EUROPEAN JOURNAL OF ENTOMOLOGY
ISSN (online): 1802-8829
http://www.eje.cz
Eur. J. Entomol. **123**: 301–313, 2026
doi: 10.14411/eje.2026.030
ORIGINAL ARTICLE

Effects of dwarf bamboo (*Sasa veitchii* var. *hirsuta*) die-off on microhabitat differentiation between two *Lethe* butterfly species (Lepidoptera: Nymphalidae)

Jun-Ya Ide

Department of Education and Creation Engineering, Kurume Institute of Technology, 2228-66 Kamitsu-machi, Kurume, Fukuoka 830-0052, Japan; e-mail: idejy@kurume-it.ac.jp

Key words. Bamboo die-off, light intensity, niche differentiation, population dynamics, reproductive interference, territorial behaviour, *Lethe diana*, *Lethe sicelis*, Japan

Abstract. Recent studies have suggested that reproductive interference plays an important role in niche differentiation among coexisting species. The closely related butterflies *Lethe diana* and *Lethe sicelis* exhibit niche differentiation, with *L. sicelis* utilising brighter locations than *L. diana*, and only territorial males of *L. sicelis* utilising slightly darker locations than *L. diana*. This study tested the hypothesis that this niche differentiation was induced by reproductive interference between *L. diana* and *L. sicelis*. Mass flowering and subsequent die-off of the dwarf bamboo *Sasa veitchii* var. *hirsuta*, the larval host plant of *L. diana*, followed by a sharp population decline in *L. diana* were used in a removal experiment to investigate subsequent changes in the microhabitat of *L. sicelis* adults. Following bamboo die-off, non-territorial *L. sicelis* males began to use locations where territorial *L. diana* males had previously been observed; furthermore, *L. sicelis* males began to establish territories in locations previously used by non-territorial *L. diana* males. In mating territories, the durations of *L. diana*-*L. sicelis* pursuit flights were shorter than those of conspecific *L. diana* pursuit flights, but equivalent to those of *L. sicelis*–*L. sicelis* pursuit flights. Therefore, while the pursuit flight between different *Lethe* butterfly species imposes a lower cost on *L. diana* than conspecific pursuit flight, it imposes a significant cost on *L. sicelis*, equivalent to that of conspecific pursuit flight. These results suggest that, prior to bamboo die-off, niche differentiation between these two species was driven by reproductive interference in mating territories, and that the species exhibiting more intense territorial behaviour gained the advantage through such interference.

INTRODUCTION

Niche differentiation among coexisting species is a widespread phenomenon observed across all living organisms. Niche differentiation is thought to be caused by interactions between species with overlapping niches, and was traditionally studied mainly as an effect of interspecific competition for resources (e.g. Pianka, 1974; Hairston, 1980; Day & Young, 2004; Sherry & Kent, 2022). However, recent studies have also investigated the role of reproductive interference in niche differentiation (e.g. Kishi & Tsubaki, 2014; Kyogoku & Kokko, 2020). Notably, resource competition among herbivorous insects has rarely been detected (Kaplan & Denno, 2007), and reproductive interference has been identified as an important factor driving host plant differentiation (Friberg et al., 2013; Noriyuki, 2015; Ohsaki et al., 2020).

Reproductive interference occurs when two different species engage in reproductive interactions that result in a fitness cost to one or both species (Gröning & Hochkirch, 2008; Shuker & Burdfield-Steel, 2017). For example, harassment by a different species during courtship can reduce conspecific mating and oviposition rates (Noriyuki et al., 2012; Kitano et al., 2018), and interspecific mating can damage female genitalia, which can negatively impact future reproduction (Kyogoku & Sota, 2015; Ujiie et al., 2025). Reproductive interference often leads to asymmetric negative fitness effects on both species (Gröning & Hochkirch, 2008; Mitchell et al., 2022), which can result in a population decline in one of the species. Because reproductive interference effects are frequency-dependent (Kuno, 1992), they can eventually lead to population extinction or niche specialisation in declining species (Kishi & Nakazawa, 2013; Nishida et al., 2015).

Field experiments can provide the strongest evidence of the effects of interspecific interactions such as competition or reproductive interference on niche differentiation (Hairston, 1989; Werner, 1998). Field experiments in which one of two interacting species is removed or introduced have made significant contributions to clarifying the importance of interspecific interactions in community organisation (e.g. Connell, 1983; Schoener, 1983; Gurevitch et al., 1992). However, field experiments can be costly and

An Open Access article distributed under the Creative Commons (CC-BY) license (http://creativecommons.org/licenses/by/4.0/). Copyright for the published material remains with the original copyright holders (authors or institutions).
OPEN ACCESS

labour-intensive, and are subject to various constraints that challenge their feasibility (Diamond, 1983). Accidental introduction of an alien species can be used as an alternative to experimentation. Some studies have clarified the effects of reproductive interference by comparing populations or environmental conditions before and after the arrival of an invasive species (Liu et al., 2007; Short & Petren, 2012; Takakura & Fujii, 2015). A sudden decrease in species abundance due to disease outbreaks or other factors may be exploited as a substitute for field experiments involving species removal (Cooper et al., 2007). However, few studies have adopted this approach because such opportunities are rare.

Dwarf bamboos are widely distributed in East Asia, where they form dense populations in the understory layers of temperate forests (Suzuki, 1978). Bamboos have a unique life history characterised by decades of vegetative growth followed by mass flowering and death (Janzen, 1976). Bamboo die-back often leads to the death or migration of other dependent organisms (Johnson et al., 1988; Areta & Cockle, 2012). Studying changes in populations and niches of organisms that depend on bamboos and those that interact with bamboo-dependent species before and after bamboo die-off, makes it possible to understand how interactions between these species influence niche differentiation.

The congeneric butterflies *Lethe diana* (Butler) and *Lethe sicelis* (Hewitson) have similar niches, with larvae feeding on dwarf bamboo leaves and adults feeding on sap and faeces (Fukuda et al., 1984). Adult males of both species establish mating territories at the tips of tree branches and drive away approaching individuals of other insect species through pursuit flight (Ide, 2001a, 2004a). Although *L. diana* and *L. sicelis* often coexist at the landscape or local scale, they have slightly different niches. For example, *L. diana* larvae prefer broadleaf bamboo species of genus *Sasa*, while *L. sicelis* larvae prefer small-leaved bamboo species of genus *Pleioblastus* (Fukuda et al., 1972; Takahashi, 1991). Additionally, *L. diana* tends to be distributed at higher altitudes than *L. sicelis* (Nishiyama, 1984). In regions where they occur sympatrically, *L. diana* adults tend to be found in darker places than *L. sicelis*, whereas their mating territories tend to be in slightly brighter places than those of *L. sicelis* (Ide, 2001a). Among Japanese butterflies, closely related species with similar host plants generally live sympatrically, suggesting that resource competition does not cause niche differentiation (Nakadai et al., 2018). Therefore, niche differentiation between these two species is suspected to be the result of reproductive interference rather than resource competition. However, it remains unknown whether reproductive interference occurs between *L. diana* and *L. sicelis*.

In northern Kyoto, where *L. diana* and *L. sicelis* live sympatrically, the broadleaf dwarf bamboo *Sasa veitchii* var. *hirsuta*, the main host plant of *L. diana*, experienced a mass flowering, fruiting, and die-off event from 2004 to 2007 (Abe & Shibata, 2012). This die-off event is thought to have caused a dramatic decline in the local *L. diana* population. If reproductive interference occurred between *L. diana* and *L. sicelis*, then this rapid *L. diana* population decline would have affected the population dynamics and microhabitat use of *L. sicelis*. Before the bamboo die-off event (1998 to 2000), surveys of the populations and microhabitat utilisation of *L. diana* and *L. sicelis* were conducted at the Kamigamo Experimental Forest Station of Kyoto University (Ide, 2001a). The present study repeated this survey at the same study site after the bamboo die-off event (2008–2009), and the results were compared to determine whether reproductive interference had occurred between *L. diana* and *L. sicelis*. Furthermore, the territorial behaviours of both butterfly species were observed, and asymmetry in the intensity of interference within their mating territories was investigated.

MATERIAL AND METHODS

Study site

This study was conducted at the Kamigamo Experimental Forest Station of Kyoto University, Kyoto, Japan (35°04′N, 135°46′E; 140 m a.s.l.). The study area is a mosaic-like environment containing both forest and clearings (Ide, 2002a). The forest comprises deciduous trees including *Quercus serrata* Murray, evergreen broadleaf trees including *Quercus glauca* Thunb. and *Ilex pedunculosa* Miq., and evergreen coniferous trees including *Pinus densiflora* Sieb. et Zucc. and *Chamaecyparis obtuse* (Sieb. et Zucc.) Endlicher (Osada et al., 2003). The understory of the forest was almost entirely covered with dwarf bamboo. Two species of dwarf bamboo grow in this area, broadleaf dwarf bamboo *S. veitchii* var. *hirsuta* and narrowleaf dwarf bamboo *Pleioblastus chino* var. *viridis*, and each form dense bushes. Both species of dwarf bamboo have an average height of about 70 cm in this area (Watanabe, 1991). Both species are evergreen and their culms live for several years; the leaves of *S. veitchii* var. *hirsuta* develop a white margin after overwintering (Ide, 2004b). The die-off event of *S. veitchii* var. *hirsuta* occurred in 2005 in this area (Abe & Shibata, 2013). Approximately 9 years are required for *S. veitchii* var. *hirsuta* bushes to regenerate to their pre-flowering size following die-off, even in the absence of herbivory by sika deer (Higashiguchi & Shibata, 2017). The 2008–2009 field survey was completed soon after the recorded die-off event, and deer grazing was shown to have inhibited natural recovery, with *S. veitchii* var. *hirsuta* populations continuing to decrease dramatically (Abe & Shibata, 2013). No die-off was observed in *P. chino* var. *viridis*, and its bushes had not spread to areas where *S. veitchii* var. *hirsuta* had died.

