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論 文 名

蛾類における特異な警告色擬態：異なる発育段階での擬態および雌雄で異なるモデルへの擬態（英文）

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Peculiar mimicry systems in moths between the different developmental stages and between the sexes

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Doctoral Theses

Peculiar mimicry systems in moths between the different developmental stages and between the sexes

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Contents

Abstract

Warning color and warning color mimicry are subjects that have long been much studied as good examples of evolution involving natural selection. Lepidopterous insects have been the focus of much of the research, although much of these has been on diurnal butterflies. In contrast, there has been little research on moths, which are predominantly nocturnal species, but I have noticed that there are multiple examples of peculiar mimicry cases in moths that are not found in other insects. In this study, experiment-based research was conducted from two main perspectives on peculiar moth mimicry, between the different developmental stages and between the sexes.

The final-instar larvae of *Pryeria sinica* Moore, 1877 (Zygaenidae) are conspicuously colored yellow-green with black stripes and are known to escape from attacks after predators learn of the cyanogenic fluids secreted on their body surface. *Ivela auripes* (Butler, 1877) (Lymantriidae) is often found in the same habitat during the same season as *Pryeria sinica*, and its pupa (not larva) is similar to larval *Pryeria sinica* in shape and color. Mature larvae of *Pryeria sinica* search for pupation sites during the daytime and pupate in cryptic, pale-brown cocoons. On the other hand, *Ivela auripes* pupates without cocoons on substrates near and above the ground, where they appear to be exposed to predators. In the chapter 2, it was observed that Japanese tits, *Parus minor* Temminck and Schlegel, 1848, ate *Ivela auripes* pupae attached to a wall, but no tit individual ever attacked them repeatedly. When fed pupae or larvae in the laboratory, Japanese grass lizards, *Takydromus tachydromoides* (Schlegel, 1838), rarely ate larval *Pryeria sinica* or pupal *Ivela auripes* or regurgitated them soon after eating them, suggesting their unpalatability. If discrimination of pupal *Ivela auripes* from larval *Pryeria sinica* is not precise for these potential predators, their similar warning colors might constitute a rare case of Müllerian mimicry between different developmental stages of unrelated moth species.

Mimicry with warning colors includes Batesian mimicry and Müllerian mimicry. If I divide mimicry by sex, there are theoretically four types of mimicry: unimodal mimicry, female-limited mimicry, male-limited mimicry, and dual mimicry. The latter three cases cause sexual dimorphism in body color and marking pattern, but are rare. In the chapter 3, I report that the tussock moth *Numenes albofascia* is possibly of dual mimicry. The wing color and marking pattern of male and female *Numenes albofascia* are completely different, with the male's pattern resembling that of the smoky moth *Pidorus atratus*, while the female pattern resembling that of the tiger moth *Arctia caja*.

Body size also differs greatly between the sexes of *Numenes albofascia*, matching the mimicry model species of each sex. These moths are distributed sympatrically in Japan, and their adult seasons overlap to each other. According to lizard feeding experiments, *Numenes albofascia* is palatable, while both male and female model species are unpalatable. Actograms in the laboratory and the light trapping in the field suggest that females of *Numenes albofascia* fly actively from sunset to midnight, while males fly during the twilight period around dawn. Therefore, male and female *Numenes albofascia* are suggested to be Batesian mimicry to diurnally active *Pidorus atratus* and nocturnally active *Arctia caja*, respectively, and the great sexual dimorphism of this moth may be caused by dual mimicry.

The evolution of sexual dimorphism in color is generally explained by same-sex competition and mate choice via color perception, or female-only mimicry via color learning of predators searching for the prey visually such as birds. Such sexual dimorphism in color is well known in lepidopteran diurnal butterflies, but is rare and little studied in moths, which are predominantly nocturnal species. In moths of the family Lymantiidae, darker wings in males compared to females are relatively common, a pattern of sexual dimorphism that is not seen in butterflies. Therefore, I first measured the daily activity rhythm in several species of lymantriid moths, and found that in species with dark males, a sexual difference in daily activity rhythm was observed, with males flying at twilight-dusk or during the day, and females flying mainly at night. Next, the repellent effect of the moths was measured by feeding to lizards, and all moths were predated by lizards and no repellent effect was observed. Furthermore, field experiments on the predation rate of males and females during twilight hours showed that dark colored males were less likely to be preyed upon than light colored females. In other words, the dark color of male wings was considered to be a result of the evolution of a concealment function due to selection pressure exerted specifically on males by birds and other visual predators. Among these moths with dark colored male wing sexual dimorphism, there are several species in which the males and females are thought to be Batesian mimics of separate models. Although the evolutionary process of this dual mimicry has been unknown in the past, it is consistent with the explanation that if the dark color of male wings is considered as "preadaptation” of mimicry.

Thus, there are several previously unknown examples of bizarre mimicry in moth species, and there may be further undiscovered examples. Studying these experimentally will be useful to reveal new ways in which natural selection may drive the mimicry system itself and its evolution.

1. General introduction

Warning color (aposematism) is a defense mechanism to promote their own toxicity or repellent effects to predators that use visual cues to search for prey (Mallet and Joron 1999, Ruxton *et al*. 2018, Caro and Koneru 2021). Insects are highly exposed to predation pressure from diurnal visual predators such as birds, lizards, or small mammals (Holling 1961), and warning color is a very common in insects. The phenomenon in which the similarity of the color and morphology of another species to such a warning color enhances its defensive effect against predators is called warning color mimicry (Mallet and Joron 1999, Ruxton *et al*. 2018), and this is also a widespread phenomenon among insects. Classically, there are two main types of interspecific relationship in warning color mimicry. Batesian mimicry is when palatablae species and unpalatable species, inhabiting the same location, resemble each other (Bates 1862). Conversely, Müllerian mimicry is a case in which cohabiting unpalatable species become similar in color to each other (Müller 1879). In the case of Batesian mimicry, the survival rate of the misidentified mimic species increases when predators learn the unpalatability of the model species. In this case, generally, the mimicry relationship functions when the number of individuals of the model species is greater than the number of individuals of the mimic species, and a negative frequency-dependent selection relationship between the number of individuals of the model species and the mimic species is constituted. In the case of Müllerian mimicry, the cost of mimic species for each individual decreases as visual predators encounter and learn more frequently the unpalatability of their prey, and the individual survival rate of the mimic species increases. In this case, a positive frequency-dependent selection relationship is established, in which the greater the number of individuals of each other species resembling each other, the greater the effectiveness of mimicry (Ayala and Campbell 1974). Thus, the relationship between mimic and model species is very different in Batesian and Müllerian mimicry, and it is important to discriminate which of these structures is adopted when studying mimicry. In addition, when multiple such warning color mimic relationships constitute complex interactions across three or more species, the entire relationship is referred to as a mimetic complex or mimetic ring (Mallet and Joron 1999, Ruxton *et al*. 2018).

As a good example of evolution with natural selection, such warning color mimicry has been actively studied since the 19th century, especially in diurnal butterflies (Wallace 1865, Osaki 2005). In this study, on the other hand, aimed to experimentally examine mimic relationships specific to moths, generally considered nocturnal, which have not been well studied, and to examine the reasons for their evolution. Two themes are addressed in this study: mimicry between different developmental stages, and sex-limited mimicry.

Warning color mimicry between different developmental stages

Warning colors in insects are found in the larval, pupal and adult developmental stages, respectively. Of these, warning color and mimicry is common in larvae and adults, but in pupae, cryptic colors and cryptic morphology are common and warning colors are rarely seen（Wiklund and Sillén-Tullberg 1985, Edmonds 1990, Janzen *et al*. 2010, Paul *et al*. 2018, Lindstedt *et al*. 2019）. The only examples of pupal warning colors known so far are those of ladybird (Coccinellidae) species (Paul *et al*. 2018, Aslam *et al*. 2019）, Geometer moths (Geometridae) (Tsubuki and Hayashi 2023), and lepidopteran pupae with an eyespot pattern (Janzen *et al*. 2010). The pupae of *Ivela auripes* are often seen in conspicuous areas of wooded areas around May. These pupae have a distinctive oval body shape and yellow-green body surface with a prominent black stripe pattern. On the other hand, the larvae of another moth, *Pryeria sinica*, are also common at the same time of year and in the same locations. This larva also has an oval body shape, yellow-green body surface and a conspicuous black stripe pattern, making them look very similar. Insects of the family Zygaenidae, including the *P. sinica*, are known to contain cyanide in their bodies and to defend themselves by secreting a liquid from their body surface when attacked (Johki and Hidaka 1979). In other words, the bright colors of the larvae *P. sinica* act as a warning color and it may serve as a model species for warning color mimicry. I made a hypothesis that this may be a unique case, not previously reported, in which a warning color mimetic relationship is established between two phylogenetically distant species, at different developmental stages, larva and pupa. The presence or absence of repellent effects and toxicity of pupae *I. auripes* are not known. This means that the mechanism of Müllerian and Batesian mimicry differs depending on whether pupae *I. auripes* has a repellent effect or not. In this study, this interspecific relationship was experimentally tested from three perspectives: morphological similarity, predator exposure and predator repellency.

Warning color mimicry with sexual dimorphism

The phenomenon of sexual dimorphism, in which males and females of the same species differ significantly in their color or morphology, is often observed in insects, and Lepidoptera are no exception (Andersson 1994). About the relationships between warning color mimicry and sexual dimorphism in color within a species (sexual dichromatism), I sorted out the relationships in following four types theoretically (Fig. 1-1) based on the preceding studies (Vane-Wright 1971, Hespenheide 1975, Kunte 2009a, Allen 2011). I. Unimodal mimicry (Both sexes of mimic species resemble the same model species. There is no sexual dimorphism in mimic species); II. Female-limited mimicry (Females of mimic species resemble the model species, but males do not. There is sexual dimorphism in mimic species); III. Male-limited mimicry (Males of mimic species resemble the model species, but females do not. There is sexual dimorphism in mimic species); IV. Dual mimicry (Each sex of mimic species resembles a different model species. There is sexual dimorphism in mimic species).

Among the four types, unimodal mimicry (type I) and female-limited mimicry (type II) have been well studied (Ohsaki 2005, Ruxton *et al*. 2018). However, only a few examples are recorded with insects and spiders so far for male-limited mimicry (type III) and dual mimicry (type IV), and the function and the evolutionary process of the relationship between warning color mimicry and sexual dimorphism in color in type III and IV remain unclear. I found the new example of suspected dual mimicry complex (type IV). The moth, *Numenes albofascia*, belong to the genus *Numenes* (Lymantriidae) in Japan, have distinctive sexual dimorphism in color: males have a white stripe on black-based forewings and have black hindwings, whereas females have complex white line patterns on black-based forewings and have vivid yellow hindwings. Male *N. albofascia* closely resembles *Pidorus atratus* (Zygaenidae) in its color, and female *N. albofascia* resembles *Arctia caja* (Arctiidae). The adult emerging seasons of each species also correspond mutually: *N. albofascia* from June to July and from August to September (bivoltine), *P. atratus* from June to July and from August to September (bivoltine), *A. caja* from August to September (univoltine) (Kishida 2011d, 2011e, Horie 2013). In the present study, I investigate experimentally the suspected mimicry complex with *N. albofascia* from the experimental study of three aspects: morphological similarity, behavioral similarity and predator avoidance, and discuss its evolutionary process based on the results.

Other than *N. albofascia*, there are many sexual dimorphisms in color in the family Lymantriidae. There is a common feature: the wing color of males is darker than the wing color of females of the same species. In diurnal butterflies, visual mate choice and strong predatory pressure on females are thought to be the main reasons for the evolution of sexual dimorphism in wing color (Ohsaki 1995, Kunte 2008, 2009b, Tsurui-Sato *et al*. 2019, van der Bijl *et al*. 2020). However, males of Lymantriidae have well-developed antennae. In these cases, mating activity is known to be mainly mediated by sex pheromones (Lees and Zilli 2019), and it is unlikely that their colors are related to visual mate choice. In addition, in the sexually dimorphic form of Lymantriidae, there are many species for which a mimetic relationship cannot be assumed, in addition to species such as *N. albofascia*, which are thought to mimic toxic species. It is therefore necessary to consider the evolutionary process of the unique sexual dimorphism itself in moths, which differs from that in butterflies.

I have therefore focused on the gap in the time of daily activity rhythm between the sexes. Males flying at dawn or during the day, when birds are already active, are presumably more likely to be exposed in flight to birds than females flying after dark after sunset (Acharya 1995). In other words, I hypothesized that color change may occur due to selection pressure from visual predators only on the males.

I experimentally tested this idea that the dark color of the males of Lymantriidae has a concealing effect on visual predators during twilight and dusk from three perspectives: diurnal activity differences between males and females, predator avoidance and sex differences in the frequency of predation in the field.

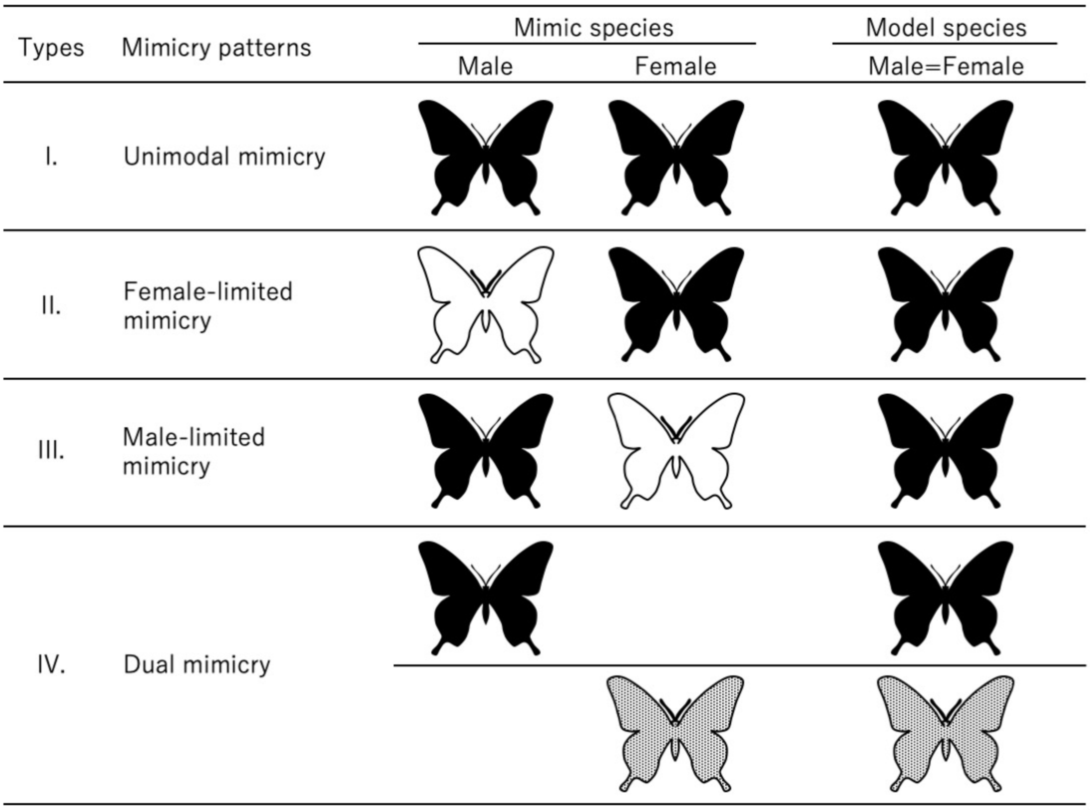


Figure 1-1. Four theoretical patterns of warning color mimicry in males and females of mimic species; I. Unimodal mimicry (Both sexes of mimic species resemble the same model species. There is no sexual dimorphism in mimic species); II. Female-limited mimicry (Females of mimic species resemble the model species, but males do not. There is sexual dimorphism in mimic species); III. Male-limited mimicry (Males of mimic species resemble the model species, but females do not. There is sexual dimorphism in mimic species); IV. Dual mimicry (Each sex of mimic species resembles a different species of model. There is sexual dimorphism in mimic species).

