < 0.01; ***P < 0.005

Fig. 4. Operative temperature (T_e) at the territorial site ($n = 90$, $r = 0.92$, $P < 0.001$) and T_{th} of territorial males ($n = 38$, $r = 0.69$, $P < 0.001$) in May–June in relation to air temperature. Thoracic temperatures of territorial males were about 5°C higher than T_e at the territorial site

T_e in July–August reached the suitable range only towards sunset or in rain. Territorial behaviour was again observed in the September–October generation when T_e was in the suitable range in the afternoon. No butterflies of any generation held territories in the morning, even when T_e was within the suitable range.

Critical thermal maxima

The mean T_{th} of male and female butterflies when no longer able to stand was 39.10 ± 1.01°C (±SE, $n = 3$) and 38.83 ± 0.38°C ($n = 12$), respectively. The maximum T_{th} did not differ between males and females (Mann–Whitney U test: $U = 15.5$, $P = 0.7180$).

Light intensity

Light intensity at locations where resting males were captured decreased significantly with increasing air temperature (Fig. 6; $r = -0.30$, $P < 0.0001$). However, the light intensity for territorial and flying males showed no correlation with air temperature (territorial males: $r = -0.03$, $P = 0.8816$; flying males: $r = -0.31$, $P = 0.1483$). The light intensity for territorial males was significantly higher than that for males of other status [ANCOVA: $F(2, 243) = 69.98$, $P < 0.0001$].
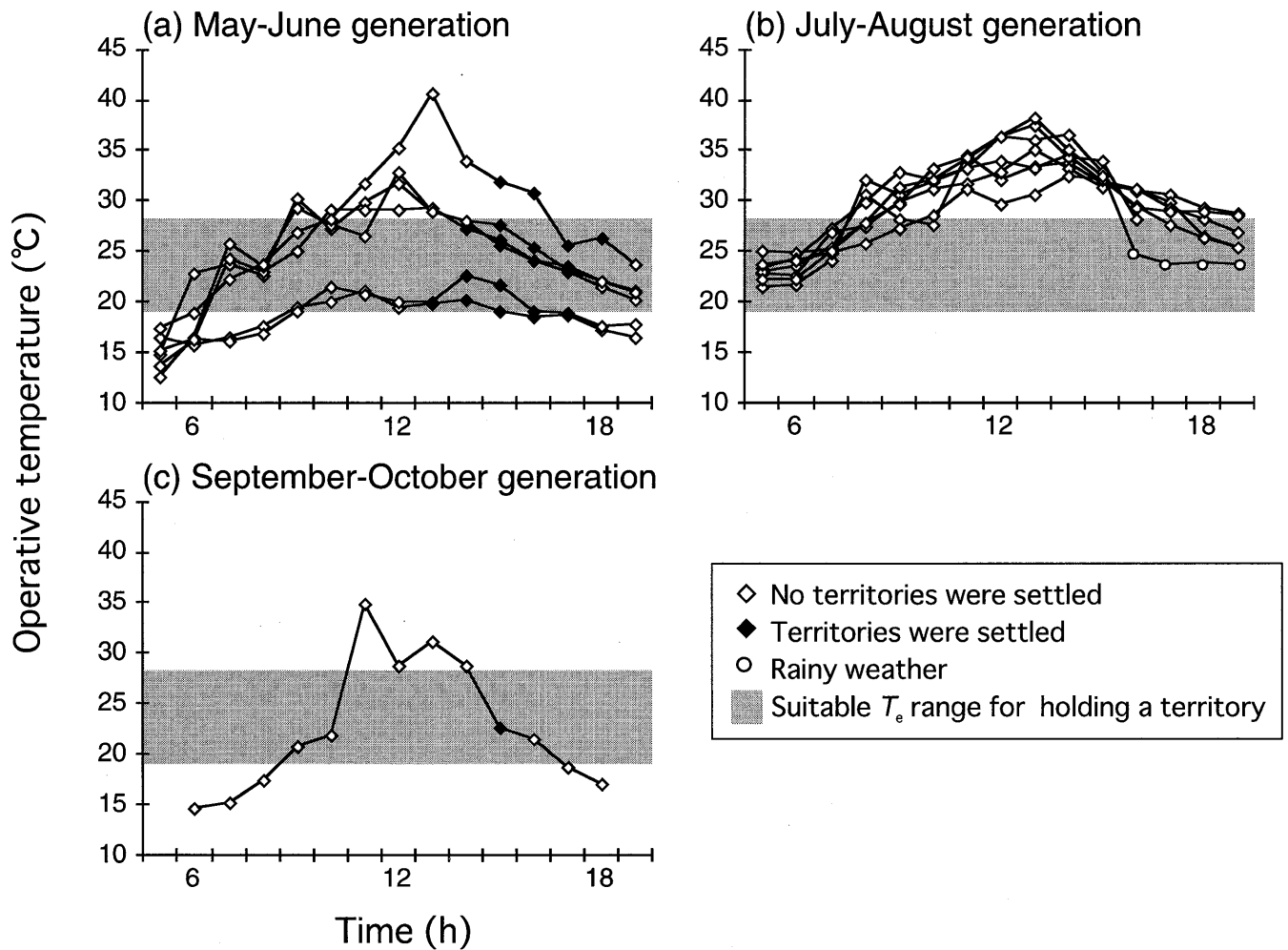
(a) May-June generation