Organisms

Both *L. diana* and *L. sicelis* are forest-dwelling species of the Satyrinae. *Lethe diana* is distributed from China and Sakhalin to Japan, while *L. sicelis* is endemic to Japan (Shirôzu, 2006). *Lethe diana* and *L. sicelis* are the dominant butterfly species in mixed forests containing dwarf bamboo bushes in central Japan (Nishinaka & Ishii, 2006). *Lethe diana* has three generations per year (May–June, July–August, and September–October) in this region, while *L. sicelis* has two (June–July and August–September) (Ide, 2001a). Neither species exhibits seasonal changes in wing patterns. Although the flight seasons of both species largely overlap, there have been no reports of interspecific hybridisation. At the study site, *L. diana* larvae have been reported to feed on *S. veitchii* var. *hirsuta* leaves (Ide, 2003), but it remains unknown whether they feed on *P. chino* var. *viridis* leaves. *Lethe sicelis* larvae have been observed feeding on leaves of *P. chino* var. *viridis*,

but not those of *S. veitchii* var. *hirsuta*, at the study site (Ide, pers. observ.). However, in other areas of Japan, both dwarf bamboo species have been reported as host plants for the larvae of both *L. diana* and *L. sicelis* (Saito et al., 2016).

Leaf biomass measurements

To understand changes in the amount of food resources available for *Lethe* butterfly larvae before and after *S. veitchii* var. *hirsuta* die-off, leaf biomass was examined in both bamboo species. Watanabe (1991) investigated leaf biomass in bamboo species at the Kamigamo Experimental Forest Station in 1990, and I conducted similar investigations at the same site in November 1999 (*S. veitchii* var. *hirsuta*) and 2008 (*S. veitchii* var. *hirsuta* and *P. chino* var. *viridis*). Four quadrats (40 cm × 40 cm) were randomly distributed among the bamboo bushes, and all aboveground parts of bamboos within each quadrat were harvested. The harvested bamboo materials were transported to the laboratory, and leaf wet weight was measured using a digital balance accurate to 1 mg. For each bamboo species, leaf samples were dried at 60°C for 3 days to calculate the percentage of dry leaf weight; this value was multiplied by the wet weight to determine leaf dry weight.

Population and microhabitat characteristics

Route surveys were conducted to characterise the populations and microhabitats of adult *Lethe* butterflies during each annual flight season from 1998 to 2000 (before bamboo die-off) and from 2008 to 2009 (after bamboo die-off). The number of surveys conducted in each year varied from 60 to 81. The timing of each survey was varied daily to cover the period 05:00–19:00. Along a fixed route of approximately 3 km (Ide, 2002a), unmarked butterflies were captured using a soft insect net and numbered on the undersurface of each hind-wing with felt-tipped pen. The code number, species, sex, and location were recorded, and the butterflies were released. When marked individuals were resighted, these variables were recorded without capture. If the butterflies appeared to be holding territories at the time of capture, this was also recorded. Male butterflies that quickly approached any intruders, but returned to their perch sites after pursuit, were recorded as holding territories. The air temperature and light intensity where each butterfly was captured were recorded. Light intensity was measured using a portable digital illumination meter (TMS 870; Tasco Japan Co., Ltd., Tokyo, Japan).

Part of the survey route (~150 m) was excluded from the 2008 and 2009 surveys, because trees along the route had been cut down. Very few butterflies were caught in this section during 1998 and 2000; therefore, it is assumed that its exclusion had no serious effects on the study results.

Territorial behaviour

The territorial behaviour of male *Lethe* butterflies was observed in the afternoon on fair days in 2001 (*L. diana*) and 2009 (*L. sicelis*). Observations began when a territorial male was found and continued throughout all subsequent activity. The entry of an insect into a sphere (radius, 2 m) around the focal butterfly was considered an approach, and the species of the approaching insect was recorded as well as the flying bout duration of the resident male butterfly. Insects that approached butterfly territories were recorded as *L. diana*, *L. sicelis*, or other insects. Observations continued until the resident male butterfly left the territory at dusk. Behaviours were recorded in seven *L. diana* males and six *L. sicelis* males, for total durations of 828 and 178 min, respectively.

Statistical analyses

Statistical analyses were performed using R v3.6.3 (R Core Team, 2020). All statistical tests were two-tailed unless otherwise stated. Significance was evaluated using a threshold of $P < 0.05$.

Population

A generalised linear model with a Poisson error structure and a log link function was used to analyse the impacts of bamboo die-off on the population dynamics of both butterfly species, with the total number of sightings (captures and resights) of individuals in each year as the dependent variable and bamboo die-off and species as the independent variables. The number of surveys was included in the model as an offset variable.

Light intensity measurements

The comparison pairs of light intensity measurements in locations where *L. diana* and *L. sicelis* were observed are listed in Table 1. To clarify whether the bamboo die-off event affected microhabitat utilisation in *Lethe* butterflies, light intensity was compared at each location before and after die-off according to butterfly species, sex, and behaviour (territorial vs. non-territorial) (Table 1A). To determine whether microhabitat utilisation of

Table 1. A list of comparison pairs of light intensity measurements in locations where *Lethe diana* and *Lethe sicelis* were observed.

(A) Microhabitat utilisation before and after bamboo die-off		(B) Microhabitat utilisation differences between individuals of different species engaging in the same behaviour		(C) Microhabitat utilisation differences between *L. diana* and *L. sicelis* individuals engaging in different behaviours	
L. diana female Before bamboo die-off vs. after bamboo die-off	Fig. 2A, Table 4	Female *L. diana* (before bamboo die-off) vs. *L. sicelis* (before bamboo die-off)	Fig. 2AB, Table 5	Territorial *L. diana* male (before bamboo die-off) vs. non-territorial *L. sicelis* male (before bamboo die-off)	Fig. 3A, Table 6
L. diana non-territorial male Before bamboo die-off vs. after bamboo die-off	Fig. 2C, Table 4	Female *L. diana* (before bamboo die-off) vs. *L. sicelis* (after bamboo die-off)	Fig. 2AB, Table 5	Territorial *L. diana* male (before bamboo die-off) vs. non-territorial *L. sicelis* male (after bamboo die-off)	Fig. 3B, Table 6
L. sicelis female Before bamboo die-off vs. after bamboo die-off	Fig. 2B, Table 4	Non-territorial male *L. diana* (before bamboo die-off) vs. *L. sicelis* (before bamboo die-off)	Fig. 2CD, Table 5	Non-territorial *L. diana* male (before bamboo die-off) vs. territorial *L. sicelis* male (before bamboo die-off)	Fig. 4A, Table 6
L. sicelis non-territorial male Before bamboo die-off vs. after bamboo die-off	Fig. 2D, Table 4	Non-territorial male *L. diana* (before bamboo die-off) vs. *L. sicelis* (after bamboo die-off)	Fig. 2CD, Table 5	Non-territorial *L. diana* male (before bamboo die-off) vs. territorial *L. sicelis* male (after bamboo die-off)	Fig. 4B, Table 6
L. sicelis territorial male Before bamboo die-off vs. after bamboo die-off	Fig. 2F, Table 4	Territorial male *L. diana* (before bamboo die-off) vs. *L. sicelis* (before bamboo die-off)	Fig. 2EF, Table 5		
		Territorial male *L. diana* (before bamboo die-off) vs. *L. sicelis* (after bamboo die-off)	Fig. 2EF, Table 5		

butterflies differed between butterfly species, light intensity was compared at each location before bamboo die-off according to sex and behaviour (territorial vs. non-territorial). To determine whether microhabitat utilisation in *L. sicelis* was affected by the *L. diana* population decline following bamboo die-off, light intensity was compared between locations where *L. sicelis* was observed after die-off and those where *L. diana* was observed before die-off (Table 1B). Microhabitats were compared between territorial and non-territorial males of different species because interspecific interactions do not necessarily occur only between territorial males (Table 1C). Light intensity at locations where butterflies were observed before bamboo die-off was compared between territorial *L. diana* males and non-territorial *L. sicelis* males, and between non-territorial *L. diana* males and territorial *L. sicelis* males. Then, light intensity was compared between locations where *L. diana* was observed before bamboo die-off and those where *L. sicelis* was observed after bamboo die-off. Linear mixed models were used for these analyses using the "lmer" function of the *lme4* R package, and model selection based on the Akaike information criterion (AIC) (Bates et al., 2015). Light intensity comparisons before and after bamboo die-off were performed using log-transformed light intensity measurements as the dependent variable, bamboo die-off and air temperature as independent variables, and year as a random effect. For interspecific comparisons, log-transformed light intensity measurements were used as the dependent variable, species and air temperature as independent variables, and year as a random effect.