2. Müllerian mimicry between cohabiting final-instar larval *Pryeria sinica* Moore, 1877 (Lepidoptera: Zygaenidae) and pupal *Ivela auripes* (Butler, 1877) (Lepidoptera: Lymantriidae)

2-1. Introduction

Many insects use their colors and patterns as camouflage to blend in with the environment and avoid detection by predators. Their bodies can resemble live or dead leaves, tree trunks, or branches, a phenomenon known as cryptic color (Edmunds 1990). However, if the insect has any defenses against predators, such as toxins or unpalatability (foul taste or smell), selection may favor warning color, resulting in Müllerian and Batesian mimicry. In Müllerian mimicry, there is close similarity in color and shape (as well as in other defensive features) between cohabiting unpalatable prey species (Rettenmeyer 1970, Mallet and Mathieu 1999, Sherratt 2008). Due to the similar color and shape between species, the warning signal to predators is shared and learned more quickly at less cost to each species, which increases expected individual survival rates. Batesian mimicry refers to cases where a palatable, non-poisonous species resembles an unpalatable species with warning color, thereby increasing its survival rate (Rettenmeyer 1970).

Cryptic color occurs in all developmental stages of insects, but warning color is typically limited to larvae and adults. Insect pupae are usually cryptic or hidden under substrates or within inconspicuous cocoons and are rarely conspicuous (Wiklund and Sillén-Tullberg 1985, Janzen *et al.* 2010, Paul *et al*. 2018). Under experimental conditions using quail as predators, larvae and adults of the monarch butterfly, *Danaus plexippus* (Linnaeus, 1758), and Old World swallowtail butterfly, *Papilio machaon* Linnaeus, 1758, with warning color usually survived attacks, while their cryptic pupae were usually consumed (Wiklund and Sillén-Tullberg 1985). An exceptions are the toxic two-spotted ladybird beetle, *Adalia bipunctata* (Linnaeus, 1758), which has warning colors in all stages of its life cycle (Paul *et al*. 2018), and the pupae of 3 species of genus *Cystidia* (Lepidoptera: Geometridae) moths in Japan, *Cystidia stratonice* (Stoll, 1782), *Cystidia truncangulata* Wehrli, 1934 and *Cystidia couaggaria* (Guenée, 1858) (Tsubuki and Hayashi 2023). Another example is the pupae of several tropical butterflies and moths, which are known to have animal eye-like or face-like color patterns. In these cases, defensive function must be discussed not only in terms of avoidance learning after encountering predators, but also in terms of innate avoidance of threats (apparent eyes or face which triggers the flight/flight response) from potential predators such as cats, hawks, and snakes (Aiello and Silberglied 1978, Janzen *et al.* 2010).

The moth *Pryeria sinica* Moore, 1877 (Zygaenidae) is univoltine; its pupae pass the summer in cocoons (summer diapause), and the adults emerge beginning in late October (Ishii *et al.* 1983). The moth spends the winter in the egg stage (Tsubaki 1981, Ishii *et al.* 1983). The duration of the larval stages is 38.6 days at 20°C (Shiotsu and Arakawa 1982). The final (4th)-instar larvae of *P. sinica* contain two different types of cuticular cavities, which are used for the storage of a cyanogenic defensive secretion (Naumann and Feist 1987). The larvae are conspicuously colored yellow-green with black stripes (Fig. 2-1A, B) and escape from attack by Japanese grass lizards, *Takydromus tachydromoides* (Schlegel, 1838), as the lizard learns the smell of fluids secreted on the larval body surface (Johki and Hidaka 1979). Therefore, larval body color functions as a warning to predators (Johki and Hidaka 1979). The larval bodies contain linamarin, lotaustralin, and sarmentosin (Nishida 1994). Fully grown larvae leave their host plants and spin pale brown cocoons between litter falls or crevices of a variety of substrates (Tsubaki 1981).

Ivela auripes (Butler, 1877) (Lymantriidae) is another moth with a univoltine life cycle. After spending the winter in the egg stage, newly hatched larvae grow and reach the final (5th) larval instar and pupate in early summer (Togashi and Kodani 1990). Yukinari (2002) suggested that color may function as a warning signal to predators in the larvae of this moth, because they have a patchy body color of yellow-green and black (Fig. 2-1F, G) and no birds attack them even in outbreak years.

I noticed that larval *P. sinica* and pupal (not larval) *I. auripes* are quite similar to each other in color and shape. These two species are common and often coexist in the same habitats. As larval *P. sinica* has warning color, pupal *I. auripes* may mimic it to avoid predation by their common enemies. If pupal *I. auripes* is also toxic or unpalatable, these two species may be showing Müllerian mimicry, but if *I. auripes* is palatable, it would suggest Batesian mimicry. In the present study, I examined the morphological similarities between larval *P. sinica* and pupal *I. auripes*, the palatability of pupal *I. auripes* to potential predators, and whether predators can discriminate between the two prey species.

2-2. Materials and methods

Pryeria sinica larvae. A total of 134 larvae were collected from their host plants, *Euonymus alatus* Siebold (Celastraceae), at Minamiosawa, Hachioji, Tokyo, central Japan (35°37'13" N, 139°23'06" E), on 6, 10, and 13 May 2018. The larvae were reared individually in plastic cups (55 mm diameter, 35 mm depth) containing *E. alatus* leaves and maintained at 15±1°C with a 13-h light/11-h dark cycle. Photographs were taken (dorsal view) of 50 randomly chosen final-instar larvae, and total body length was measured using the free software, ImageJ (version 1.4.3.67; National Institutes of Health, Bethesda, Maryland, U.S.A.). Seven larvae were used for measurements of daily locomotory activity. The larvae were individually placed into a glass vessel (18 mm diameter, 14 mm height) set on a single *E. alatus* leaf (Fig. 2-2). A fine infrared beam (1 mm diameter) was passed through the central part of each glass vessel, and all interruptions of the beam by larval locomotion were recorded on a chart of a pen recorder (PR8112; Hioki, Nagano, Japan) until they began spinning their cocoon. The locomotory recording was done at 25±1°C with a 14-h light/10-h dark cycle.

Ivela auripes pupae. A total of 41 pupae were collected around the host plant *Cornus controversa* Hemsley (Cornaceae) from the same study site as larval *P. sinica* on 13 and 15 May 2018. Photographs of 22 randomly chosen pupae were taken (dorsal view), and their total lengths were measured using ImageJ. On 13, 14 and 16 May, I measured the above-ground heights of all pupae found on concrete walls of buildings, tree trunks, and iron lampposts at the study site. I also measured the heights of all pupae found on tree trunks in Sayama, Saitama, central Japan (35°46'58" N, 139°23'59" E) on 28 May and those found on wooden walls of houses in Todori, Hachioji, Tokyo, central Japan (35°38'46" N, 139°16'45" E) on 13 May. To examine the pupal predation rate in the field, two trail cameras (6210MC; Shenzhen Ltl Acorn Electronics Co. Ltd., Guangdong, China) were positioned to view wooden house walls in Todori. These cameras were equipped with a passive infrared sensor and two ‘prep sensors’ to detect heat and motion and were set to video mode at the highest video quality (1,080 pixels) with medium trigger sensitivity, a 10-s trigger interval, and a 20-s video length; the time and date stamp functions were activated. One camera monitored 27 pupae during a period of 11 days from 13 to 23 May; the other monitored 26 pupae during a period of 10 days from 14 to 23 May.

Predation Experiments. Four field-caught *T. tachydromoides* were used as predators: #1, female, collected at Hino, Tokyo, on 1 May 2018 (54.5 mm snout–vent length [SVL], 105.0 mm tail length [TL]); #2, male, Hino, 3 May 2018 (60.0 mm SVL, 153.0 mm TL); #3, female, Minamiosawa, 6 May 2018 (57.0 mm SVL, 120.5 mm TL); and #4, female, Minamiosawa, 12 May 2018 (48.0 mm SVL, 110.5 mm TL). They were kept individually in plastic cages (200 mm × 350 mm × 200 mm) at 20–25°C under a 13-h light/11-h dark cycle. Tree twigs and fallen leaves were included in the cages to simulate their natural habitats. Water was always available in a cup (90 mm diameter, 50 mm depth). They were fed between three and five mealworms (larvae of *Tenebrio molitor* Linnaeus, 1758) and small-sized nymphs of the Mediterranean field cricket, *Gryllus bimaculatus* De Geer, 1773, every other day. On 13 May, one larval *P. sinica* and one pupal *I. auripes* were given to individual lizards. These experimental prey items were presented to the lizards by hanging each prey with a fine nylon string (0.09 mm diameter). The feeding experiments were carried out in the morning after 30 min of basking in artificial light. From 14 to 19 May, the lizards were fed every day with one larval *P. sinica*, one pupal *I. auripes*, and one mealworm in various orders (see Table 2-1).

2-3. Results

Pryeria sinica Larvae. The final-instar larvae were oval in shape and yellow-green in body color, with seven blackish longitudinal lines on the dorsal body surface (Fig. 2-1A, B). The mean body length was 13.84 mm (SD = 0.41, N = 50, range 10.66–16.36). These larvae generally showed diurnal activity rhythms in the wandering phase before prepupation (Fig. 2-2). In the field, I could easily observe such wandering larvae in the daytime. After wandering, they pupated in pale brown cocoons (Fig. 2-1C). The faint blackish stripes of the pupae (Fig. 2-1D, E) were not visible through the brownish cocoon (Fig. 2-1C).

Ivela auripes Pupae. The final-instar larvae had rather elongated bodies, with somewhat complex color patterns of yellow and black (Fig. 2-1F, G). The pupae, however, were oval in shape and had seven longitudinal blackish lines on the dorsal half of their yellow green bodies, just like larval *P. sinica* (Fig. 2-1H, I). The mean pupal length was 21.72 mm (SD = 0.70, N = 22, range 18.10-25.13). The pupae lack a cocoon (Fig. 2-1H, I). The above-ground height of pupation sites ranged from close to the ground to the tops of the concrete walls, wooden walls, iron posts, and tree trunks (Fig. 2-3) and, thus, exposed to potential predators. One of the camera traps took 57 video recordings capturing 21 small flying insects, 10 humans, and 26 unknowns. The other took 15 recordings: 3 Japanese tits (*Parus minor* Temminck and Schlegel, 1848), 5 adult *I. auripes*, 4 small flying insects, 1 human, and 2 unknowns. Two of the tits grabbed a pupa in their beaks and flew away on 15 May (12:44 p.m.) and 16 May (18:15 p.m.); the third flew away on 22 May (17:50 p.m.). The two predatory tits were different individuals, as determined by their ventral and tail feather color patterns; thus, the same individuals never returned to pick up additional pupae during the recording periods.

Predation Experiments. On the first day of experiments, two lizards feeding on larval *P. sinica* and pupal *I. auripes* regurgitated them after 33 and 74 min, respectively (Fig. 2-4); the other two lizards did not bite the larval *P. sinica* (Table 2-1). During the subsequent six days, all mealworms were eaten normally, but larval *P. sinica* and pupal *I. auripes* were not bitten (except for one biting and one regurgitation by lizard #1; Table 2-1).

2-4. Discussion

Larval *P. sinica* and pupal *I. auripes* have similar color patterns: their bodies are oval, with seven longitudinal black stripes on yellow-green bodies, although the body size of *P. sinica* is slightly smaller. These larvae and pupae appeared simultaneously at the same places within our study site; wandering larvae of *P. sinica* were observed during early to mid-May, and the pupae of *I. auripes* appeared mostly in mid-May. Larvae of *P. sinica* wander in the daytime before pupation. Pupae of *I. auripes* lack cocoons or any other cryptic materials and are found at higher aboveground locations. Therefore, these two prey animals are highly exposed to visual predators.

Birds and small mammals are the most important predators of insect pupae and larvae and sometimes reduce the population sizes of butterflies (West and Hazel 1982, Stefanescu 2004), moths (Campbell and Sloan 1976, Campbell and Torgersen 1983, Torgersen *et al*. 1983, Tanhuanpää *et al*. 1999, Battisti *et al*. 2000), and other groups (e.g., sawflies, Wheelwright *et al*. 2017). Survival rates of moth and butterfly pupae are affected mostly by small mammal (mice and shrews) predation on the ground or by birds on tree trunks (Campbell and Sloan 1976, West and Hazel 1982). Campbell and Torgersen (1983) found that pupae of western spruce budworm, *Choristoneura freeman* Razowski, 2008, at 20 m above the ground were more vulnerable to birds than those at 2 m. In our study site, *I. auripes* pupated on walls near and above ground level, and two Mediterranean tits were observed preying on these pupae. Predators often use a "searching image" when hunting prey, which represents a specialized form of learning

(Tinbergen 1981), and therefore they visit hunting sites repeatedly and eat the same prey items. In our camera trap experiments, however, the tits never preyed upon additional pupae at the site of capture. The lack of repeat visits to this food-rich patch suggests that pupal *I. auripes* is toxic or unpalatable to the tits.

Diurnally active lizards are another potential predator of insects. *Takydromus tachydromoides* feeds on insects and spiders on and near the ground (Jackson and Telford 1975). Larvae of *P. sinica* are protected from predation by *T. tachydromoides*, since the lizards learn the smell of the fluid secreted on their body surface and their conspicuous color (Johki and Hikida 1979). In our feeding experiments, three individuals of *T. tachydromoides* rejected larval *P. sinica* and pupal *I. auripes* after encountering these prey on the first day. They may have learned the prey's unpalatability without discriminating between larval *P. sinica* and pupal *I. auripes*, however, due to their similar body color patterns. This would suggest that their color patterns function as warning signals to potential predators, suggesting Müllerian mimicry between the different developmental stages. However, another individual of the lizard bit the prey or regurgitated after eating prey in 3 of 13 feeding trials, suggesting misidentification of these two prey types. Future studies should focus on the lizards' ability to discriminate larval *P. sinica* and pupal *I. auripes*. In this study, the body color of both prey species appears similar, at least to the human eye. However, visual pigments of avian and lizard predators generally absorb ultraviolet light, which humans cannot perceive (e.g., Chen *et al.* 1984, Chen and Goldsmith 1986, Fleishman *et al.* 1993, Pérez i de Lanuza and Font 2014). Therefore, measurement of the reflectance spectra of prey bodies could be used to evaluate their conspicuousness and similarity to potential predators that possess ultraviolet-sensitive vision.