(b) July-August generation

(c) September-October generation

◇ No territories were settled
◆ Territories were settled
○ Rainy weather
▨ Suitable T_e range for holding a territory

Time (h)

Fig. 5a–c. Diurnal change in T_e at the territorial site. **a** May–June; **b** July–August; **c** September–October. Territorial behaviour was observed when T_e was in the suitable T_e range for holding a territory in May–June and September–October. However, T_e stayed above suitable range during almost all the afternoon in July–August, and males could not display territorial behaviour

Discussion

Several studies have reported seasonal changes in the mate-locating behaviour of butterflies, but the changes are slight, as shown in starting time of territorial behaviour (Rutowski et al. 1996; Fric and Konvička 2000). However, the mate-locating behaviour of *L. diana* changes greatly with season; territorial behaviour was observed in May–June and September–October, but not in July–August. The presence or absence of territorial behaviour depending on generations has not been reported in other butterfly species.

When males of *L. diana* were engaged in territorial behaviour, their T_{th} ranged from 23.8 to 33.6°C, a range agreeing with that of flying individuals (24.0–34.0°C). The minimum of the T_{th} was higher than that of resting individuals. Since the performance of the thoracic flight muscle is dependent on the temperature, a higher thoracic temperature is required for active flight (Heinrich 1974). *L. diana* must bask to raise its body temperature for flight when air temperature is low (Ide 2000b). Territorial behaviour,

including repelling intruders, also requires higher thoracic temperatures. Thus, *L. diana* may be unable to hold a territory when their T_{th} is low.

In contrast, upper limits of T_{th} were roughly the same irrespective of behaviour or generation. The upper limit of T_{th} measured in the field was slightly lower than the critical T_{th} (about 39°C) that was estimated by the experiments. It is likely that insects regulate their body temperature before it reaches the critical level (Heinrich 1996). Thus, *L. diana* probably cannot hold a territory when T_{th} is above or below the range of T_{th} of territorial males measured in the field.