Territorial behaviour

A linear mixed model with maximum likelihood estimation was used to identify factors that influence flying bout duration in resident male butterflies; the individual identity of the resident male was included in the model as a random intercept effect. Because no *L. diana* butterflies approached focal territories during territorial behaviour observations of *L. sicelis* resident males, data on the pursuit flight duration of *L. sicelis* males towards *L. diana* could not be obtained. Therefore, one-way analysis was performed, with flying bout duration as the dependent variable and approaching insect category and resident male butterfly species as independent variables. Thus, the flying bout durations of resident males were compared among groups of insects that approached the defended territories and between resident male species. Additionally, the durations of pursuit flights between resident males and conspecifics were compared between resident male butterfly species.

RESULTS

Dwarf bamboo leaf biomass

Sasa veitchii var. *hirsuta* leaf dry weight was similar between 1990 (329 g/m^2) and 1999 (379.5 ± 76.3 g/m^2, mean ± standard deviation), but dropped dramatically in 2008 (1.5 ± 0.9 g/m^2) after bamboo die-off. Dead culms remained densely packed in areas where *S. veitchii* var. *hirsuta* had once thrived, with no invasion by *P. chino* var. *viridis*. Leaf dry weight showed little variation in *P. chino* var. *viridis* between 1990 (92 g/m^2) and 2008 (85.5 ± 63.0 g/m^2).

Table 2. Number of individual *Lethe diana* and *Lethe sicelis* butterflies recorded annually in surveys conducted during 1998–2000 and 2008–2009. Mean number of individuals per survey was shown in parentheses.

	Before bamboo die-off			After bamboo die-off	
	1998	1999	2000	2008	2009
L. diana	473 (7.9)	631 (8.1)	433 (5.3)	9 (0.1)	9 (0.1)
L. sicelis	88 (1.5)	59 (0.8)	60 (0.7)	263 (3.9)	365 (5.2)
No. survey	60	78	81	67	70

Table 3. Generalised linear model analysis result showing the effects of bamboo die-off and butterfly species on *Lethe diana* and *Lethe sicelis* numbers. The base category for the 'bamboo die-off' and 'species' variables were 'after die-off' and '*L. diana*', respectively.

Variable	Estimate	SE	*z*	*P*
Intercept	–2.030	0.236	–8.611	<0.0001
Bamboo die-off (before)	3.978	0.237	16.780	<0.0001
Species (*L. sicelis*)	3.552	0.239	14.859	<0.0001
Bamboo die-off × species	–5.557	0.250	–22.205	<0.0001

Lethe butterfly population dynamics

Hundreds of *L. diana* butterflies were marked and resighted annually from 1998 to 2000, whereas after bamboo die-off, only nine individuals were found annually in 2008 and 2009 (Table 2). Several dozen *L. sicelis* butterflies were marked and resighted annually before bamboo die-off, whereas their numbers greatly increased after bamboo die-off. Generalised linear model analysis showed significant effects of bamboo die-off, butterfly species, and their interaction on the number of individual butterflies recorded per survey (Table 3). Thus, population changes following bamboo die-off differed between the two butterfly species.

Microhabitat utilisation

Microhabitat utilisation before and after bamboo die-off?

In locations where territorial males of both *Lethe* butterfly species were observed, light intensity was not affected by air temperature, whereas in locations where non-territorial males and females were observed, higher air temperature was associated with lower light intensity (Table 4, Fig. 1). Thus, temperature effects were significant only where *Lethe* butterflies other than territorial males were observed.

Table 4. Linear mixed model results showing associations between light intensity and locations where *Lethe diana* and *Lethe sicelis* butterflies were observed. Variables included in the selected models (lowest AIC) are shown.

Variable	Estimate	SE	df	*t*	*P*
L. diana female					
Intercept	11.166	0.623	240.1	17.910	<0.0001
Temperature	–0.125	0.020	255.7	–6.206	<0.0001
Bamboo die-off (before)	–1.324	0.393	114.6	–3.366	0.0010
L. diana non-territorial male					
Intercept	9.601	0.669	469.0	14.360	<0.0001
Temperature	–0.074	0.018	449.4	–4.163	<0.0001
Bamboo die-off (before)	–1.207	0.506	334.7	–2.384	0.0177
L. sicelis female					
Intercept	10.497	0.816	240.7	12.858	<0.0001
Temperature	–0.112	0.030	278.8	–3.713	0.0002
L. sicelis non-territorial male					
Intercept	10.645	0.769	93.0	13.851	<0.0001
Temperature	–0.109	0.027	330.1	–3.989	<0.0001
Bamboo die-off (before)	–0.722	0.364	2.04	–1.986	0.183
L. sicelis territorial male					
Intercept	6.706	0.073	157.0	92.347	<0.0001
Bamboo die-off (before)	1.382	0.276	157.0	5.004	<0.0001

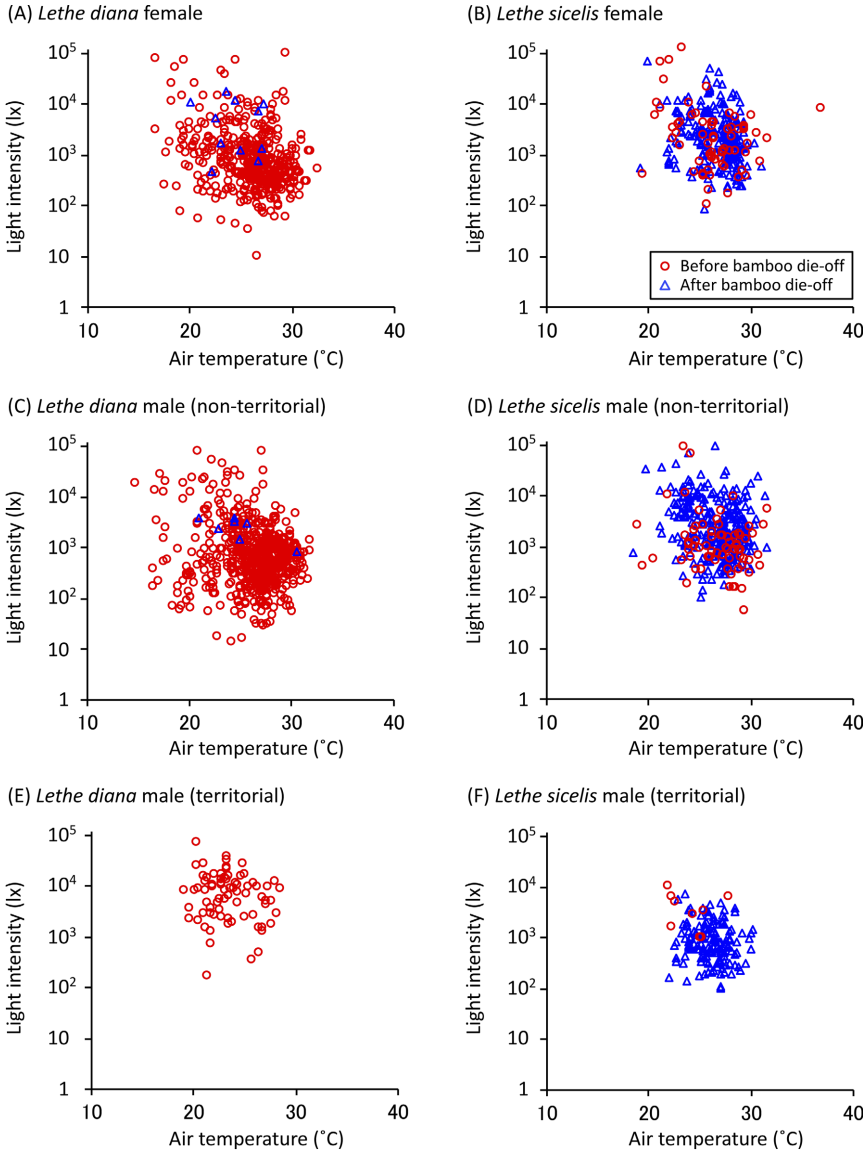


Fig. 1. Light intensity measurements at locations where *Lethe* butterflies were observed: (A) *L. diana* females, (B) *L. sicelis* females, (C) non-territorial *L. diana* males, (D) non-territorial *L. sicelis* males, (E) territorial *L. diana* males, and (F) territorial *L. sicelis* males. Red circles, before bamboo die-off; blue triangles, after bamboo die-off.

Bamboo die-off was significantly associated with light intensity in locations where *L. diana* butterflies were observed, and non-territorial males and females were observed in brighter locations after the bamboo die-off event (Fig. 1A, C). However, because only 11 females and 7 males of *L. diana* were observed after bamboo die-off, these results may be due to chance alone. No territorial *L. diana* males were observed after bamboo die-off; therefore, differences in light intensity before and after bamboo die-off could not be analysed.

In locations where female *L. sicelis* were observed, light intensity did not differ before and after bamboo die-off (Fig. 1B). Non-territorial males were observed in slightly brighter locations after bamboo die-off than before die-off (Fig. 1D), but territorial males were observed in significantly darker locations after bamboo die-off (Fig. 1F). Therefore, with the exception of *L. sicelis* females, light intensity differed before and after bamboo die-off in locations where *Lethe* butterflies were observed.