Table 2-1. Feeding results of larval *Pryeria sinica* (*ps*), pupal *Ivela auripes* (*ia*), and mealworms for four *Takydromus tachydromoides* lizards (#1–4) over 1 week. E, bitten and eaten; R, bitten and eaten but regurgitated; B, bitten but not eaten; N, not bitten.

Date	Individual lizards			
	#1	#2	#3	#4
May 13	*ia* R	*ps* N	*ps* R	*ps* N
May 14	*ia* N	*ia* N	*ps* N	*ps* N
	ps N	*ps* N	*ia* N	*ia* N
	mw E	mw E	mw E	mw E
May 15	mw E	mw E	mw E	mw E
	ia N	*ia* N	*ps* N	*ps* N
	ps B	*ps* N	*ia* N	*ia* N
May 16	*ia* N	*ia* N	*ps* N	*ps* N
	ps N	*ps* N	*ia* N	*ia* N
	mw E	mw E	mw E	mw E
May 17	mw E	mw E	mw E	mw E
	ia R	*ia* N	*ps* N	*ps* N
	ps N	*ps* N	*ia* N	*ia* N
May 18	*ps* N	*ps* N	*ia* N	*ia* N
	ia N	*ia* N	*ps* N	*ps* N
	mw E	mw E	mw E	mw E
May 19	mw E	mw E	mw E	mw E
	ps N	*ps* N	*ia* N	*ia* N
	ia N	*ia* N	*ps* N	*ps* N

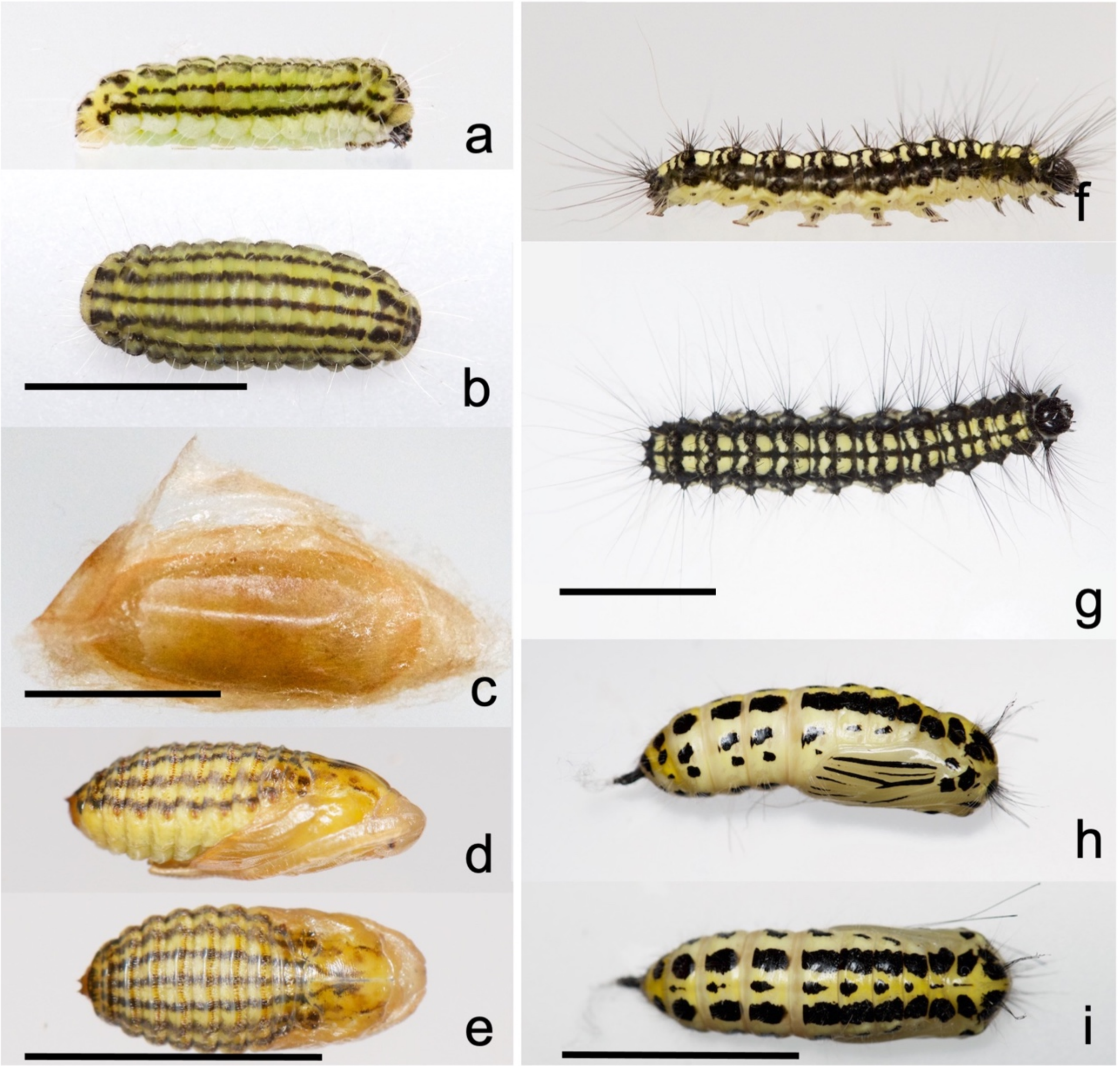


Figure 2-1. Immature stages of *Pryeria sinica* (A–E) and *Ivela auripes* (F–I). Larvae (A, F in lateral; B, G in dorsal). Pupae (C in a cocoon; D, H in lateral; E, I in dorsal). Scale bars: 10 mm. Larval *P. sinica* and pupal *I. auripes* appear similar to each other.

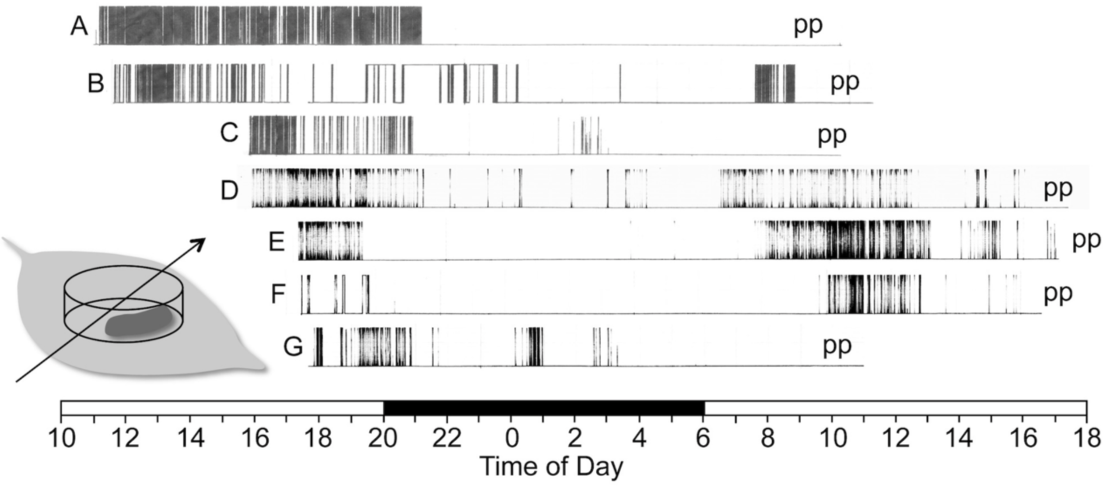


Figure 2-2. Daily locomotory activity patterns of seven fully grown larvae (A–G) of *Pryeria sinica* before prepupation (pp) in cocoons. Blocking of a fine infrared beam (arrow) by a larva in a glass vessel on a leaf was noted on a chart sending at 10 mm/h on pen recorders. The period from 20:00 to 6:00 the next day was dark, and the remaining period was light.

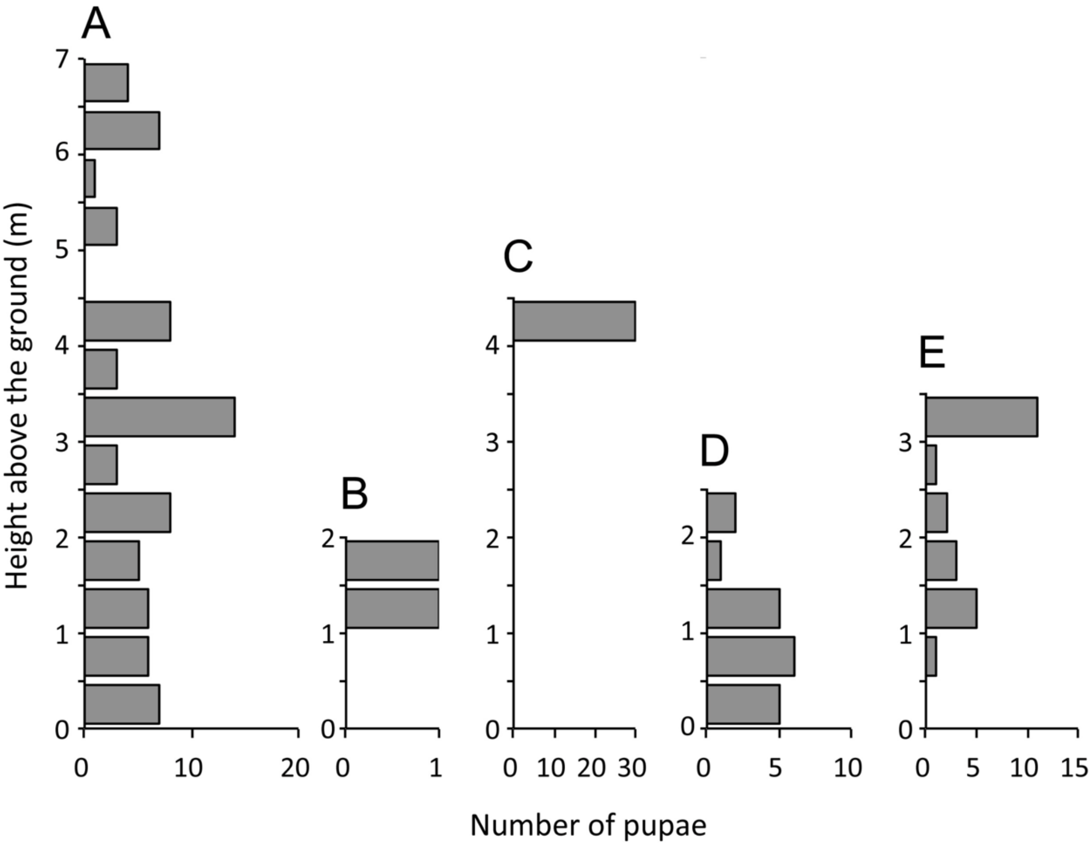


Figure 2-3. Distributions of the aboveground pupating height in *Ivela auripes* on five studied substrates: A, concrete wall at Minamiosawa (N = 75); B, single tree at Minamiosawa (N = 2); C, iron lamppost (N = 30); D, three trees at Sayama (N = 19); and E, house wall at Todori (N = 23). The y-axes only indicate the available heights at each substrate.

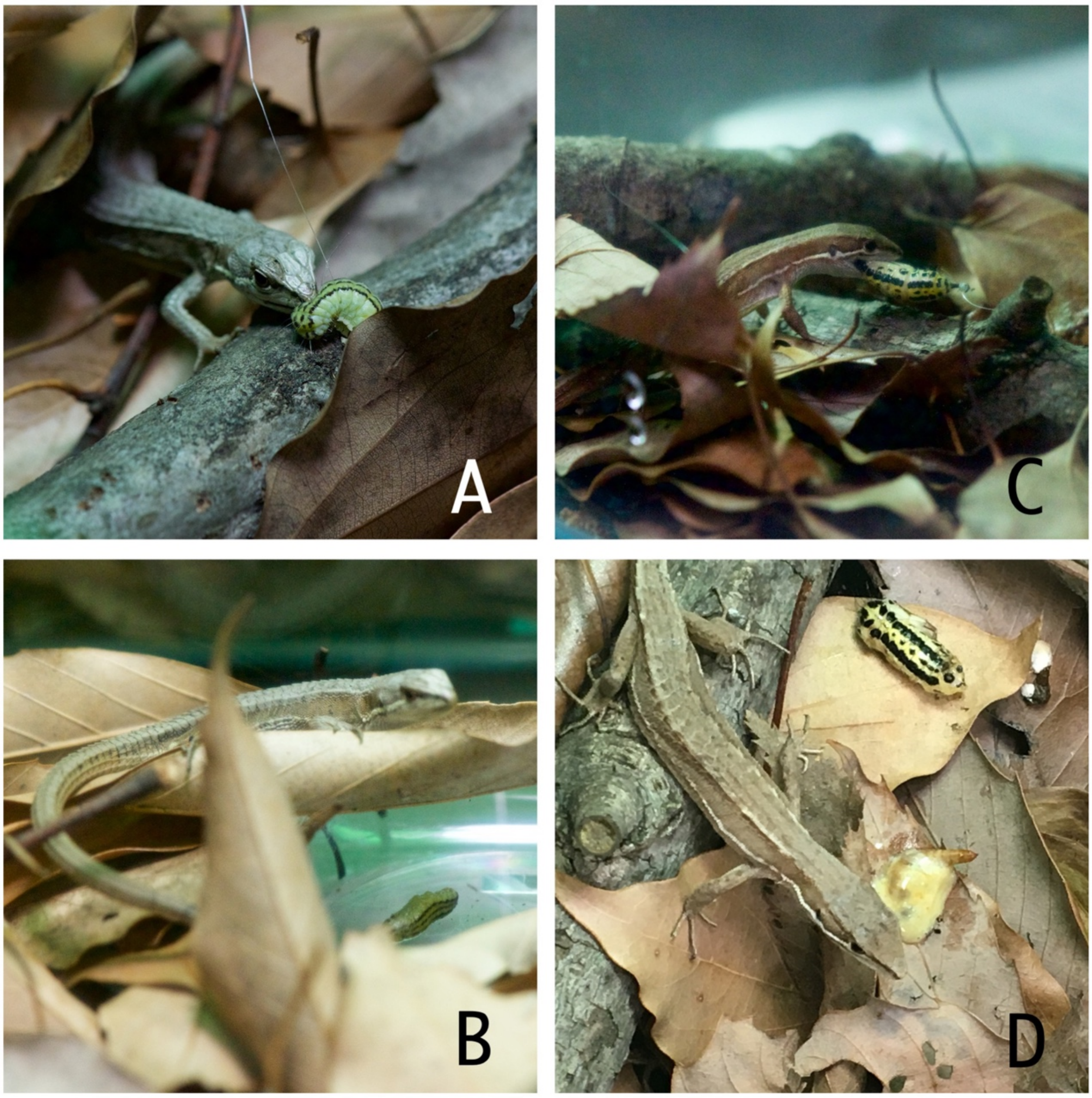


Figure 2-4. Biting (A, C) and regurgitation (B, D) of larval *Pryeria sinica* (A, B) and pupal *Ivela auripes* (C, D) by the lizard *Takydromus tachydromoides*. Arrows show the bitten or regurgitated larval *Pryeria sinica* and pupal *Ivela auripes*. In D, the mealworm eaten first was also regurgitated (lower arrow), with the pupal *I. auripes* consumed second.