T_{th} of *L. diana* was mainly influenced by the thermal environment represented by T_e. The suitable range of T_e for holding a territory was estimated to be 18.8–28.6°C. Male territories were usually established on sunny branch tips facing an open space. In these sites, exposed to solar radiation, the thermal environment may become very hot around noon, and T_e at the territorial site may often exceed the suitable range. In the May–June and September–October generations, territorial behaviour was rare when T_e at the territorial site exceeded the suitable range (around noon-
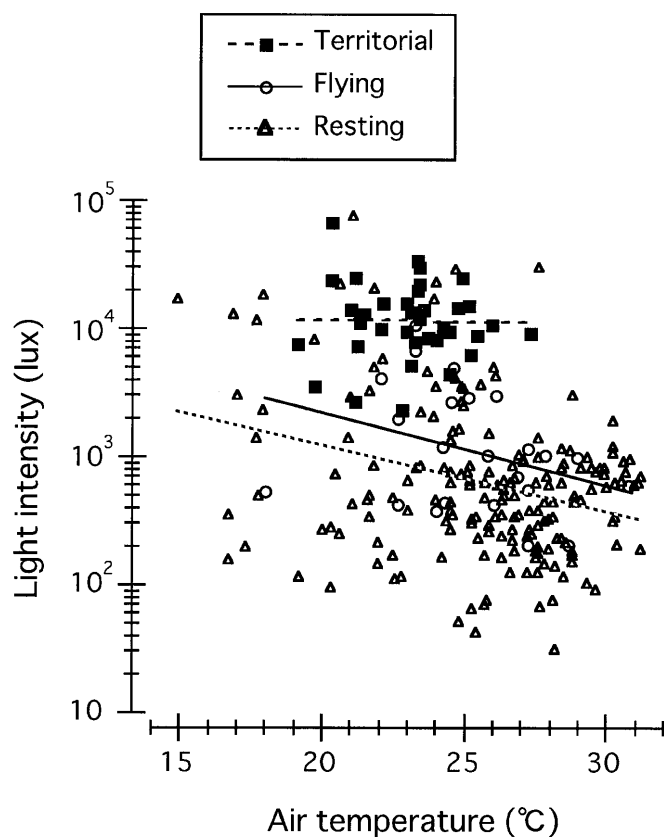
Fig. 6. The relationship between air temperature and light intensity at the locations where male *L. diana* were captured. All generations are shown together. Although the light intensity at locations where territorial and flying males were captured was not correlated with air temperature, regression lines are included for comparison

time), but territories were held by *L. diana* when T_e was kept in the suitable range in the afternoon.

Like other butterfly species (Ohsaki 1986), *L. diana* adopted a behavioural thermoregulation strategy by selecting sites with suitable light intensity. However, the light intensity and air temperature at territories were not correlated, suggesting that *L. diana* does not shift territorial sites for thermoregulation, unlike other butterfly species (Shreeve 1984, 1987; Ravenscroft 1994; Rutowski et al. 1994). This may be because males of *L. diana* select territorial sites where they can easily meet females (e.g. Cordero and Soberón 1990). Consequently, *L. diana* of the May–June and September–October generations hold a territory only when the thermal environment is suitable at a territorial site.

Since the relationship between air temperature and T_{th} for each generation showed a constant pattern, T_e at the territorial site of each generation that was suitable for territorial behaviour was also probably constant. In July–August, T_e at the territorial site was suitable only towards sunset, and *L. diana* had a short time to hold a territory. The seasonal changes in mate-locating behaviour of *L. diana* are thus caused by temperature.

Butterflies usually eclose synchronously in the early morning and females usually copulate within the day (Iwasa and Obara 1989; Rutowski et al. 1996; Watanabe and Ishii 1997; Hirota et al. 2001). Thus, males are engaged in mate-locating behaviour mainly in the morning (Iwasa and Obara 1989; Hirota and Obara 2000). *L. diana* males may patrol in pursuit of females in the morning and display territorial behaviour in the afternoon, although it is not known whether they locate mates in the morning. Such a temporal switching of mate-locating behaviour is known in the skipper butterfly *Ochlodes venata* (Dennis and Williams 1987) and in the chironomid midge *Tokunagayusurika akamusi* (Kon et al. 1986). Ide and Kondoh (2000) suggest theoretically that the switching of mate-locating behaviour from an easy-to-search tactic (patrol is thought to be fit for this tactic in *L. diana*) to a costless tactic (territorial behaviour) may occur when the reproductive value of females decreases within a day (e.g. Wickman and Jansson 1997). Thus, the mate-locating tactic in the latter half of the day, which contributes a little to fitness, is not predicted when costs increase in the too-hot thermal condition, and *L. diana* males probably only use patrol tactics in summer. Further research is necessary to clarify the mate-locating behaviour of *L. diana* in the morning.

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