Microhabitat utilisation differences between individuals of different species engaging in the same behaviour

Before bamboo die-off, *L. sicelis* females were observed in significantly brighter locations than *L. diana* females (Table 5, Fig. 1A, B). Even after bamboo die-off, when *L. diana* butterfly numbers were dramatically reduced, *L. sicelis* females were observed in significantly brighter locations than those previously used by *L. diana* females.

Non-territorial *L. sicelis* males were also observed in significantly brighter locations than non-territorial *L. diana* males before bamboo die-off (Table 5, Fig. 1C, D). After bamboo die-off, non-territorial *L. sicelis* males were observed in significantly brighter locations than those previously used by non-territorial *L. diana* males, and the difference in light intensity became greater.

Table 5. Linear mixed model results showing associations between light intensity and locations where *Lethe diana* was observed before bamboo die-off and those where *Lethe sicelis* was observed before or after bamboo die-off. Variables included in the selected models (lowest AIC) are shown.

Variable	Estimate	SE	df	*t*	*P*
Female: *L. diana* (before bamboo die-off) vs. *L. sicelis* (before bamboo die-off)					
Intercept	9.640	0.517	223.2	18.635	<0.0001
Temperature	–0.118	0.019	464.4	–6.124	<0.0001
Species (*L. sicelis*)	1.008	0.166	504.9	6.088	<0.0001
Female: *L. diana* (before bamboo die-off) vs. *L. sicelis* (after bamboo die-off)					
Intercept	9.810	0.467	234.9	21.028	<0.0001
Temperature	–0.124	0.018	369.7	–7.039	<0.0001
Species (*L. sicelis*)	1.103	0.127	3.3	8.680	0.0022
Non-territorial male: *L. diana* (before bamboo die-off) vs. *L. sicelis* (before bamboo die-off)					
Intercept	8.470	0.457	323.5	18.527	<0.0001
Temperature	–0.077	0.017	514.2	–4.531	<0.0001
Species (*L. sicelis*)	0.497	0.165	679.3	3.016	0.0027
Non-territorial male: *L. diana* (before bamboo die-off) vs. *L. sicelis* (after bamboo die-off)					
Intercept	8.521	0.432	293.9	19.742	<0.0001
Temperature	–0.079	0.016	860.2	–5.019	<0.0001
Species (*L. sicelis*)	1.324	0.179	2.9	7.405	0.0059
Territorial male: *L. diana* (before bamboo die-off) vs. *L. sicelis* (before bamboo die-off)					
Intercept	8.561	0.381	2.2	22.49	0.0011
Territorial male: *L. diana* (before bamboo die-off) vs. *L. sicelis* (after bamboo die-off)					
Intercept	8.583	0.338	3.5	25.406	<0.0001
Species (*L. sicelis*)	–1.876	0.509	3.0	–3.686	0.0345

Table 6. Linear mixed model results comparing light intensity at the locations where *Lethe diana* and *Lethe sicelis* individuals engaging in different behaviours were observed. Variables included in the selected models (lowest AIC) are shown.

Variable	Estimate	SE	df	*t*	*P*
L. diana territorial male (before bamboo die-off) vs. *L. sicelis* non-territorial male (before bamboo die-off)					
Intercept	10.131	0.910	112.0	11.138	<0.0001
Temperature	–0.068	0.037	148.3	–1.861	0.0647
Species (*L. sicelis*)	–1.401	0.237	138.0	–5.903	<0.0001
L. diana territorial male (before bamboo die-off) vs. *L. sicelis* non-territorial male (after bamboo die-off)					
Intercept	10.353	0.731	111.3	14.160	<0.0001
Temperature	–0.087	0.027	339.2	–3.242	0.0013
L. diana non-territorial male (before bamboo die-off) vs. *L. sicelis* territorial male (before bamboo die-off)					
Intercept	8.366	0.479	297.6	17.477	<0.0001
Temperature	–0.073	0.018	474.9	–4.107	<0.0001
Species (*L. sicelis*)	1.535	0.400	650.4	3.840	0.0001
L. diana non-territorial male (before bamboo die-off) vs. *L. sicelis* territorial male (after bamboo die-off)					
Intercept	8.386	0.442	499.6	18.978	<0.0001
Temperature	–0.071	0.017	685.5	–4.312	<0.0001

An interspecific comparison of light intensity in locations used by territorial males revealed no significant differences before bamboo die-off (Table 5, Fig. 1E, F). After bamboo die-off, territorial *L. sicelis* males were observed in significantly darker locations than those previously used by territorial *L. diana* males.

Thus, there were significant interspecific differences in the locations where butterflies were observed prior to bamboo die-off. Following the dramatic *L. diana* population decline after bamboo die-off, *L. sicelis* was observed in locations where *L. diana* had not previously been observed, rather than in spaces previously occupied by *L. diana*.

Microhabitat utilisation differences between *L. diana* and *L. sicelis* individuals engaging in different behaviours

A comparison of light intensity between locations used by territorial *L. diana* males and non-territorial *L. sicelis* males before bamboo die-off showed that non-territorial *L. sicelis* males were observed in significantly darker locations (Table 6, Fig. 2A). After bamboo die-off, light intensity did not differ significantly between locations where non-territorial *L. sicelis* males were observed and territorial *L. diana* males had been observed before bamboo die-off (Fig. 2B). These results indicate that after the bamboo die-off event, the locations where non-territorial *L. sicelis*

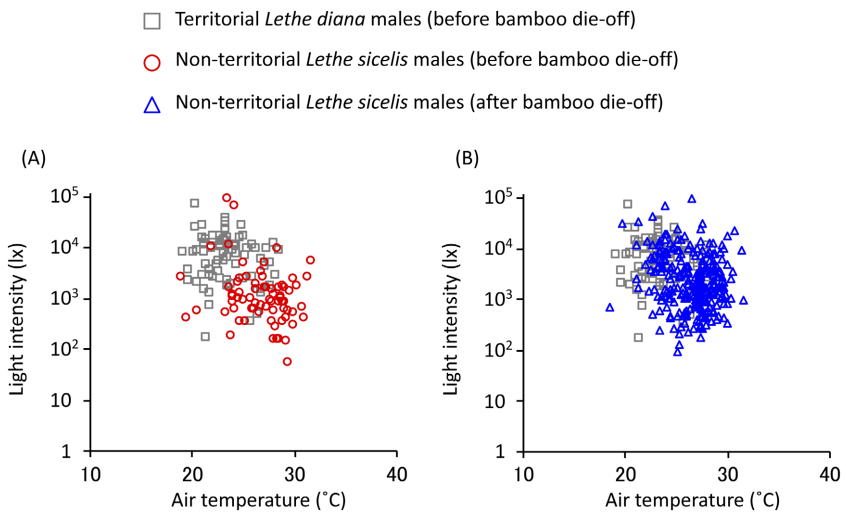


Fig. 2. Light intensity measurements at locations where territorial *Lethe diana* males and non-territorial *Lethe sicelis* males were observed. (A) Territorial *L. diana* males and non-territorial *L. sicelis* males before bamboo die-off. (B) Territorial *L. diana* males before bamboo die-off and non-territorial *L. sicelis* males after bamboo die-off.

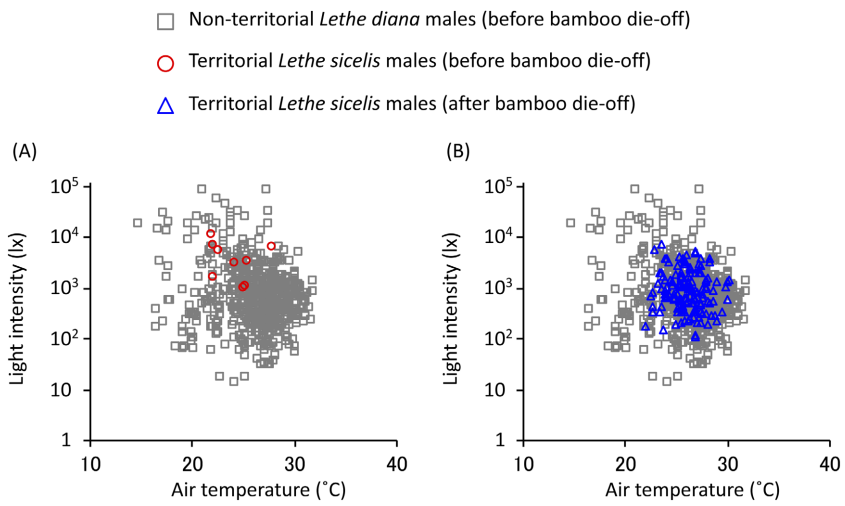


Fig. 3. Light intensity measurements at locations where non-territorial *Lethe diana* males and territorial *Lethe sicelis* males were observed. (A) Non-territorial *L. diana* males and territorial *L. sicelis* males before bamboo die-off. (B) Non-territorial *L. diana* males before bamboo die-off and territorial *L. sicelis* males after bamboo die-off.

males were observed shifted to spaces where territorial *L. diana* males had previously been observed.

A comparison of light intensity between locations used by non-territorial *L. diana* males and territorial *L. sicelis* males before bamboo die-off showed that territorial *L. sicelis* males were observed in significantly brighter locations (Table 6, Fig. 3A). However, after bamboo die-off, light intensity did not differ between *L. sicelis* territories and locations where non-territorial *L. diana* males had been observed before bamboo die-off (Fig. 3B). These results suggest that after bamboo die-off, *L. sicelis* males began to establish territories in spaces previously used by non-territorial *L. diana* males.