3. Possible Batesian mimicry to sexually different models in the tussock moth *Numenes albofascia* with a great sexual color dimorphism

3-1. Introduction

Animals that reproduce sexually exhibit primary and secondary sexual characteristics. Primary sexual traits are directly connected with reproduction, such as gonads and copulatory organs, that are necessary for breeding and hence are favored by natural selection (Andersson 1994). However, secondary sexual traits increase the success of intrasexual competition for mates and/or mate choice by each sex, and thus that is a result of sexual selection (Andersson 1994). Sexual dimorphism caused by sexual selection includes differences in male and female physiology, morphology and behavior, which has been reported particularly in body size dimorphism (e.g., Blanckenhorn 2005), exaggerated male weaponry (e.g., Emlen 2008), conspicuous male color (e.g., Andersson 1994; Wiens and Tuschhoff 2020), and also sexually selected female-specific secondary characteristics (Rubenstein and Alcock 2019).

Sexually dimorphic color patterns of animals also derived from mimetic evolution between the species with warning color. Theoretically, the following four types of mimicry evolution should occur; unimodal mimicry, female-limited mimicry, male-limited mimicry, and dual mimicry (Vane-Wright 1971, Hespenheide 1975, Kunte 2009a, Allen *et al*. 2011, Ruxton *et al*. 2018). In the unimodal mimicry, both sexes resemble the same poisonous or unpalatable model species, and therefore, sexual dimorphism in color does not occur. In male- and female-limited mimicries, only the male or female resembles the model species, and therefore, the warning color is seen in only one sex. The dual mimicry, in which each sex resembles a different model species, cause a great difference in color between the sexes. Among the latter three types causing sexually dimorphic color, female-limited mimicry has been studied well since 1865 when Wallace (1865) recorded seven examples of female-limited mimicking butterflies (Ruxton *et al*. 2018). However, only a few examples are recorded so far for the male-limited mimicry (Reiskind and Levi 1967, Vane-Wright 1974, Gilbert 2005, Hespenheide 1975, Waldbauer and Sternburg 1975, 1987, Sternburg *et al*. 1977, Jeffords *et al*. 1979, 1980) and dual mimicry (Evans 1968, 1969, Vane-Wright 1971, 1974, Heal 1981, Takiya *et al*. 1999, Kunte 2008, 2009a, Wei *et al*. 2017, Panettieri *et al*. 2018, Ruttenberg *et al*. 2021, Morinaka *et al*. 2018).

Thus, sexual dimorphism in color and marking pattern can be approached either from sexual selection and mimetic mechanisms. The tussock moth *Numenes albofascia* (Leech, 1889) (Lepidoptera: Lymantriidae) has distinctive sexual dimorphism in wing color; a single white stripe apically on the blackish forewing and the entirely black hindwing in male (Fig. 3-1a), but multiple white lines on the blackish forewing and the vivid yellow hindwing with a few marginal dark spots in females (Fig. 3-1c). Body color also differ between the sexes; blackish in males whereas yellowish in females. Under considering such a great color difference of *N. albofascia*, I noticed that the male resembles the smoky moth *Pidorus atratus* Butler, 1877 (Lepidoptera: Zygaenidae) and the female resembles the tiger moth *Arctia caja* (Linnaeus, 1758) (Lepidoptera: Arctiidae) (Fig. 3-1g, i). Inter-specifically similar warning colors warn predators more frequently that the prey is not profitable and promote predator learning, and so increasing individual survival rate of the mimicry type (Mappes *et al*. 2005, Ruxton *et al*. 2018). To examine this dual mimicry hypothesis of *N. albofascia* and to determine which type of mimicry occurs, I need information of distribution, adult emerging season, morphological and behavioral similarity, and palatability of mimic and model species.

So far known distribution area of *N. albofascia* is Japan, Korean Peninsula and the mainland China, which is similar to the models *P. atratus* (Japan, Korean Peninsula and the mainland China) and *A. caja* (Japan, Eurasia and North America) (Kishida 2011d, e; Horie 2013). The adult emerging seasons of each species also correspond to each other, *N. albofascia* (bivoltine, June to July and August to September), *P. atratus* (bivoltine, June to July and August to September) and *A. caja* (univoltine, August to September) (Kishida 2011d, e, Horie 2013). However, the other information is unavailable.

In this study, to examine the dual mimicry hypothesis of *N. albofascia*, first, I describe the wing color patterns under visible and also ultraviolet light, because visual pigments of the potential predators such as birds and lizards can absorb ultraviolet light (Chen *et al*. 1984, Fleishman *et al*. 1993). Second, the body size is compared between the mimic and model species, because it is expected the mimetic species become similar also in body size. Third, daily flight activities are recorded in the laboratory because mimicry seems to be more effective if their behavior such as the locomotor activity patterns is similar between mimicry and model species. The laboratory-recorded activity pattern is also confirmed in the field by intensive light trapping. Finally, palatability is assessed using the lizards with visual cue to perceive prey, which are often used as one of the potential predators of insects (Sexton 1960, Boyden 1976, Johki and Hidaka

1979, McLain 1984, Hasegawa and Taniguchi 1994, Thery and Gomez 2010, Chapter 2). Although avian predators are assumed to be a main potential predators of *N. albofascia* in the wild, lizards, for which a large number of samples can be prepared, were used as predators in this predation experiment. Lizards share the visual search for insects and other prey as avian and non-avian reptiles do, and they also share the ability to use near ultraviolet light as well as visible light (e.g., Chen *et al*. 1984, Chen and Goldsmith 1986, Fleishman *et al*. 1993, Pérez i de Lanuza and Font 2014). From these data, I discuss the relative importance of mimicry as the evolutionary background of sexually dimorphic color patterns in insects.

3-2. Materials and methods

Morphological measurements

The color patterns of mimic (*N. albofascia*) and possible model species (*P. atratus* and *A. caja*) were compared under visible and also ultraviolet light. The photographs were taken from just above the wing-expanded dry specimen in direct sunlight at 14:00. First, I used a digital single-lens reflex camera (D3300; NIKON, Tokyo, Japan) with a macro lens (NIKKOR AF-S DX Micro NIKKOR 85mm f/3.5G ED VR; NIKON, Tokyo, Japan), setting 1/320s SS, f9, ISO100, 4800K color temperature, and jpg. saved. The images were taken into the PC and trimmed by using a free software ImageJ (version 1.52q; National Institutes of Health, Bethesda, Maryland, USA). Next, I took another photograph after an ultraviolet filter (U330; HOYA, Tokyo, Japan) was added to the head of the lens, setting ISO3200. The ultraviolet images were trimmed, split into RGB channels, and only the blue channel images were saved by ImageJ. Brightness and contrast settings in ImageJ of the blue channel images were adjusted as minimum 0 and maximum 100.

To compare the adult body size of mimic and possible model species, the forewing length from its base to the tip was measured with a digital slide caliper to the nearest 0.01mm or using ImageJ on the photographs of wing-expanded dry specimens taken from the dorsal side. I measured a total of 104 male and 50 female *N. albofascia* collected across Japan: 26 males and 21 females in F. Hayashi Collection of Tokyo Metropolitan University, Hachioji, Tokyo (HFC); 18 males and 8 females in Y. Kishida Collection, Setagaya, Tokyo (KYC); and 60 males and 21 females in National Museum of Nature and Science, Tsukuba, Ibaraki (NMNS). In the model species, a total of 238 *P. atratus* (23 males and 11 females in HFC and 147 males and 57 females in NMNS) and 66 *A. caja* (15 males and 1 female in HFC and 31 males and 19 females in NMNS) were measured. The forewing length was compared between mimic and model species and tested using Student's *t*-test because of equal variances.

Palatability assessments

Palatability of mimic and model species was assessed using the lizard *Plestiodon finitimus*. A total of 15 *P. finitimus* were used from the lizard stock collected in Hino (35°40'N 139°23'E), Tama (35°38'N 139°26'E), and Hachioji (35°39'N 139°18'E) cities in western Tokyo in 2019 and 2020. They were kept individually in the plastic cages (200 × 350 mm, 200 mm in depth) at 25 ± 1°C with a 14-h light (6:00–20:00) and 10-h dark (20:00–6:00) cycle. Red clay and roofing tiles were included in the cages to simulate their natural habitats, and water was always available in a cup (90 mm in diameter, 50 mm in depth). They were fed one mealworm (larvae of *Tenebrio molitor*) daily during the 3-h basking time to artificial light.

Feeding experiments were conducted after maintained in the cage for at least one week. After 30-min basking, to check feeding willingness of the lizard, one mealworm was given by dropping it in the cage. If it was eaten, the moth was next given. To prevent the moth from flying out of the cage bottom, adults were given after partly cutting both forewings at their frontal edges. Lizard's feeding behavior was recorded using a video camera of a smartphone (iPhone 6; Apple, California, USA), and classified into three categories; "eaten" when the lizard swallowed the moth (Fig. 3-1e, f); "bitten" when the lizard bit but released it, and "unbitten" when the lizard did not bite it within 30 s. If eaten, the time from biting to completely swallowing the moth wings was measured, and if bitten, the time from biting to releasing the moth was measured. This procedure was done in three consecutive days for individual lizard. If the moth was eaten, to starve the lizard, only one mealworm was given in the next day, and after that day feeding of the moth was repeated. The lizards once used for the experiment were released to the capture site after checking their sex and measuring their snout to vent length (SVL).

This 3-day feeding experiment was conducted for three lizards in each male and female *N. albofascia* on September 24 to 28, 2020. The adult moths were obtained by rearing larvae hatched from eggs deposited by the field-collected females in Okutama, western Tokyo, in June, 2020. The hatched larvae were placed into individual plastic cups (120 mm in diameter, 55 mm in height) and kept at 25 ± 1°C with a 16-h light (4:00–20:00) and 8-h dark (20:00–4:00) cycle, giving fresh leaves of the tree *Carpinus* *tschonoskii* (Betulaceae). The feeding experiments were conducted for each three lizards of male and female *P. atratus* on September 8 to 20, 2019. Adult *P. atratus* was collected at streetlights at night in Koto (35°40'N 139°49'E), eastern Tokyo, on 12 September 2019. For male *A. caja* collected in Hirosaki (40°36'N 140°27'E), Aomori, on 15 September 2019 (females not collected), they were fed to three lizards. Adults of *N. albofascia* lack a functional proboscis and do not feed, but those of *P. atratus* and *A. caja* feed liquids, so that wet cotton was provided on the bottom of rearing vessels.

Daily activity patterns

Daily activity patterns (actograms) were recorded using a hand-made actograph in which a fine infrared beam (1 mm in diameter) passes the central part of a moth keeping hyaline glass vessel and interruptions of the beam by the moth movements are recorded on a chart sent at 10 mm/h of a pen recorder (PR8112; Hioki, Nagano, Japan). A total of 10 male and 5 female *N. albofascia*, 6 male and 4 female *P. atratus*, and 5 male and 1 female *A. caja* were recorded for 2 to 9 consecutive days. The size of the vessel was 70 mm in diameter and 90 mm in height for *N. albofascia* and *A. caja*, and 45 mm in diameter and 60 mm in height for *P. atratus*. A wet paper filter was placed on the bottom and a short twig (4 mm in diameter) was placed as a perch. The top of the vessel was covered with fine cloth. The actograph was kept at 25±1°C with a 14-h light (6:00–20:00) and 10-h dark (20:00–6:00) cycle and water was added to the filter paper once a day to prevent desiccation and provide water for the moths to drink.

To know daily activity patterns of the mimic species *N. albofascia* in the field, they were collected using a light trap at Okutama, western Tokyo, from the sunset to the sunrise of the next day for a total of 25 days (27, 28 August, 11 September in 2018; 22, 23, 27, 29 June, 4, 8, 10, 17 July, 19, 25 September, 28 October in 2019; 10, 16 ,17, 20, 26 June, 2, 3, 24, 26, 28 August, 3 September in 2020), but the light trapping was stopped in midnight by heavy rain on 11 September 2018. The light sources were one 400W mercury vapor lamp (H400; Toshiba, Tokyo, Japan), two 18W fluorescent lamps (FL20SS/ECW/18X; Panasonic, Osaka, Japan), and two 20W black lights (FL20S-BLB; Toshiba, Tokyo, Japan), which illuminated two white cloths. A gasoline generator (EX6; Honda, Tokyo, Japan) was used as the power source.

3-3. Results

Morphology

Wing color and marking pattern were similar between male *N. albofascia* and *P. atratus* (Fig. 3-1a, g) and between female *N. albofascia* and *A. caja* (Fig. 3-1c, j), although the wing color differs individually from yellow to red in *A. caja* (Fig. 3-1i, k. l) (Kishida 2011e). The wing marking patterns in all of them did not differ under the visible and ultraviolet light (Fig. 3-1).

The mean forewing length of male *N. albofascia* and *P. atratus* differed statistically (Student's *t*-test; $t = 12.7$, df = 340, $P < 0.0001$), but the size range overlapped fully between these two groups (Fig. 3-2a). In female *N. albofascia*, the mean forewing length did not differ from the length of *A. caja* (Fig. 3-2b; $t = 0.2$, df = 114, $P = 0.85$).

Palatability

The lizards used for 3-day feeding trials was 55–70 mm in SVL (64.1 ± 4.6 SD, $N = 15$). Male and female *N. albofascia* were all eaten by the lizards during the feeding trials (Table 3-1). The feeding time was 97–1257 s (364.4 ± 306.1 SD, $N = 15$). However, only 4 of 18 individuals of male and female *P. atratus* and only 1 of 9 individuals of male *A. caja* (no female was available) were bitten but released after 3–33 s and 231 s from biting, respectively (Table 3-1). Thus, *N. albofascia* is palatable, but *P. atratus* and *A. caja* are highly unpalatable for lizards. Lizards bit unpalatable *P. atratus* and *A. caja* more frequently in the 1st-day feeding trials than the 2nd-trials, and no lizards bite it in the last-trials (Table 3-1), which suggesting some learning processes of lizards for such unpalatable moths by experience, although the pre-captive history of these field-caught lizards is unknown.

Daily activity

Most actograms show that male *N. albofascia* becomes active around the light is turned on, whereas the female is activity after the light is turned off (Figs. 3-3, S3-1). The model *P. atratus* show diurnal activities, but *A. caja* is nocturnal (Figs. 3-3, S3-1).

A total of 57 male and 17 female *N. albofascia* were collected by the light traps in the field (Fig. 3-4). The time of sunset and sunrise for each day was referred to the time of sunset and sunrise in Tokyo near the light trapping site (National Astronomical Observatory of Japan 2018, 2019, 2020), and a crepuscular period was defined as 120 min centered around the time of sunset and sunrise (Hu *et al.* 2016). As a result, the flight time of males was in early hours of the morning from 2:00 and at least 5:00 when insect attraction to the artificial light ceased. Among 57 males, 28 (49.1%) were trapped in crepuscular around the sunrise. In contrast, the time when females were collected ranged early hours of evening from sunset to midnight (19:00–23:00). Females were never recorded in crepuscular. This tendency that males fly in the early morning but females fly in the early evening seems to correspond to their respective activity patterns recorded as actograms (Fig. 3-3).