Territorial behaviour

Territorial behaviour was observed in *L. diana* males 83 times during route surveys before the bamboo die-off event, between 13:12 and 18:13. In contrast, territorial behaviour was observed in *L. sicelis* males 11 and 148 times before and after bamboo die-off, respectively, between 13:28 and 17:37. Thus, territorial behaviour was observed within a similar temporal window for both species.

During observations of *L. diana* territories conducted before bamboo die-off, 10 approaches by *L. diana*, 42 approaches by *L. sicelis*, and 102 approaches by other insects were observed; in all cases, the resident male butterfly chased off the approaching insect. The flying bout duration of the resident *L. diana* male was significantly longer when approached by an *L. diana* individual than when approached by *L. sicelis* or another insect species (Fig. 4, Table 7). During observations of *L. sicelis* territories conducted after bamboo die-off, 79 approaches by *L. sicelis* and 31 approaches by other insects were observed, but no *L. diana* approaches were observed. Resident *L. sicelis* males also chased off approaching insects. The flying bout duration of a resident *L. sicelis* male was significantly longer in response to an approach by *L. sicelis* than in response to approaches by other insects.

There was no significant difference in flying bout duration between resident *L. diana* and *L. sicelis* males regardless of whether the approaching insect was *L. sicelis* (t = 0.988, P = 0.349) or another insect species (t = –1.468, P = 0.17). When the approaching species was a conspecific butterfly (i.e. resident male *L. diana* and approaching *L.*

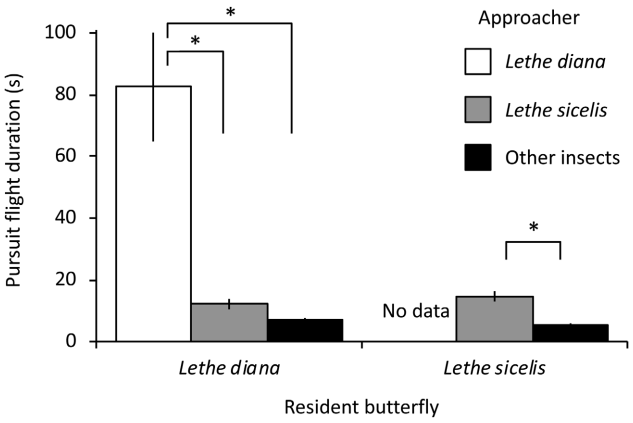


Fig. 4. Mean flying bout duration of a resident male in a territory approached by *Lethe diana* (white bars), by *Lethe sicelis* (grey bars), or by other insects (black bars). Error bars indicate standard error. Data on resident *L. diana* males were collected before bamboo die-off, while data on resident *L. sicelis* males were collected after bamboo die-off. No approach by an *L. diana* male to a territory of *L. sicelis* was observed. Asterisks indicate significant differences (*P < 0.05).

Table 7. Linear mixed model results showing flying bout durations of resident male butterflies of each species towards approaching individuals.

Resident butterfly	Fixed effect	Estimate	SE	df	t	P
Lethe diana	Intercept	80.631	5.217	145	15.456	<0.0001
	Approacher (*L. sicelis*)	–67.451	5.283	145	–12.768	<0.0001
	Approacher (other insects)	–72.660	4.803	145	–15.127	<0.0001
Lethe sicelis	Intercept	14.658	1.417	103	10.343	<0.0001
	Approacher (other insects)	–9.368	2.670	103	–3.5091	<0.0001

diana, or resident male *L. sicelis* and approaching *L. sicelis*), the flying bout durations of resident males were significantly longer for *L. diana* than for *L. sicelis* ($t = –4.271$, $P = 0.0021$).

DISCUSSION

Following the *S. veitchii* var. *hirsuta* die-off event in 2005 (Abe & Shibata, 2013), which significantly decreased the number of leaves remaining on bushes, *L. diana* approached extirpation at the study site (Table 2). The population dynamics of *L. diana* are thought to be influenced by various factors including vegetation succession (Nishinaka & Ishii, 2007; Kobayashi et al., 2010) and predation pressure (Ide, 2006). However, the only possible explanations for the drastic population decrease observed at the study site are habitat destruction and the loss of food resources. Although some trees in the study area were cut down between the two survey periods, there was no other human disturbance; therefore, it is reasonable to suppose that the sudden loss of food resources resulting from bamboo die-off caused the near-extinction of *L. diana*.

In the study area, *L. diana* larvae have been reported to feed on *S. veitchii* var. *hirsuta* leaves (Ide, 2003), although some studies listed *P. chino* var. *viridis* as a host plant (Fukuda et al., 1984; Saito et al., 2016), which suggests that they may also consume *P. chino* var. *viridis* leaves. However, the amount of *P. chino* var. *viridis* leaves at the study site remained unchanged after the *S. veitchii* var. *hirsuta* die-off event, whereas the *L. diana* population declined dramatically, which indicates that *L. diana* did not feed on *P. chino* var. *viridis* leaves. This finding implies resource differentiation in the study area, with *S. veitchii* var. *hirsuta* as the host plant for *L. diana* and *P. chino* var. *viridis* as the host plant for *L. sicelis*. *Lethe diana* adults prefer shade and frequently fly within or along forest edges, making it challenging for these butterflies to move between forests (Ide, 2000a, b). This preference may have increased the likelihood of local evolution of host preferences in *L. diana*.

The population density of *L. sicelis* increased roughly 7-fold after the bamboo die-off event (Table 2). Previous studies using transect surveys have shown that the population density of *L. sicelis* can sometimes fluctuate by as much as 10-fold from year to year (Matsumoto, 2008; Inoue, 2018). Some forest lepidopteran insects experience more dramatic population fluctuations (Myers & Cory, 2013; Garnas et al., 2023), such that the *L. sicelis* population increase may be considered within the limits of random fluctuation. However, the population density of *L. sicelis* was always higher in the 2 years after bamboo die-off than in the 3 years before die-off; therefore, the bamboo die-off event may have led to a steady rise in the *L. sicelis* population.

The *L. sicelis* population increase observed after the bamboo die-off event could not have been caused by an increase in available resources, because its host plant, *P. chino* var. *viridis*, did not expand after *S. veitchii* var. *hirsuta* died off. Another possibility is that there had been reproductive interference between *L. diana* and *L. sicelis* prior to the bamboo die-off, and that the *L. sicelis* population subsequently increased because it was no longer exposed to reproductive interference. When interspecific interference competition occurs, species that are more sensitive to the interference often shift their niches (Haskins et al., 1997; Culbertson & Herrmann, 2019), and the interference-sensitive species begins to use the niche following the removal of the other species (McEachin et al., 2024). If *L. sicelis* was affected by interference from *L. diana* before the bamboo die-off event, then its realised niche may have been more restricted than its original niche. Freed from interference following the bamboo die-off event, *L. sicelis* would have exploited parts of the niches formerly occupied by *L. diana*.

Light intensity in microhabitats used by *Lethe* butterflies differed between non-territorial males of both species before bamboo die-off (Fig. 1C, D). Following bamboo die-off, *L. sicelis* did not subsume microhabitats formerly occupied by *L. diana*, but rather extended its range in the opposite direction. At first glance, this result appears to indicate a lack of interference between the two *Lethe* butterfly species. However, a comparison of light intensity between microhabitats used by territorial and non-territorial males showed that spaces used by *L. sicelis* within its expanded range were those previously used by *L. diana* (Figs 2 and 3). Thus, interspecific interference between territorial and non-territorial males, in the form of chasing, appears to have led to differential microhabitat use before the bamboo die-off event. The elimination of this interference after bamboo die-off allowed territorial *L. sicelis* males to use the spaces vacated by *L. diana* and non-territorial *L. sicelis* males to use the spaces previously used by territorial *L. diana* males. The impact of the interspecific interference on the fitness of *L. sicelis* males may have differed between territorial males and non-territorial males; this is because territorial males subjected to the interference had their reproductive activities disrupted, whereas this was not necessarily the case for non-territorial males. If the interference did not significantly affect non-territorial *L. sicelis* males, it is likely that the effect on the species' population growth was also minor. Nonetheless, given that various butterfly species use both perching tactics (sitting and waiting for mates, including territorial behaviour) and patrolling tactics (actively searching for mates) during mate-locating (Wickman, 1985, 1988; Ide, 2004, 2010; Peixoto et al., 2012), it cannot be asserted that non-territorial *L. sicelis* males did not engage in reproductive activities.