3-4. Discussion

Wing color and marking pattern are similar between male *N. albofascia* and its possible model *P. atratus*, whereas female *N. albofascia* resembles its possible model *A. caja* (Fig. 3-1). The marking patterns are also similar between these two combinations of mimic and model species in ultraviolet light (Fig. 3-1), suggesting the similarity for the predators, such as birds and lizards, that can use ultraviolet vision. The body size in forewing length does not differ between these two mimic/model species combinations (Fig. 3-2). While there are statistically significant differences between the measurements of males *N. albofascia* and *P. atratus*, the difference is marginal compared to the differences between female *N. albofascia* or *A. caja*, and the trends between the two are similar. Great sexual size dimorphism in *N. albofascia* may be explained as the result that the males resemble a smaller species *P. atratus* but the females resembles a larger species *A. caja* (Fig. 3-2). In Japan, their distribution ranges and adult appearance periods overlap; *N. albofascia* is distributed in Hokkaido, Honshu, Shikoku and Kyushu and appear bivoltine, June to July and August to September; *P. atratus* in Honshu, Shikoku and Kyushu appears bivoltine, June to July and August to September; and *A. caja* in Hokkaido and Honshu appears univoltine, August to September (Kishida 2011d, e; Horie 2013).

Feeding experiments using lizards as one of the potential predators of moths revealed that both sexes of *N. albofascia* are palatable and their possible models *P. atratus* and *A. caja* are unpalatable (Table 3-1). The former species belongs to the family Zygaenidae, most genera (also *Pidorus*) of which are known to contain toxic hydrogen cyanide (Sbordoni *et al*. 1979, Yen *et al*. 2005a, b, Niehuis *et al*. 2006). The latter species uses both self-generated chemicals (e.g., histamine, acetylcholine, toxic protein) and plant-derived chemicals (e.g., Cardenolides and Pyrrolizidine alkaloids) for defense against predators (Nishida 2002).

Our data suggest Batesian mimicry occurs between male *N. albofascia* and *P. atratus* and between female *N. albofascia* and *A. caja*. This type of mimicry is dual mimicry. So far, eight cases of dual mimicry have been suggested in insects. In the spider wasps, *Chirodamus* spp. and *Austrochares* spp. (Hymenoptera: Pompilidae), the stingless males resemble several species of female wasps (Batesian mimicry), but the females with a sting resemble other groups of female wasps (Müllerian mimicry) (Evans 1968, 1969). In the flower fly *Eristalis arbustorum* (Diptera: Syrphidae), the male is similar to the female wasps or bees with the yellow and black color pattern, but the female is similar to the mining bees (Heal 1981). In the leaf hopper *Propetes schmidti* (Heteroptera: Cicadellidae), the male and female are similar to the paper wasps *Polvbia rejecta* and *Myschocyttarus ypiranguensis*, respectively (Takiya *et al*. 1999）. The other four cases are in butterflies: *Mycalesis drusillodes* (Lepidoptera: Nymphalidae) (Vane-Wright 1971, 1974), *Elymnias hypermnestra* (Lepidoptera: Nymphalidae) (Wei *et al*. 2017, Panettieri *et al*. 2018, Ruttenberg *et al*. 2021), *Papilio erostratus* (Lepidoptera: Papilionidae) (Kunte 2008, 2009a), and *Delias lemoulti* (Lepidoptera: Pieridae) (Morinaka *et al*. 2018). In the former three butterflies, the palatable males and females resemble respective model butterflies likely to be unpalatable, such as *Taenaris*, *Danaus* and *Parides* species (Batesian mimicry), but in the last case, the males and females of unpalatable *D. lemoulti* resemble both unpalatable *D. splendeida* and *D. eileenae*, respectively (Müllerian mimicry). However, these studies defined the similarity between mimic and suspected model species by the human visionary identification.

Active flight of male *N. albofascia* in crepuscular in the early morning differed from the female pattern being active from sunset to the midnight (Figs. 3-3, 3-4). Male *N. albofascia* overlap their flight period to the diurnally active unpalatable *P. atratus*. In general, mating of moths occurs by encountering between the mate searching male and the calling female via female stopping and releasing pheromone (Lee and Zilli 2019). Although I could not confirm when mating occurs, the male flight activity in crepuscular may be caused by the female calling in this time. The female nocturnal flight activity may depend on her oviposition behavior, because adult *N. albofascia* does not feed. Both nocturnal female *N. albofascia* and unpalatable *A. caja* have peculiar wing color that seems effective as the warning color when predators attack individuals that rest on the substrates in the daytime. The mimicry of male *Callosamia promethea* (Lepidoptera: Saturniidae) to the distasteful butterfly *Battus philenor* is suggested to evolve as they shifted their hours of flight activity to the late afternoon, but females are still nocturnal and cryptic in wing color (Sternburg *et al*. 1977, Jeffords *et al*. 1979, 1980). This example is male-limited mimicry; however, the process of male mimicry to the diurnally active model by shifting their flight time is presumed to be the same as in *N. albofascia*. In *C. promethea*, calling by females occurs from 15:00 to 20:00, and flight of males becomes active from 13:00 to 20:00, although the flight of females is limited at night (Jeffords *et al*. 1980).

To investigate further detailed relationships among the members of dual mimicry, I need to examine predator’s ability to discriminate mimic and possible model species. This process involves predator’s learning by experiences. Our study does not include experiments to reveal such processes and it is necessary to develop a new research method including memorize experiments of the repellent effect to the predators based on the similarity of wing color and marking pattern (Brower 1958, Sexton 1960, Edmonds 1974, Pinheiro 2003, Wüster *et al*. 2004). In addition, although lizards were used in this experiment to measure repellent effects, conducting learning experiments to measure mimicry effects using birds, which are considered potential predators of moths in the field, is an important future task to prove that mimicry relationships.

Table 3-1. Results of 3-day feeding trials (eaten, bitten, or unbitten) in which individual male (m) and female (f) moths of *Numenes albofascia*, *Pidorus atratus* and *Arctia caja* were given to a total of 15 lizards (SVL, snout to vent length in mm; m, male; f, female). If the moth was eaten, the time from biting to swallowing it was measured in s. If bitten, the time from biting to releasing it was measured based on the recoded movie.

Moths		Lizards		Feeding results					
Species	Sex	SVL (mm)	Sex	1st day	Time in s	2nd day	Time in s	3rd day	Time in s
N. albofascia	m	67	m	eaten	230	eaten	167	eaten	221
N. albofascia	m	68	m	eaten	360	eaten	855	eaten	321
N. albofascia	m	65	f	eaten	131	eaten	120	eaten	97
N. albofascia	f	67	f	eaten	1250	eaten	312	eaten	253
N. albofascia	f	61	f	eaten	412	eaten	226	eaten	187
N. albofascia	f	68	f	eaten	834	eaten	336	eaten	248
P. atratus	m	68	m	unbitten		unbitten		unbitten	
P. atratus	m	68	m	bitten	4	unbitten		unbitten	
P. atratus	m	70	m	bitten	33	bitten	14	unbitten	
P. atratus	f	58	m	bitten	3	unbitten		unbitten	
P. atratus	f	65	f	unbitten		unbitten		unbitten	
P. atratus	f	55	f	unbitten		unbitten		unbitten	
A. caja	m	61	m	unbitten		unbitten		unbitten	
A. caja	m	63	f	bitten	231	unbitten		unbitten	
A. caja	m	58	m	unbitten		unbitten		unbitten	

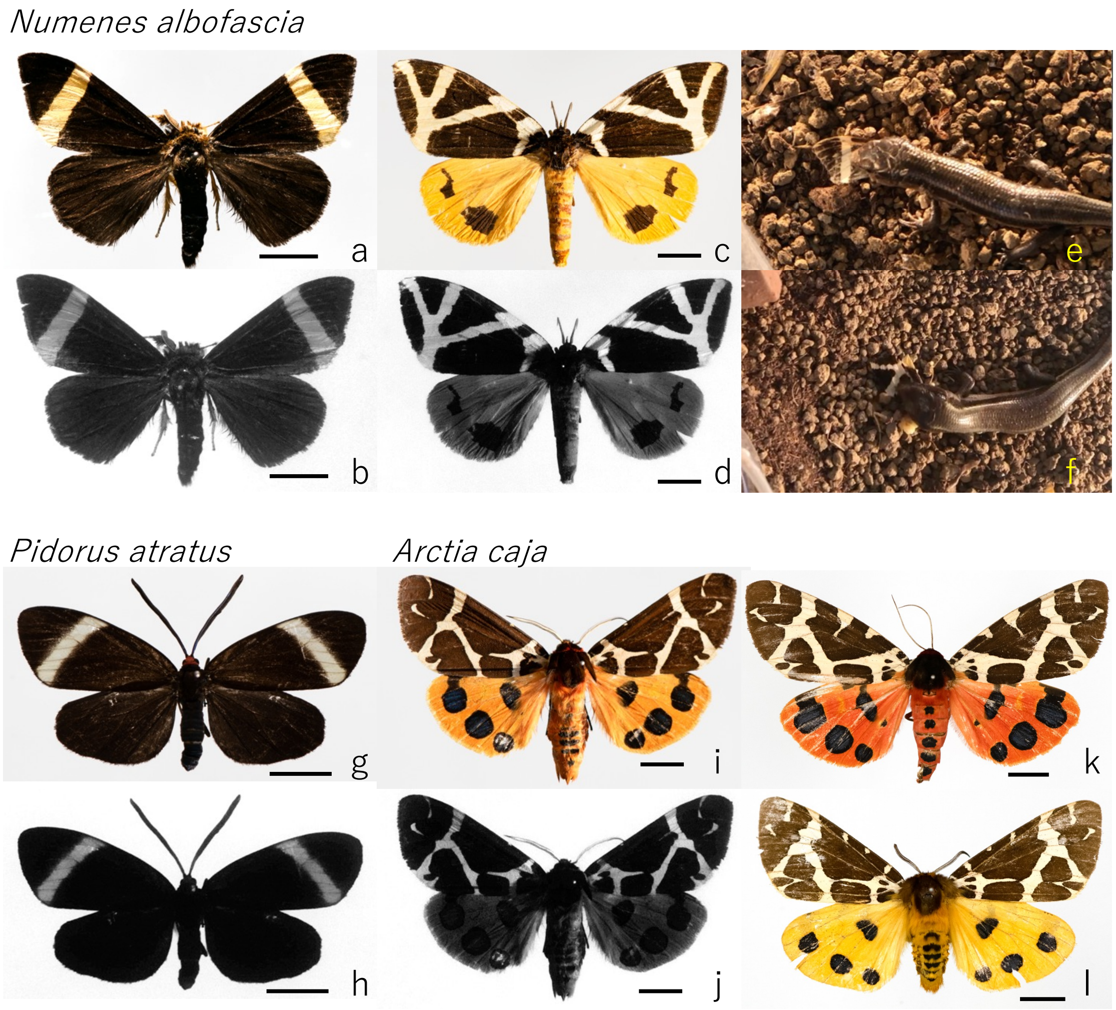


Figure 3-1. Possible dual mimicry of *Numenes albofascia* with *Pidorus atratus* (g) in males (a) and with *Arctia caja* (i, k, l) in females (c) under visible light. Photographs of them under ultraviolet light are also shown (b, d, h, j). Scale bars: 10 mm. The inserted photographs show male and female *N. albofascia* (e, f) bitten and swallowed by the lizards in the experiments of prey palatability assessment.

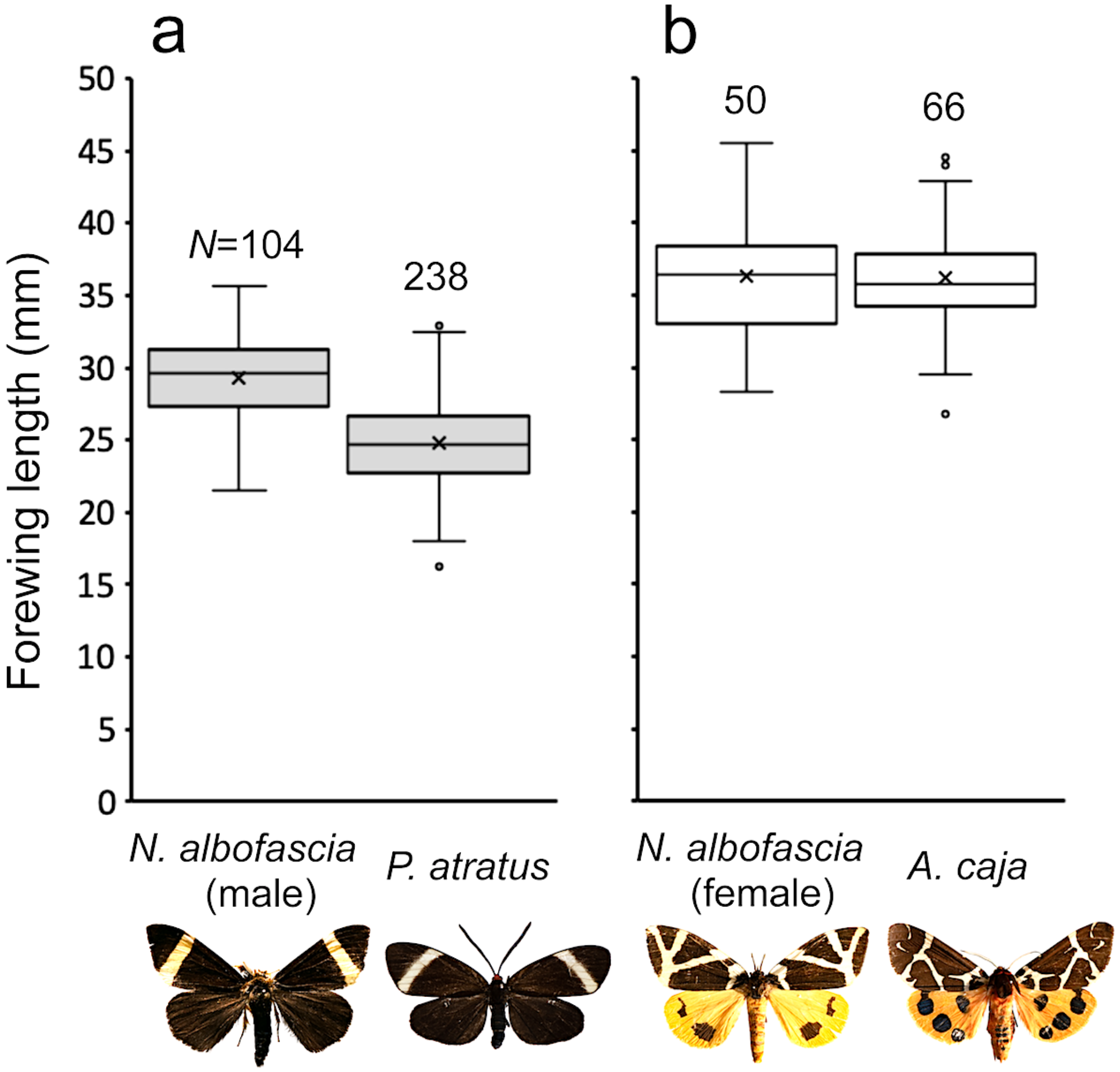


Figure 3-2. Forewing lengths of male *Numenes albofascia* and *Pidorus atratus* (a) and fmale *N. albofascia* and *Arctia caja*. *N*: number of individuals measured. Crosses are the mean values.

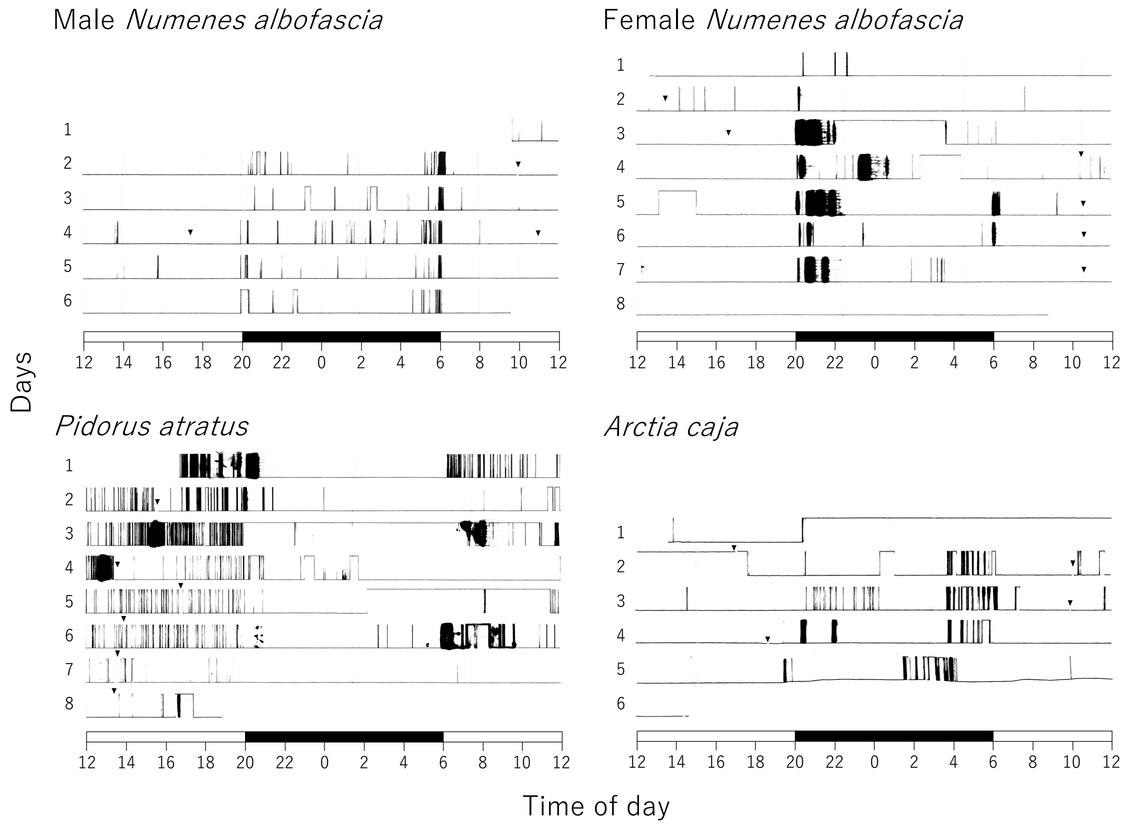


Figure 3-3. Actograms of male *Numenes albofascia*, female *N. albofascia*, female *Pidorus atratus*, and male *Arctia caja* obtained in the laboratory. All interceptions of a fine beam through the rearing glass vessel are recorded on a chart sent at 10 mm/h of the pen recorder. The recording condition was at 25±1°C with a 14-h light (6:00–20:00) and 10-h dark (20:00–6:00) cycle. Each arrow head shows the time when water is added to the filter paper on the bottom of the vessel.

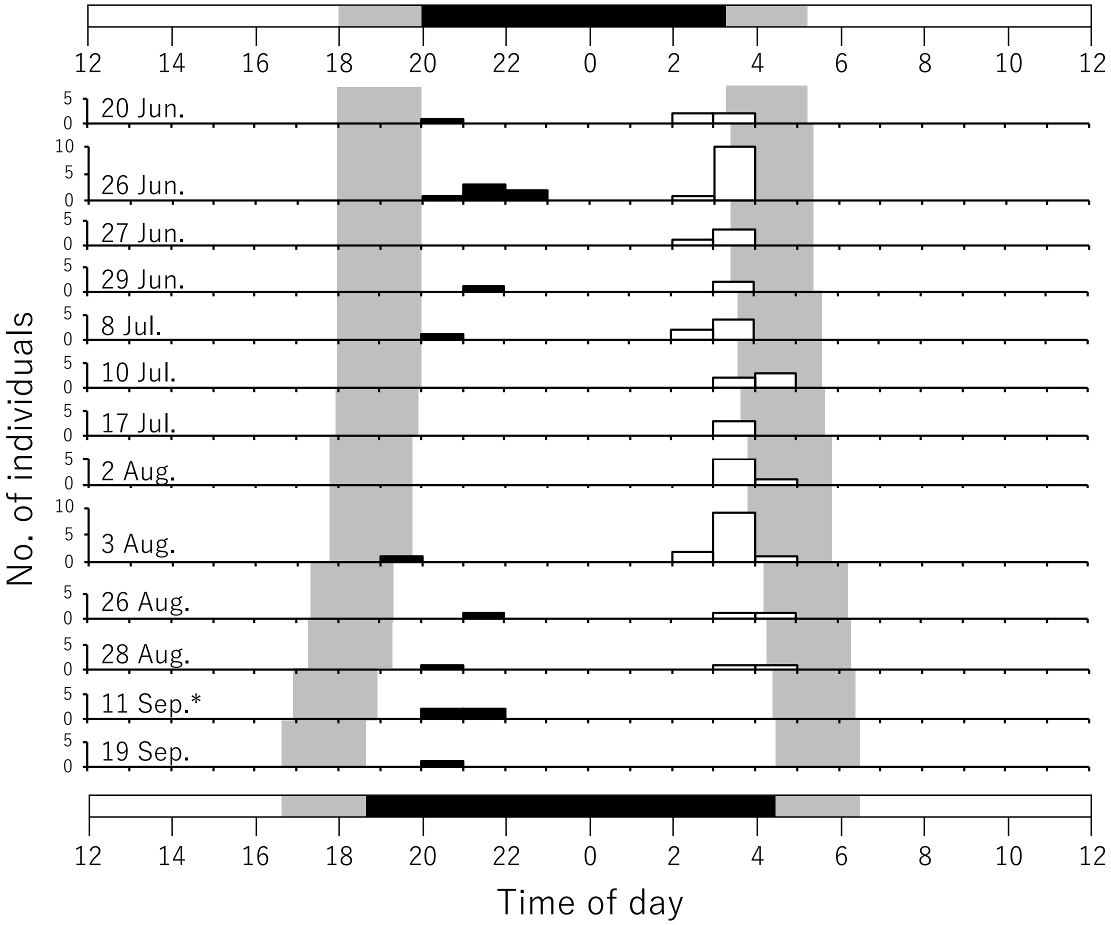
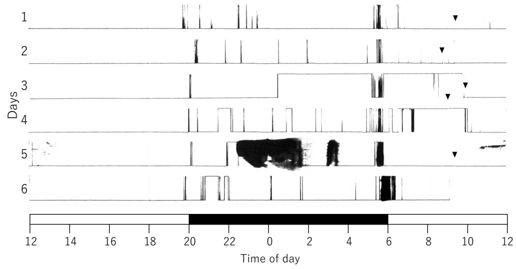


Figure 3-4. Number of males (open bars) and females (closed bars) of *Numenes albofascia* collected by the overnight light traps at Okutama, western Tokyo, on 13 nights during late June to mid-September (*until the midnight because of heavy rain). A crepuscular period is shown with gray by defining it as 120 min centered around the time of sunset and sunrise.

Male *Numenes albofascia*

#1



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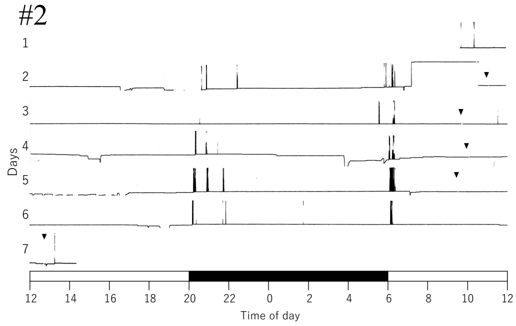

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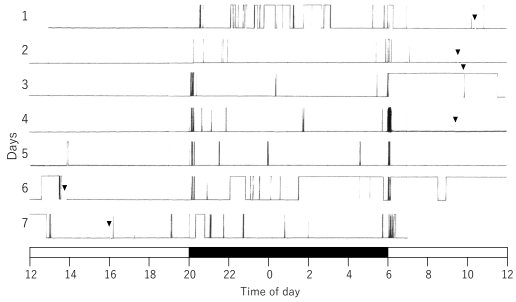

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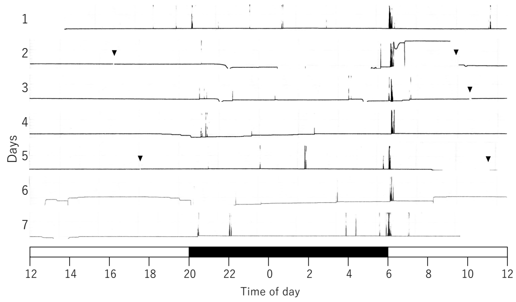

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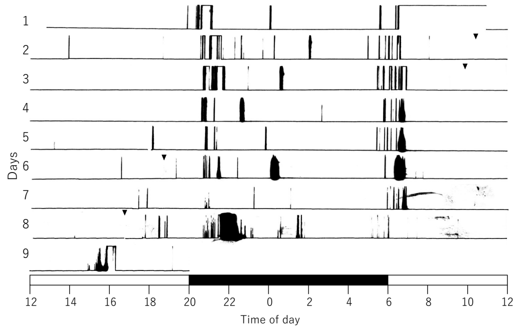

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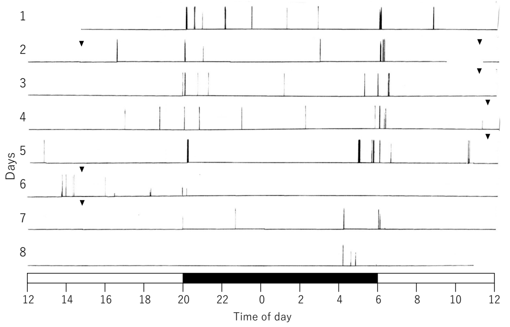

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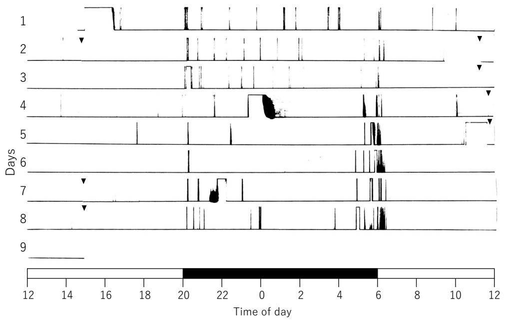

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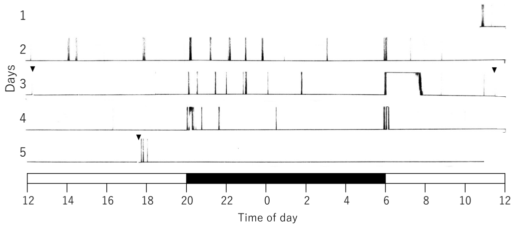
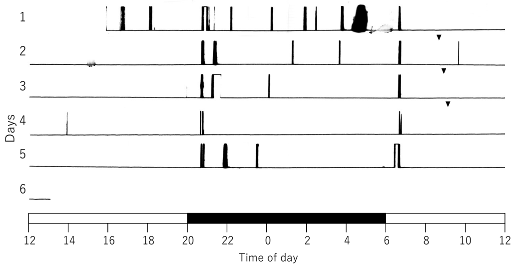
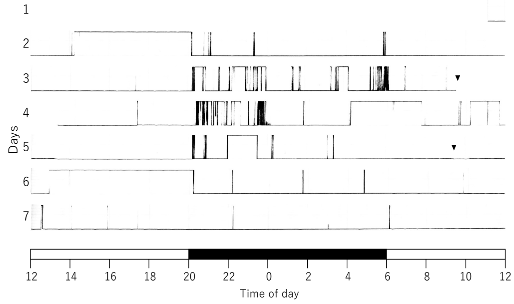


#9



Female *Numenes albofascia*

#1



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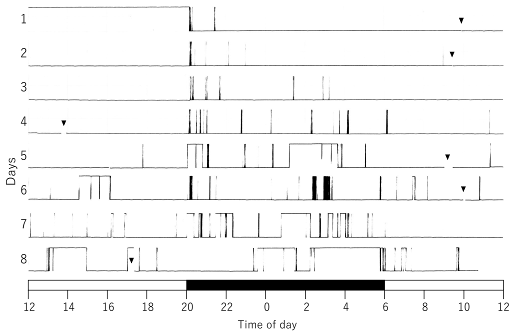

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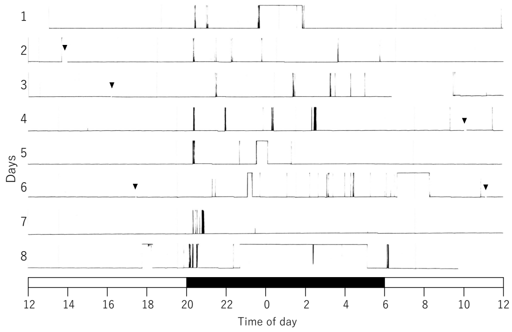

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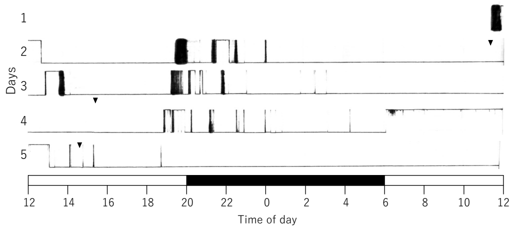
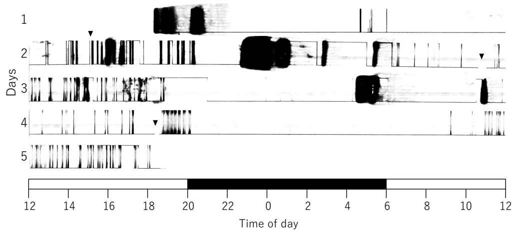


Male *Pidorus atratus*

#1



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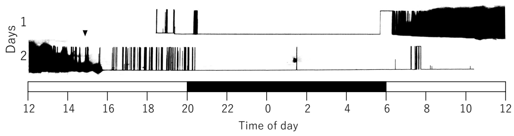

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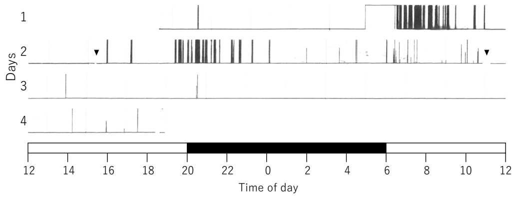

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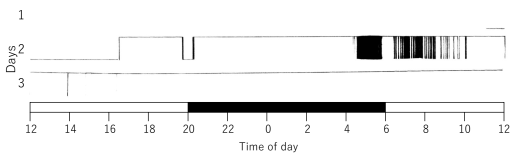