Because the *S. veitchii* var. *hirsuta* die-off caused a sharp population decline in *L. diana*, the effects of interspecific interference were detected only in *L. sicelis*. It is interesting to consider whether a *P. chino* var. *viridis* die-off, which could have caused an *L. sicelis* population decline, would have led to clearly detectable reproductive interference between these two *Lethe* butterfly species. The effects of reproductive interference are often asymmetric between species, with only one species experiencing a reduction in fitness (Gröning & Hochkirch, 2008; Mitchell et al., 2022). The mechanism by which asymmetry in reproductive in-

terference occurs may be related to intrasexual selection intensity and sexual conflict within a species (Kyogoku & Sota, 2015; Yassin & David, 2016; Onishi & Matsumura, 2024). Male–male aggression and sexual coercion behaviours such as persistent courtship and forced copulation by males generally evolved based on sex differences in offspring investment (Clutton-Brock & Parker, 1995; Emlen, 2008; Rico-Guevara & Hurme, 2019). These aggressive behaviours may also be directed towards other species if species identification is inaccurate. Indeed, territorial behaviour is sometimes observed between species without resource overlap, and is often thought to arise from misdirected intraspecific aggression (Schultz & Switzer, 2001; Tynkkynen et al., 2004; Peiman & Robinson, 2010; Cowen et al., 2020). Furthermore, misdirected courtship behaviour is sometimes perceived as aggressive behaviour towards other species (McLain & Shure, 1987). Pursuit flight by male butterflies within their mating territories is likely misdirected courtship behaviour rather than aggression (Suzuki, 1976). Such intraspecific courtship behaviour may lead to interspecific interference if species are not accurately identified. The intensity of such "aggressive behaviour" (including mating attempts) toward different species reflects courtship persistence and aggression intensity within a species. Species with intense intraspecific "aggressive behaviour" have typically evolved traits that aid in defence (Arnqvist & Rowe, 2005; Rico-Guevara & Hurme, 2019). Such species would be less susceptible to interspecific interference, whereas species that do not exhibit intense intraspecific "aggressive behaviour" likely incur high costs from interspecific interference due to insufficient defences. For example, males of the broad-horned flour beetle *Gnatocerus cornutus* use their large mandibles as weapons during male–male combat (Okada et al., 2006), while males of the red flour beetle *Tribolium castaneum* are less aggressive and do not have exaggerated weapon traits (Onishi & Matsumura, 2024). When the two species coexist, *G. cornutus* males attack *T. castaneum* males, reducing mating and oviposition rates in *T. castaneum* (Onishi & Matsumura, 2024). Thus, the species that is more aggressive in intraspecific interactions exerts a stronger interference effect on the less aggressive species; as a result, the less aggressive species may undergo a niche shift (Reif et al., 2015; Grether et al., 2017; Culbertson & Herrmann, 2019).

In mating territories, the durations of pursuit flights between conspecifics were longer for *L. diana* than for *L. sicelis* (Fig. 4). That is, *L. diana* males were more "aggressive" than *L. sicelis* males. When *L. sicelis* approached an *L. diana* territory, the flying bout duration of the resident male was shorter than an *L. diana–L. diana* pursuit flight, but equivalent to that of an *L. sicelis–L. sicelis* pursuit flight. Territorial flight in butterflies causes energy depletion, despite the absence of physical contact (Peixoto & Benson, 2011; Vande Velde & Van Dyck, 2013). Furthermore, as butterflies fly more, their wings suffer more significant wear and damage (Niitepõld & Boggs, 2015). Consequently, the duration of pursuit flight is considered a valid proxy for the cost of territorial behaviour and is indeed used as such in many studies (Pinto et al., 2019). For *L. diana*, the cost involved in pursuing a different *Lethe* species is a fraction of that required to pursue a conspecific, whereas for *L. sicelis*, it is likely equivalent to the cost of pursuing a conspecific. Therefore, compared to a situation where interspecific pursuit flights do not occur, such a pursuit flight between different *Lethe* butterflies imposes a relatively small additional cost on *L. diana*, whereas it imposes a significant additional cost on an approaching *L. sicelis*. No data are available for an *L. diana* approaching *L. sicelis* territory, because the territorial behaviour of *L. sicelis* was not investigated before the bamboo die-off event. However, because these butterfly species chase each other during pursuit flight, the flying bout duration of a resident male in this situation would likely be similar to that of heterospecific pursuit flight in *L. diana* territory. Under any circumstances, pursuit flights between different *Lethe* butterflies are costly for *L. sicelis*. Therefore, it appears that interspecific interference effects were greater in *L. sicelis*. If the *L. sicelis* population had drastically decreased, a clearly detectable influence of reproductive interference on *L. diana* would appear unlikely.

The microhabitat of *L. sicelis* females did not change after bamboo die-off, which suggests that they experienced little interference from territorial *L. diana* males, likely because female butterflies often fly near their host plants, dwarf bamboos on the forest floor. Because interference between males does not directly reduce the number of eggs laid by females, any fitness loss due to reproductive interference may have been negligible (Gröning & Hochkirch, 2008). Simulations have shown that two species can coexist when reproductive interference is weak (Nishida et al., 2015), which may explain why, despite reproductive interference between the two *Lethe* species, one species was not excluded. However, even weak interference can result in resource differentiation (Noriyuki, 2015), such that differential host plant use between the two *Lethe* species may have been caused by reproductive interference.

Closely related butterfly species in sympatry sometimes exhibit temporal segregation in mating activities such as territorial behaviours (Kuno, 1992; Le Roy et al., 2021). Such butterflies are thought to experience temporal niche differentiation as a result of interspecific interactions such as reproductive interference (Bouinier et al., 2025). However, in *L. diana* and *L. sicelis*, territorial behaviour was observed within roughly the same temporal window (13:00–18:00). Because the overall territories of these species differ slightly (Ide, 2001a), they may not have required temporal niche differentiation. The start and end times of territorial behaviour in *L. diana* have been reported to depend on air temperature and solar radiation, which allow this species to maintain an optimum body temperature for flight (Ide, 2002b). Territorial behaviour in *L. sicelis* may also be affected by air temperature (Ide, 2001b). Diurnal activity patterns in animals are often constrained by physiological traits (Kronfeld-Schor & Dayan, 2003); the territorial behaviour of *L. diana* and *L. sicelis* may also be constrained by thermoregulation. However, this study did

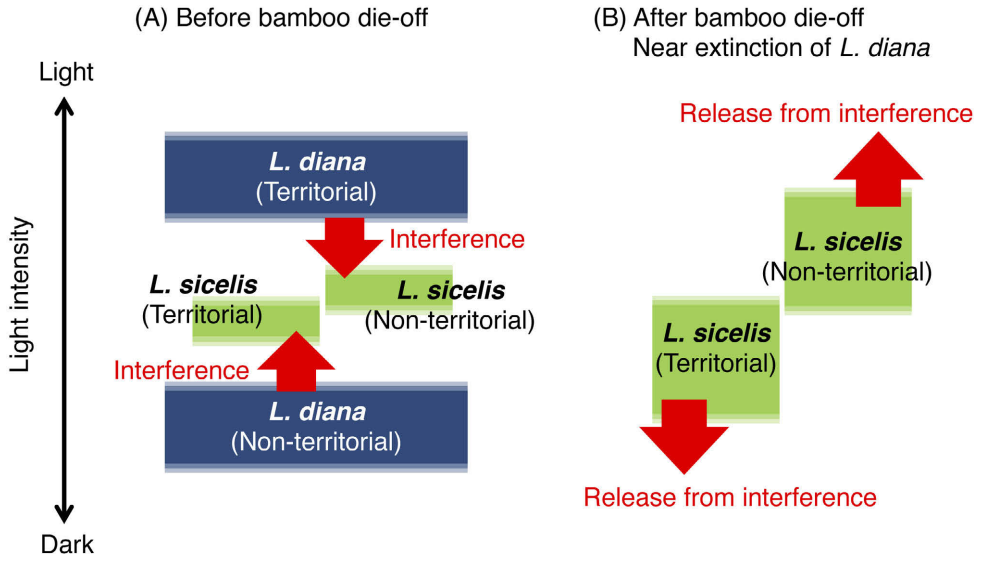


Fig. 5. Schema of microhabitat utilisation of *Lethe diana* and *L. sicelis* males before and after bamboo die-off. Height of boxes represents range of light intensity levels utilised by each butterfly species. (A) Before bamboo die-off, (B) after bamboo die-off.

not systematically investigate the timing of territorial behaviour; more precise investigations are needed to evaluate temporal niche differentiation in these species.

CONCLUSION

Changes in the microhabitats used by *L. sicelis* males after bamboo die-off are thought to have been caused by release from interference by *L. diana* males (Fig. 5). Resource differentiation in terms of host plant availability occurred between these two *Lethe* species, suggesting that reproductive interference was not necessarily one-sided, and that *L. diana* was also affected to some extent. However, given that *L. diana* was more persistent in chasing approaching insects from its territories and that *L. sicelis* expended greater effort in interspecific chases, it appears likely that interference had a greater effect on *L. sicelis*. The *L. sicelis* population increase that followed the bamboo die-off event may also have been caused by its release from reproductive interference.

Kyogoku & Sota (2017) proposed that sexual selection intensity within a species determines its capacity for reproductive interference. Male traits that are harmful to females evolve through sexual selection (Arnqvist & Rowe, 2005), and these traits also harm females of other sympatric species. Heterospecific females may incur higher fitness costs than conspecific females because heterospecific females are unlikely to have evolved counter-adaptations to harmful male traits (Kawatsu, 2013). As a result, weak sexual selection makes species more susceptible to reproductive interference. This hypothesis would also hold true for male–male interference, as supported by the present findings.

ACKNOWLEDGEMENTS. I thank the reviewers for valuable comments and suggestions. I also thank the Kamigamo Experimental Forest Station, Kyoto University, for permission to conduct this research.

REFERENCES

Abe Y. & Shibata S. 2012: Spatial and temporal flowering patterns of the monocarpic dwarf bamboo *Sasa veitchii* var. *hirsuta*. — *Ecol. Res.* **27**: 625–632.

Abe Y. & Shibata S. 2013: *Sasa veitchii* (Carrière) Rehder var. *hirsuta* seedling growth under various light conditions. — *J. Jpn. Soc. Reveget. Tech.* **39**: 295–300 [in Japanese, English abstract].

Areta J.I. & Cockle K.L. 2012: A theoretical framework for understanding the ecology and conservation of bamboo-specialist birds. — *J. Ornithol.* **153**: S163–S170.

Arnqvist G. & Rowe L. 2005: *Sexual Conflict*. Princeton Univ. Press, Princeton, NJ, 330 pp.

Bates D., Maechler M., Bolker B. & Walker S. 2015: Fitting linear mixed-effects models using lme4. — *J. Stat. Software* **67**: 1–48.

Bouinier T., Smadi C. & Llaurens V. 2025: Vertical and temporal niche partitioning in Amazonian butterflies: implications for the evolution of thermal tolerance. — *Oikos* **2025**: e11567, 13 pp.

Clutton-Brock T.H. & Parker G.A. 1995: Sexual coercion in animal societies. — *Anim. Behav.* **49**: 1345–1365.

Connell J.H. 1983: On the prevalence and relative importance of interspecific competition: evidence from field experiments. — *Am. Nat.* **122**: 661–696.

Cooper C.B., Hochachka W.M. & Dhondt A.A. 2007: Contrasting natural experiments confirm competition between house finches and house sparrows. — *Ecology* **88**: 864–870.

Cowen M.C., Drury J.P. & Grether G.F. 2020: Multiple routes to interspecific territoriality in sister species of North American perching birds. — *Evolution* **74**: 2134–2148.

Culbertson K.A. & Herrmann N.C. 2019: Asymmetric interference competition and niche partitioning between native and invasive *Anolis* lizards. — *Oecologia* **190**: 811–820.

Day T. & Young K.A. 2004: Competitive and facilitative evolutionary diversification. — *BioScience* **54**: 101–109.

Diamond J.M. 1983: Laboratory, field and natural experiments. — *Nature* **304**: 586–587.

Emlen D.J. 2008: The evolution of animal weapons. — *Annu. Rev. Ecol. Evol. Syst.* **39**: 387–413.

Friberg M., Leimar O. & Wiklund C. 2013: Heterospecific courtship, minority effects and niche separation between cryptic butterfly species. — *J. Evol. Biol.* **26**: 971–979.

Fukuda H., Kubo K., Kuzuya T., Takahashi A., Takahashi M., Tanaka B. & Wakabayashi M. 1972: *Insects' Life in Japan. Vol. 3. Butterflies.* Hoikusha, Osaka, 278 pp. [in Japanese].

Fukuda H., Hama E., Kuzuya T., Takahashi A., Takahashi M., Tanaka B., Tanaka H., Wakabayashi M. & Watanabe Y. 1984: *The Life Histories of Butterflies in Japan. Vol. 4.* Hoikusha, Osaka, 373 pp. [in Japanese].

Garnas J.R., Ayres M.P. & Lombardero M.J. 2023: Forest insect population dynamics. In Allison J.D., Paine T.D., Slippers B. & Wingfield M.J. (eds): *Forest Entomology and Pathology. Vol. 1. Entomology.* Springer, Cham, pp. 115–140.

Grether G.F., Peiman K.S., Tobias J.A. & Robinson B.W. 2017: Causes and consequences of behavioral interference between species. — *Trends Ecol. Evol.* **32**: 760–772.

Gröning J. & Hochkirch A. 2008: Reproductive interference between animal species. — *Quart. Rev. Biol.* **83**: 257–282.

Gurevitch J., Morrow L.L., Wallace A. & Walsh J.S. 1992: A meta-analysis of competition in field experiments. — *Am. Nat.* **140**: 539–572.

Hairston N.G. 1980: The experimental test of an analysis of field distributions: competition in terrestrial salamanders. — *Ecology* **61**: 817–826.

Hairston N.G. 1989: *Ecological Experiments: Purpose, Design, and Execution*. Cambridge University Press, Cambridge, 390 pp.

Haskins K.E., Sih A. & Krupa J.J. 1997: Predation risk and social interference as factors influencing habitat selection in two species of stream-dwelling waterstriders. — *Behav. Ecol.* **8**: 351–363.

Higashiguchi R. & Shibata S. 2017: Effect of removing the impact of continuous herbivory by sika deer on regeneration of dwarf bamboo (*Sasa veitchii* var. *hirsuta*) after mass flowering. — *J. Jpn. Soc. Reveget. Tech.* **43**: 74–79 [in Japanese, English abstract].

Ide J.-Y. 2000a: Seasonal change in flight behaviour of the satyrine butterfly *Lethe diana* (Lepidoptera: Nymphalidae). — *Entomol. Sci.* **3**: 591–596.

Ide J.-Y. 2000b: Seasonal change in factors affecting spatial microdistribution in a population of the satyrine butterfly *Lethe diana*. — *Trans. Lepid. Soc. Jpn.* **52**: 13–24.

Ide J.-Y. 2001a: Microhabitat differences in two *Lethe* butterflies (Lepidoptera: Nymphalidae) concerning thermoregulation. — *Entomol. Sci.* **4**: 279–285.

Ide J.-Y. 2001b: Summer disappearance of territoriality in the satyrine butterfly *Lethe sicelis*. — *Trans. Lepid. Soc. Jpn.* **52**: 168–170.

Ide J.-Y. 2002a: Mating behaviour and light conditions cause seasonal changes in the dispersal pattern of the satyrine butterfly *Lethe diana*. — *Ecol. Entomol.* **27**: 33–40.

Ide J.-Y. 2002b: Seasonal changes in the territorial behaviour of the satyrine butterfly *Lethe diana* are mediated by temperature. — *J. Ethol.* **20**: 71–78.

Ide J.-Y. 2003: Age patterns in leaves used by larvae of the satyrine butterfly *Lethe diana*. — *Trans. Lepid. Soc. Jpn.* **54**: 40–46.

Ide J.-Y. 2004a: Diurnal and seasonal changes in the mate-locating behavior of the satyrine butterfly *Lethe diana*. — *Ecol. Res.* **19**: 189–196.

Ide J.-Y. 2004b: Selection of age classes of *Sasa* leaves by caterpillars of the skipper butterfly *Thoressa varia* using albomargination of overwintered leaves. — *J. Ethol.* **22**: 99–103.

Ide J.-Y. 2006: Sexual and seasonal differences in the frequency of beak marks on the wings of two *Lethe* butterflies. — *Ecol. Res.* **21**: 453–459.

Ide J.-Y. 2010: Weather factors affecting the male mate-locating tactics of the small copper butterfly (Lepidoptera: Lycaenidae). — *Eur. J. Entomol.* **107**: 369–376.

Inoue T. 2018: Recent change in the butterfly assemblage of the Forestry and Forest Products Research Institute, Tsukuba City, Ibaraki Prefecture, central Japan. — *Jpn. J. Entomol. N.S.* **21**: 211–229 [in Japanese, English abstract].

Janzen D.H. 1976: Why bamboos wait so long to flower. — *Annu. Rev. Ecol. Syst.* **7**: 347–391.

Johnson K.G., Schaller G.B. & Hu J. 1988: Responses of giant pandas to a bamboo die-off. — *Natl. Geogr. Res.* **4**: 161–177.

Kaplan I. & Denno R.F. 2007: Interspecific interactions in phytophagous insects revisited: a quantitative assessment of competition theory. — *Ecol. Lett.* **10**: 977–994.

Kawatsu K. 2013: Sexually antagonistic coevolution for sexual harassment can act as a barrier to further invasions by parthenogenesis. — *Am. Nat.* **181**: 223–234.

Kishi S. & Nakazawa T. 2013: Analysis of species coexistence co-mediated by resource competition and reproductive interference. — *Popul. Ecol.* **55**: 305–313.

Kishi S. & Tsubaki Y. 2014: Avoidance of reproductive interference causes resource partitioning in bean beetle females. — *Popul. Ecol.* **56**: 73–80.

Kitano D., Fujii N., Sujiono, Yamaue S., Kitamura T., Honma A., Tsukada M., Nishida T., Sawada H. & Takakura K.I. 2018: Reproductive interference between two serious pests, oriental fruit flies *Bactrocera carambolae* and *B. dorsalis* (Diptera: Tephritidae), with very wide but partially overlapping host ranges. — *Appl. Entomol. Zool.* **53**: 525–533.

Kobayashi T., Kitahara M., Ohkubo T. & Aizawa M. 2010: Relationships between the age of northern Kantou plain (central Japan) coppice woods used for production of Japanese forest mushroom logs and butterfly assemblage structure. — *Biodiv. Conserv.* **19**: 2147–2166.

Kronfeld-Schor N. & Dayan T. 2003: Partitioning of time as an ecological resource. — *Annu. Rev. Ecol. Evol. Syst.* **34**: 153–181.

Kuno E. 1992: Competitive exclusion through reproductive interference. — *Res. Popul. Ecol.* **34**: 275–284.

Kyogoku D. & Kokko H. 2020: Species coexist more easily if reinforcement is based on habitat preferences than on species recognition. — *J. Anim. Ecol.* **89**: 2605–2616.

Kyogoku D. & Sota T. 2015: Exaggerated male genitalia intensify interspecific reproductive interference by damaging heterospecific female genitalia. — *J. Evol. Biol.* **28**: 1283–1289.