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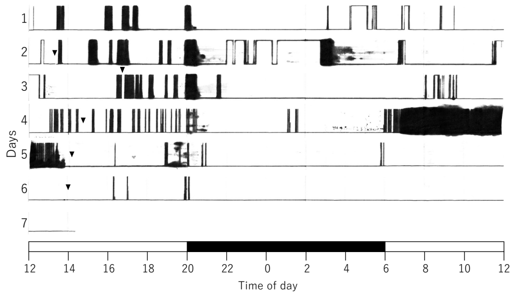
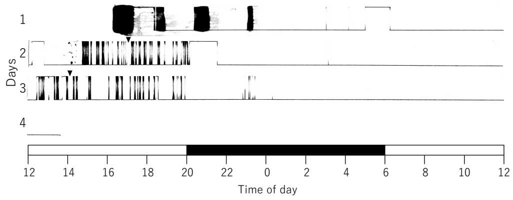


Female *Pidorus atratus*

#1



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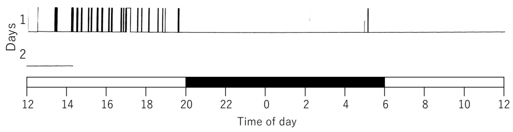

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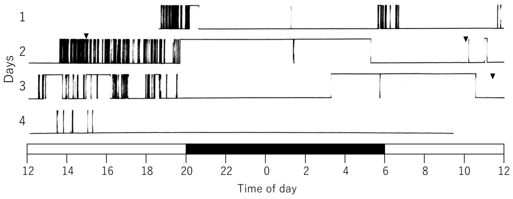

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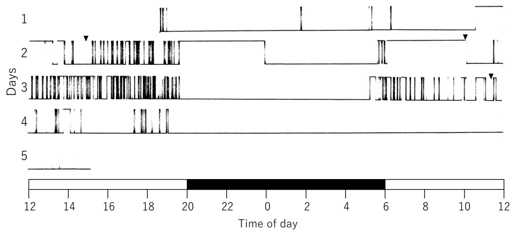
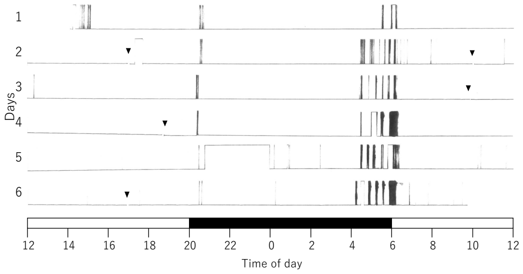


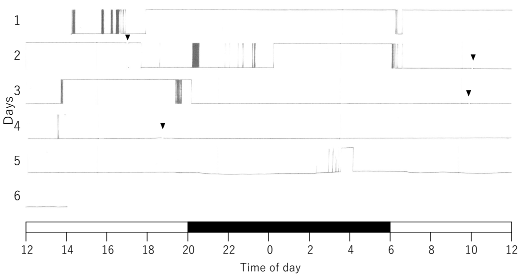
Male *Arctia caja*

#1



Female *Arctia caja*

#1



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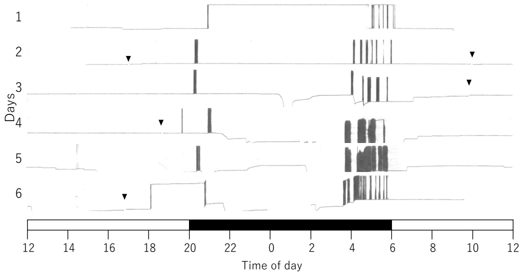
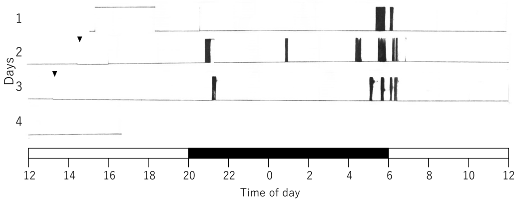


#3



#4

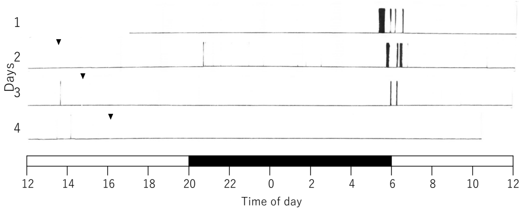


Figure S3-1. Additional actograms to Fig. 3-3 of 9 males and 4 females of *Numenes albofascia*, 5 males and 4 females of *Pidorus atratus*, and 4 males and 1 female of *Arctia caja*. All interceptions of a fine beam through the rearing glass vessel are recorded on a chart sent at 10 mm/h of the pen recorder. The recording condition was at 25±1°C with a 14-h light (6:00-20:00) and 10-h dark (20:00-6:00) cycle. Each arrow head shows the time when water is added to the filter paper on the bottom of the vessel.

4. Evolution of sexual dimorphism in wing color and preadaptation to sex-limited mimicry in tussock moths

4-1. Introduction

Sexual dimorphism, in which males and females of the same species differ markedly in their morphology, is a frequent phenomenon in many animals, including insects (Andersson 1994). Sexual dimorphism, in which wing color differs markedly between males and females of the same species, has been studied mainly in diurnal butterflies in the Lepidoptera (Wallace 1865, Ohsaki 2005, Allen *et al*. 2011). Sexual dimorphism in wing color in butterflies firstly involves males having brighter wings than females. This is mainly due to sexual selection, such as male territoriality and gamete choice by females (van der Bijl *et al*. 2020). Secondly, only females are known to mimic toxic species, which is thought to be mainly due to natural selection, such as strong predatory pressure on females (Ohsaki 1995, Kunte 2008, Tsurui-Sato *et al*. 2019) On the other hand, there is a plenty of nocturnal species in moths and the number of species with sexual dimorphism in wing color is significantly lower than in butterflies which are mostly diurnal (Kettlewell 1973).

A well-known example of the evolution of sexual dimorphism in wing color in moths is the swift moths (Hepialidae). In one species of them, Ghost swift (*Hepialus humuli*), only the male has bright silver wings. This moth has a mating behavior in which males swarm and mate with females under dusk. In other words, the bright wings of the males seem to be attributed to gamete selection by the females, and a similar evolutionary process to that of the above-mentioned butterflies is assumed (Turner 1976, Mallet 1984, Andersson 1998, Rydell 1998).

I focused on sexual dimorphism in wing color in the Japanese tussock moths (Lymantriidae). Sexual dimorphism in wing color is relatively common in this family, where the male wing color is dark, and the female wing color is relatively light. However, this feature does not correspond to the evolutionary process of the sexual dimorphism of wing color in the above-mentioned butterflies. In other words, it may be necessary to assume a new evolutionary pattern in moths, many of which are also active at night, that differs from butterflies.

In the present study, it is noteworthy that lymantriid adults degenerate their proboscis (Kishida 2011d). If the proboscis of moth degenerates and they do not feed as adults, the purpose of their flight behavior is generally expected to be restricted to a search flight for the female during calling (stopping and releasing sex pheromones) for males and a search flight for egg-laying sites for females (Jeffords *et al.* 1980). In other words, as there is no 'feeding' period during which male and female flight behavior is likely to overlap, it is assumed that the time of day when males and females fly is likely to be separated and the frequency of exposure to visual predators (mainly birds) may differ between males and females.

Similar example is studies on a moth species of Saturn moths (Saturniidae), *Callosamia promethea*. This species also has a sexually dimorphic pattern, with females having light brown wing color, whereas males have dark wing color. It has been suggested that this species also has a sex difference in daily activity rhythm, with males being diurnal and females nocturnal, and that only the males may mimic the toxic diurnal butterfly, *Battus philenor*, to have a defensive effect against natural enemies such as birds (Walbauer and Sternburg 1975, Sternburg *et al.* 1977, Jeffords *et al.* 1979, Jeffords *et al.* 1980, Waldbauer and Sternburg 1987). However, unlike this species, there are many species of the Japanese Lymantriidae in which males are not thought to mimic toxic species, so the evolution of sexual dimorphism in wing color cannot be explained solely on the basis of mimicry. It is also difficult to explain the existence of related species of *C. promethea*, where the males are non-mimetic and dark colored, and daily activity rhythm differs between the sexes (Morton 2017). In the family of Tiger moths (Arctiidae) and the family Erebidae, a link between sexual dimorphism in wing color and differences in daily activity rhythm between males and females has also been suggested, but none of this has been experimentally demonstrated (Kettlewell 1973, Moraes *et al.* 2016).

Based on these studies, the present study hypothesizes that when the daily activity rhythm of males and females differs, with females flying at night and males flying during light hours such as twilight and dusk, males are subjected to greater visual predation pressure by birds and other visual predators, and that males specifically evolved dark colors as a cryptic color. To test the hypothesis experimentally, five species with dark wing colors in males and light wing colors in females, *Numenes albofascia* (Fig. 4-1a, b), *Numenes disparilis* (Fig. 4-1c, d), *Kuromondokuga niphonis* (Fig. 4-1e, f), *Orgyia thyellina* (Fig. 4-1g, h), *Orgyia triangularis* (Fig. 4-1i, j), and one species with light wing colors in both sexes as a control, *Cifuna locuples* (Fig. 4-1k, l), were used in the experiment. Among the moths treated in this study, the male of *N. albofascia* closely resembles the toxic dark colored moth, *Pidorus atratus*, in its spots; both males and females of *P. atratus* are diurnal and overlap in their hours of activity with the male of *N. albofascia*, suggesting that they may be in a mimetic relationship.

Furthermore, the female of *N. albofascia* may be in a mimetic relationship with a toxic, brightly colored moth, *Arctia caja*, and both the female of *N. albofascia* and *A. caja* have been shown to be nocturnal (see Chapter 3). The data from the daily activity rhythm and predation experiments in *N. albofascia* (see Chepter 3) are also recapitulated in this report.

Firstly, the time of flight activity was recorded in the laboratory and in the field to measure differences in the daily activity rhythm between the sexes. I also recorded the time of day when mating was initiated in pairs in the laboratory. Secondly, palatability is assessed using the lizards with visual cue to perceive prey, which are often used as one of the potential predators of insects (Sexton 1960, Boyden 1976, Johki and Hidaka 1979, McLain 1984, Hasegawa and Taniguchi 1994, Thery and Gomez 2010, Chapter 2). Finally, predation experiments were conducted in which moths were hung in the field to determine whether the wing colors of males functioned as a cryptic color and to determine the rate of predation by birds and other predators.

4-2. Materials and methods

Daily activity patterns

Daily activity patterns (actograms) were recorded using a hand-made actograph in which a fine infrared beam (1 mm in diameter) passes the central part of a moth keeping hyaline glass vessel and interruptions of the beam by the moth movements are recorded on a chart sent at 10 mm/h of a pen recorder (PR8112; Hioki, Nagano, Japan). A total of 10 male and 5 female *N. albofascia*, 13 male and 14 female *N. disparilis*, 7 male and 10 female *K. niphonis*, 10 male and 7 female *O. thyellina*, 10 male and 8 female *O. triangularis* and 9 male and 6 female *C. locuples* were recorded for 2 to 9 consecutive days. The size of the vessel was 70 mm in diameter and 90 mm in height for *N. albofascia*, and 60 mm in diameter and 35 mm in height for the other species. A wet paper filter was placed on the bottom and a short twig (4 mm in diameter) was placed as a perch. The top of the vessel was covered with fine cloth. The actograph was kept at 25±1°C with a 14-h light (6:00–20:00) and 10-h dark (20:00–6:00) cycle and water was added to the filter paper once a day to prevent desiccation and provide water for the moths to drink. The adult moths were obtained by rearing larvae hatched from eggs deposited by the field-collected females of *N. albofascia* in Okutama, western Tokyo on June 2020, *N. disparilis* in Shinshiro, Aichi, central Japan (34°53'N 137°29'E) on June 2019 and in Wakasa, Tottori, western Japan (34°24'N 134°27'E) on July 2022, *K.*

niphonis in Okutama, western Tokyo on June 2020, *O. thyellina* in Kamoenai, Hokkaido, northern Japan (43°27'N 140°34'E) on July 2021 and in Higashimatsuyama, Saitama, eastern Japan (36°02'N 139°24'E) on July 2021, *O. triangularis* in Ogimi, Okinawa, southern Japan (26°42'N 128°07'E) on March 2022, *C. locuples* in Hachioji, Tokyo, eastern Japan (35°39'N 139°18'E) on June 2021. The hatched larvae were placed into individual plastic cups (120 mm in diameter, 55 mm in height) and kept at 25 ± 1°C with a 16-h light (4:00–20:00) and 8-h dark (20:00–4:00) cycle, giving fresh leaves of the tree *Carpinus tschonoskii* (Betulaceae) for *N. albofascia,* N. disparilis and *K. niphonis*, *Cerasus* × *subhirtella f. hisauchiana* (Rosaceae) for *O. thyellina*, *Eurya japonica* (Pentaphylacaceae) for *O. triangularis*, *Wisteria floribunda* (Fabaceae) for *C. locuples*.

To know daily activity patterns of *N. albofascia*, *K. niphonis*, *O. thyellina* and *C. locuples* in the field, they were collected using a light trap at Okutama, western Tokyo, from the sunset to the sunrise of the next day for a total of 26 days (27, 28 August, 11 September in 2018; 22, 23, 27, 29 June, 4, 8, 10, 17 July, 19, 25 September, 28 October in 2019; 10, 16 ,17, 20, 26 June, 2, 3, 24, 26, 28 August, 3 September in 2020; 12 June in 2021), Hachioji, western Tokyo, for 1 day (20 June 2021), Matsumoto, Nagano, central Japan for 6 days (12, 13 July in 2018; 25, 26 July in 2019; 6, 7 August in 2020), but the light trapping was stopped in midnight by heavy rain on 11 September 2018 at Okutama. The light sources were one 400W mercury vapor lamp (H400; Toshiba, Tokyo, Japan), two 18W fluorescent lamps (FL20SS/ECW/18X; Panasonic, Osaka, Japan), and two 20W black lights (FL20S-BLB; Toshiba, Tokyo, Japan), which illuminated two white cloths. A gasoline generator (EX6; Honda, Tokyo, Japan) was used as the power source.

To test the prediction that the time of male activity coincides with the time of mating, one male and one female of each moth species were placed in a case and video recorded them for 24 hours using an infrared camera (FDR-AX55; SONY, Tokyo, Japan) to measure the onset time of mating. The cases were made of clear plastic, 140 mm long, 80 mm wide, 10 mm high, with two lightly moistened and rolled papers (Kimwipe; Kimberly-Clark Corp., Roswell, GA, USA) inside for moisture retention. The top of the case was covered with a fine cloth and the lid was placed over it and sealed with plastic wrap. The laboratory room was kept at 25±1°C with a 14-h light (6:00–20:00) and 10-h dark (20:00–6:00) cycle. The experiment was terminated either after 24 hours of mating, after 3 days without mating, or after the moths died. All experiments were conducted using individuals reared in the laboratory and within 2 days of hatching. For *K. niphonis*, a total of 23 pairs of experiments were conducted from 15 August 2020 to 6 November 2021. For *O. thyellina*, a total of 28 pairs of experiments were conducted from 1 November 2021 to 10 November 2021. For *C. locuples*, 21 pairs of experiments were conducted from 12 October 2020 to 3 November 2021.