Kyogoku D. & Sota T. 2017: The evolution of between-species reproductive interference capability under different within-species mating regimes. — *Evolution* **71**: 2721–2727.

Le Roy C., Roux C., Authier E., Parrinello H., Bastide H., Debat V. & Llaurens V. 2021: Convergent morphology and divergent phenology promote the coexistence of *Morpho* butterfly species. — *Nat. Commun.* **12**: 7248, 9 pp.

Liu S.S., De Barro P.J., Xu J., Luan J.B., Zang L.S., Ruan Y.M. & Wan F.H. 2007: Asymmetric mating interactions drive widespread invasion and displacement in a whitefly. — *Science* **318**: 1769–1772.

Matsumoto K. 2008: Butterfly assemblages and assessment of the forest environment in the Tama Experimental Station of Forestry and Forest Products Research Institute and the Tokyo Metropolitan Sakuragaoka Park in Tama City, Tokyo. — *Jpn. J. Environ. Entomol. Zool.* **19**: 1–16 [in Japanese, English abstract].

McEachin S., Drury J.P. & Grether G.F. 2024: Competitive displacement and agonistic character displacement, or the ghost of interference competition. — *Am. Nat.* **203**: 335–346.

McLain D.K. & Shure D.J. 1987: Pseudocompetition: interspecific displacement of insect species through misdirected courtship. — *Oikos* **49**: 291–296.

Mitchell C., Leigh S., Alphey L., Haerty W. & Chapman T. 2022: Reproductive interference and Satyrisation: mechanisms, outcomes and potential use for insect control. — *J. Pest Sci.* **95**: 1023–1036.

Myers J.H. & Cory J.S. 2013: Population cycles in forest Lepidoptera revisited. — *Annu. Rev. Ecol. Evol. Syst.* **44**: 565–592.

Nakadai R., Hashimoto K., Iwasaki T. & Sato Y. 2018: Geographical co-occurrence of butterfly species: the importance of niche filtering by host plant species. — *Oecologia* **186**: 995–1005.

Niitepõld K. & Boggs C.L. 2015: Effects of increased flight on the energetics and life history of the butterfly *Speyeria mormonia*. — *PLoS ONE* **10**: e0140104, 16 pp.

Nishida T., Takakura K. & Iwao K. 2015: Host specialization by reproductive interference between closely related herbivorous insects. — *Popul. Ecol.* **57**: 273–281.

Nishinaka Y. & Ishii M. 2006: Effects of experimental mowing on species diversity and assemblage structure of butterflies in a coppice on Mt Mikusa, northern Osaka, central Japan. — *Trans. Lepid. Soc. Jpn.* **57**: 202–216.

Nishinaka Y. & Ishii M. 2007: Mosaic of various seral stages of vegetation in the *Satoyama*, the traditional rural landscape of Japan as an important habitat for butterflies. — *Trans. Lepid. Soc. Jpn.* **58**: 69–90.

Nishiyama T. 1984: Distribution and ecology of *Lethe sicelis* in Tochigi prefecture. — *Gekkan-Mushi* **155**: 2–5 [in Japanese].

Noriyuki S. 2015: Host selection in insects: reproductive interference shapes behavior of ovipositing females. — *Popul. Ecol.* **57**: 293–305.

Noriyuki S., Osawa N. & Nishida T. 2012: Asymmetric reproductive interference between specialist and generalist predatory ladybirds. — *J. Anim. Ecol.* **81**: 1077–1085.

Ohsaki N., Ohata M., Sato Y. & Rausher M.D. 2020: Host plant choice determined by reproductive interference between closely related butterflies. — *Am. Nat.* **196**: 512–523.

Okada K., Miyanoshita A. & Miyatake T. 2006: Intra-sexual dimorphism in male mandibles and male aggressive behavior in the broad-horned flour beetle *Gnatocerus cornutus* (Coleoptera: Tenebrionidae). — *J. Insect Behav.* **19**: 457–467.

Onishi R. & Matsumura K. 2024: Heterospecific interaction in two beetle species: Males with weapons decrease the reproductive success of species with weaponless males. — *Ecol. Evol.* **14**: e11518, 9 pp.

Osada N., Sugiura S., Kawamura K., Cho M. & Takeda H. 2003: Community-level flowering phenology and fruit set: comparative study of 25 woody species in a secondary forest in Japan. — *Ecol. Res.* **18**: 711–723.

Peiman K.S. & Robinson B.W. 2010: Ecology and evolution of resource-related heterospecific aggression. — *Quart. Rev. Biol.* **85**: 133–158.

Peixoto P.E.C. & Benson W.W. 2011: Fat and body mass predict residency status in two tropical satyrine butterflies. — *Ethology* **117**: 722–730.

Peixoto P.E.C., Muniz D. & Benson W.W. 2012: Do feeding resources induce the adoption of resource defence polygyny in a lekking butterfly? — *Ethology* **118**: 311–319.

Pianka E.R. 1974: Niche overlap and diffuse competition. — *Proc. Natl. Acad. Sci. U.S.A.* **71**: 2141–2145.

Pinto N.S., Palaoro A.V. & Peixoto P.E.C. 2019: All by myself? Meta-analysis of animal contests shows stronger support for self than for mutual assessment models. — *Biol. Rev.* **94**: 1430–1442.

R Core Team 2020: *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, URL: https://www.R-project.org/.

Reif J., Jiran M., Reifová R., Vokurková J., Dolata P.T., Petrusek A. & Petrusková T. 2015: Interspecific territoriality in two songbird species: potential role of song convergence in male aggressive interactions. — *Anim. Behav.* **104**: 131–136.

Rico-Guevara A. & Hurme K.J. 2019: Intrasexually selected weapons. — *Biol. Rev.* **94**: 60–101.

Saito M.U., Jimbo U., Yago M., Kurashima O. & Ito M. 2016: Larval host records of butterflies in Japan. — *Ecol. Res.* **31**: 491.

Schoener T.W. 1983: Field experiments on interspecific competition. — *Am. Nat.* **122**: 240–285.

Schultz J.K. & Switzer P.V. 2001: Pursuit of heterospecific targets by territorial amberwing dragonflies (*Perithemis tenera* Say): a case of mistaken identity. — *J. Insect Behav.* **14**: 607–620.

Sherry T.W. & Kent C.M. 2022: Extensions and limitations of MacArthur (1958): A review of ecological and evolutionary approaches to competition and diet in the New World wood warblers (Parulidae). — *Ornithology* **139**: 1–17.

Shirôzu T. 2006: *The Standard of Butterflies in Japan*. Gakken, Tokyo, 336 pp. [in Japanese].

Short K.H. & Petren K. 2012: Rapid species displacement during the invasion of Florida by the tropical house gecko *Hemidactylus mabouia*. — *Biol. Invas.* **14**: 1177–1186.

Shuker D.M. & Burdfield-Steel E.R. 2017: Reproductive interference in insects. — *Ecol. Entomol.* **42**: 65–75.

Suzuki S. 1978: *Index to Japanese Bambusaceae*. Gakken, Tokyo, 384 pp. [in Japanese].

Suzuki Y. 1976: So-called territorial behaviour of the small copper, *Lycaena phlaeas daimio* Seitz (Lepidoptera, Lycaenidae). — *Kontyû* **44**: 193–204.

Takahashi M. 1991: *Lethe diana*. — *Insectarium* **28**: 193 [in Japanese].

Takakura K.I. & Fujii S. 2015: Island biogeography as a test of reproductive interference. — *Popul. Ecol.* **57**: 307–319.

Tynkkynen T., Rantala M.J. & Suhonen J. 2004: Interspecific aggression and character displacement in the damselfly *Calopteryx splendens*. — *J. Evol. Biol.* **17**: 759–767.

Ujiie M., Kubota K. & Takami Y. 2025: Interspecific difference and frequency dependence in habitat use of coexisting *Ohomopterus* ground beetle species under reproductive interference. — *Popul. Ecol.* **67**: 6–14.

Vande Velde L. & Van Dyck H. 2013: Lipid economy, flight activity and reproductive behaviour in the speckled wood butterfly: on the energetic cost of territory holding. — *Oikos* **122**: 555–562.

Watanabe M. 1991: Recovering from the weeding of Sasa undergrowth in *Metasequoia* experiment plantation stand. — *Rept. Kyoto Univ. Forests* **22**: 153–162 [in Japanese].

Werner E.E. 1998: Ecological experiments and a research program in community ecology. In Resetarits W.J. & Bernardo J. (eds): *Experimental Ecology: Issues and Perspectives*. Oxford University Press, Oxford, pp. 3–26.

Wickman P.-O. 1985: The influence of temperature on the territorial and mate locating behaviour of the small heath butterfly, *Coenonympha pamphilus* (L.) (Lepidoptera: Satyridae). — *Behav. Ecol. Sociobiol.* **16**: 233–238.

Wickman P.-O. 1988: Dynamics of mate-searching behaviour in a hilltopping butterfly, *Lasiommata megera* (L.): the effects of weather and male density. — *Zool. J. Linn. Soc.* **93**: 357–377.

Yassin A. & David J.R. 2016: Within-species reproductive costs affect the asymmetry of satyrization in *Drosophila*. — *J. Evol. Biol.* **29**: 455–460.

Received April 23, 2026; revised and accepted October 21, 2026
Published online November 16, 2026