Palatability assessments in the laboratory

Palatability of the species was assessed using the lizard *Plestiodon finitimus*. A total of 30 *P. finitimus* were used from the lizard stock collected in Hino (35°40'N 139°23'E), Tama (35°38'N 139°26'E), and Hachioji (35°39'N 139°18'E) cities in western Tokyo from 2019 to 2022. They were kept individually in the plastic cages (200 × 350 mm, 200 mm in depth) at 25 ± 1°C with a 14-h light (6:00–20:00) and 10-h dark (20:00–6:00) cycle. Red clay and roofing tiles were included in the cages to simulate their natural habitats, and water was always available in a cup (90 mm in diameter, 50 mm in depth). They were fed one mealworm (larvae of *Tenebrio molitor*) daily during the 3-h basking time to artificial light.

Feeding experiments were conducted after maintained in the cage for at least one week. After 30-min basking, to check feeding willingness of the lizard, one mealworm was given by dropping it in the cage. If it was eaten, the moth was next given. To prevent the moth from flying out of the cage bottom, adults were given after partly cutting both forewings at their frontal edges. Lizard’s feeding behavior was recorded using a video camera of a smartphone (iPhone 6; Apple, California, USA), and classified into three categories; “eaten” when the lizard swallowed the moth; “bitten” when the lizard bit but released it, and “unbitten” when the lizard did not bite it within 30 s. If eaten, the time from biting to completely swallowing the moth wings was measured, and if bitten, the time from biting to releasing the moth was measured. This procedure was done in three consecutive days for individual lizard. If the moth was eaten, to starve the lizard, only one mealworm was given in the next day, and after that day feeding of the moth was repeated. The lizards once used for the experiment were released to the capture site after checking their sex and measuring their snout to vent length (SVL).

This 3-day feeding experiment was conducted for three lizards in each male and female *N. albofascia* on 24 to 28 September 2020, *N. disparilis* on 8 to 13 September 2019, *K. niphonis* on 31 July to 6 August, 2020, *O. thyellina* on 7 November 2021 to 18 May 2022, *O. triangularis* on 13 to 18 May 2022, *C. locuples* on 16 October to 1

November 2021. The adult moths were obtained by rearing larvae hatched from eggs deposited by the field-collected females.

Palatability assessments in the field

To determine whether the dark color of the male wings has a cryptic effect at twilight-dusk on visual predators such as birds, frozen *K. niphonis* and *O. thyellina* were hung from trees at dawn and their predation rates were measured. Experiments were conducted on 17, 18, 23, 24, and 25 April 2022, for *K. niphonis*, and on 11, 12, 17, 18, and 23 April 2022, for *O. thyellina*.

A study site of 2 km square was set up in Karuizawa, Nagano, central Japan (36°20'N 138°35'E, 1000 m elevation), and subsites were placed in 10 forest locations within the study site. Each subsite was at least 300 m away from the other. The illuminance in the forest was measured every 30 minutes from 3:30 to 8:30 a.m. in the shade using an illuminance meter (LX-204; CUSTOM, Tokyo, Japan) at the subsites on 23 and 25 April (about 1 km apart). Bird calls were recorded with an IC recorder (ICD-UX570F; SONY, Tokyo, Japan) at three points in the same subsite (30-50 m apart) at the same time, and the number of species and total number of individuals of birds were counted every 30 minutes for 5 minutes.

For the predation experiment, 50 each of frozen male and female moths (male and female sizes were matched as much as possible) were hung from a 1-2 m high branch with 0.6 mm nylon fishing line (Fighter keiryu; YAMATOYO, Shiga, Japan) at a distance of 3-6 cm (Fig. 4-4a, b), with each sample approximately 1 m apart. Setting was completed one hour before sunrise (around 4:00), and collection began by the time direct sunlight reached the study site (around 8:00). After retrieval, the number of samples lost and the number of samples with clear predator damage were counted.

4-3. Results

Daily activity patterns

Most actograms show that male *N. albofascia* becomes active around the light is turned on, whereas the female is activity after the light is turned off (Fig. 4-2, S4-1). Male *N. disparilis* shows diurnal activities, but the female is active mainly at night (Fig. 4-2, S4-1). Male *K. niphonis* becomes active after the light is turned on, but the female is activity after the light is turned off (Fig. 4-2, S4-1). Male *O. thyellina* becomes active around the light is turned off, but the female is active at night (Fig. 4-2, S4-1). Male *O.*

triangularis becomes active before the light is turned off, but the female is active at night (Fig. 4-2, S4-1). On the other hand, male *C. locuples* becomes active after the light is turned off, and the female is also active at night (Fig. 4-2, S4-1).

A total of 57 male and 17 female *N. albofascia*, 11 female *K. niphonis*, 2 male and 3 female *O. thyellina* and 6 male and 6 female *C. locuples* were collected by the light traps in the field (Fig. 4-3a, b, c, d). The time of sunset and sunrise for each day was referred to the time of sunset and sunrise in Tokyo near the light trapping site (National Astronomical Observatory of Japan 2018, 2019, 2020), and a crepuscular period was defined as 120 min centered around the time of sunset and sunrise (Hu *et al*. 2016). As a result, the flight time of male *N. albofascia* was in early hours of the morning from 2:00 and at least 5:00 when insect attraction to the artificial light ceased. Among 57 male *N. albofascia*, 28 (49.1%) were trapped in crepuscular around the sunrise. In contrast, the time when female *N. albofascia* were collected ranged early hours of evening from sunset to midnight (19:00–23:00). Female *N. albofascia* were never recorded in crepuscular. This tendency that male *N. albofascia* fly in the early morning but female *N. albofascia* fly in the early evening seems to correspond to their respective activity patterns recorded as actograms (Fig. 4-3a).

None of the male *K. niphonis* flew into the light trap, whereas the time when female *K. niphonis* were collected ranged early hours of evening from sunset to midnight (19:00–22:00). Female *K. niphonis* were never recorded in crepuscular. This tendency that male *K. niphonis* do not fly in the morning before sunrise and female *N. albofascia* fly in the early evening seems to correspond to their respective activity patterns recorded as actograms (Fig. 4-3b).

The flight time of male *O. thyellina* was in early hours of the evening (20:00-21:00) when insect attraction to the artificial light started, whereas the time when female *O. thyellina* were collected ranged in the evening from sunset to midnight (19:00–22:00). Female *O. thyellina* were never recorded in crepuscular. This tendency that male *O. thyellina* fly around the sunset and female *O. thyellina* fly at night seems to correspond to their respective activity patterns recorded as actograms (Fig. 4-3c).

The flight time of male *C. locuples* was collected ranged early hours of evening from sunset to midnight (20:00–0:00), whereas the time when female *C. locuples* were collected ranged in the evening from sunset to sunrise (20:00–3:00). Male and female *C. locuples* were never recorded in crepuscular. This tendency that male *C. locuples* fly in the early evening and female *C. locuples* fly at night seems to correspond to their respective activity patterns recorded as actograms (Fig. 4-3d).

In the mating time measurements in the laboratory, *K. niphonis* had 17 cases of mating that were captured on video, all of which were concentrated during the time period immediately after the lights turned on in the morning (6:00-8:00) (Fig. 4-3e). This time period coincided with the peak activity period of males as measured in actgram.

O. thyellina had 13 cases of mating that were captured on video, 11 cases of which were concentrated during the time period around the lights turned off in the evening (18:00-21:00) (Fig. 4-3e). This time period coincided with the peak activity period of males as measured in actgram.

C. locuples had 15 cases of mating that were captured on video, 14 cases of which were concentrated during the time period after the lights turned off at night (21:00-1:00) (Fig. 4-3e). This time period coincided with the peak activity period of males as measured in actgram.

Palatability assessments in the laboratory

The lizards used for 3-day feeding trials was 53–72 mm in SVL (62.1 ± 4.9 SD, *N* = 36). Male and female *N. albofascia*, *N. disparilis*, *K. niphonis*, *O. thyellina*, *O. triangularis* and *C. locuples* were all eaten by the lizards during the feeding trials (Table 4-1). The feeding time of *N. albofascia* was 97–1257 s (364.4 ± 306.1 SD, *N* = 18), *N. disparilis* was 25–126 s (55.4 ± 30.2 SD, *N* = 18), *K. niphonis* was 19–85 s (48.2 ± 17.8 SD, *N* = 18), *O. thyellina* was 16–69 s (34.8 ± 16.4 SD, *N* = 18), *O. triangulari* was 18–313 s (105.2 ± 88.9 SD, *N* = 18) and *C. locuples* was 13-114 s (39.8 ± 23.6 SD, *N* = 18) .

Palatability assessments in the field

The environmental conditions for the field foraging experiment were as follows: the illumination level began to increase around sunrise, and was almost saturated around 8:00 a.m. at the end of the experiment. Bird calls also began to be heard actively around sunrise, and then gradually decreased in frequency. A total of 29 insectivorous bird species calls were recorded during the two days of measurements (Fig. 4-4c, d, Table S4-1), and 6 insectivorous bird species were observed during the two days of measurements in addition (Table S4-1).

A total of 250 males (forewing length: 16.6±0.1 SE) and 250 females (forewing length: 16.8±0.1 SE) of *K. niphonis* were presented in the field, and the probability of damage or loss in females exceeded that in males in all four trials, except for the fourth trial in which no damage or loss was observed (Table 4-2a).

In the same manner, A total of 250 males (forewing length: 13.8±0.1 SE) and 250females (forewing length: 18.3±0.1 SE) of *O. thyellina* were presented in the field, and the probability of damage or loss in females exceeded that in males in all four trials, except for the fourth trial in which no damage or loss was observed (Table 4-2b).

4-4. Discussion

Laboratory measurements of daily activity rhythm showed that all five species with sexual dimorphism in wing color in the family Lymantriidae were also sexually dimorphic in their daily activity rhythm. The peak of activity existed during the male diurnal or twilight-dusk hours and the female at night. In contrast, in the control moth, *C. locuples*, which lacked wing-color sexual dimorphism, peak activity was present in both sexes at night. The measurement of flight times in the field light traps was consistent with the laboratory measurements, confirming the reliability of the actograph measurements. Measurements of mating times in the laboratory coincided with the peak activity time of males, experimentally confirming the expectation that the purpose of male flight is to search for females. Thus, the evolution of sexual dimorphism in wing color in Lymantriidae is likely to be closely related to the different activity times of males and females. In particular, it was observed that dark colored males flew during light hours in order to search for females.

In a predation experiment using the lizard, all moths of all species treated in this study were preyed upon by the lizards. Therefore, no repellent effect could be confirmed. Finally, in field predation experiments conducted at twilight, dark colored males were less likely to be preyed upon than light colored females at all trials. As a result, I succeeded in experimentally testing the hypothesis that in some sexually dimorphic species, males fly during light hours, such as twilight and dusk, and are thus subjected to stronger visual predation pressure by birds and other predators than females, resulting in the evolution of dark colors as cryptic colors specifically in the males. In other words, unlike the evolution of sexual dimorphism in diurnal butterflies due to sexual selection and predation pressure on females, predation pressure on males due to diurnal activity shifts can be assumed to be related to the evolution of sexual dimorphism in color in the family Lymantriidae (Fig. 4-5)

Such an evolutionary model of sexual dimorphism with dark colored males could be adapted to other species of the family Lymantriidae (Table 4-3). For example, gypsy moth (*Lymantria dispar*), a species of the same family Lymantriidae has been reported to have repellent effects on predators such as birds, and the males have darker colors than the females. Furthermore, males of this species are known to be active during the day and females at night (Odell and Mastro 1980, Koshio 1996, Koshio 1997, Iwaizumi 2010).

About the genus *Numenes*, it includes 14 species from Northeast Asia to South Asia. Among them, the relationship between *Numenes contrahens* and *Numenes insignis*, both living in Indonesia, is noteworthy. Both male and female *N. contrahens* have generally the same white colored wing. In contrast, male *N. insignis* has dark black wing, although the female wing of *N. insignis* is wholly similar white color to that of *N. contrahens* (Holloway 1999). This case suggests that sexual dimorphism in color in *Numenes* moths can be caused by changing color in males.

There are other diurnal species in the family Lymantriidae, of which *Ivela auripes* is an example. Both sexes of this species are active during the day (Fig. S4-2), but there is little difference in color between the sexes, with both sexes having white wings. When predation experiments were conducted with lizards, all individuals of both sexes were not preyed upon by lizards（Table S4-2, the data was taken from a joint experiment with Makoto Tsubuki）. This confirms the existence of a repellent effect against predation in this species. Thus, even in the family Lymantriidae, which is active during the daytime and has a predator repellent effect, the color functions as a warning color and the evolution of sexual dimorphism in wing color is unlikely to occur (Table 4-3).

An example of a male that is active during light hours becoming blackened due to the effects of predation by birds and other predators is *Hepialus humuli*, mentioned in the example of sexual dimorphism of color. It is known that males of the species in high Arctic latitudes have an increasing number of individuals with blackened wings, and it has been postulated that this is due, in part, to the effect of predation pressure caused by the extended activity hours of birds due to the midnight sun although not experimentally proven (Kaabar *et al*. 2009).

In saturniid moth, also lacking their mouthparts, there are nine cases known to have sexual difference in their activity time between daytime and nighttime in the field (Table 4-3), *Rhodinia fugax* (Mitamura 2003), *Anisota* ssp., *Automeris phrynon*, *Callosamia promethea*, *Callosamia securifera*, *Eupackardia calleta*, *Hemileuca burnsi*, *Saturnia albofasciata* and *Saturnia pavonia* (Morton 2017). Flight of the males in these species occurs in daytime, and coincides with the time of pheromone calling by the females. In the case of *C. promethea*, calling by females occurs from 15:00 to 20:00, and flight of males becomes active from 13:00 to 20:00 (Jeffords *et al*. 1980). On the contrary, the flight of females in all these species occurs in nighttime. In addition, six species among them also have sexual dimorphism in color which females have similar colors to those of closely related species whereas males are more darkly or deeply colored. Regarding the remaining three species, adult *E. calleta*, in which both males and females have black wings, has defense chemicals in common with the larval stage (Louwagie and Peigler 2016). Also, the *Hemileuca* moths including *H. burnsi*, in which both sexes have white wings, contain toxic chemicals in the larval stage at least (Pesce and Delgado 1971). And although the toxicity of *Automeris phrynon*, in which both sexes have brown wings, is not clear, *Automeris io* of the same genus is known to be toxic at least in larvae (Gilmer 1925). As these three species are likely to be toxic, it is expected that wing color functions as a warning color and, as in case *Ivela auripes*, sexual dimorphism in color was less likely to evolve. For *E. calleta* in particular, it has been suggested that both sexes may mimic for *Battus philenor* (Walbauer and Sternburg 1975).

Walbauer and Sternburg indicated that females of *C. promethea* and *C. securifera* have similar colors to those of closely related species, whereas males are more darkly colored. They suspected that the colors of male *Callosamia* moths and *E. calleta* derived from Batesian mimicry to the poisonous diurnal butterfly *Battus philenor* (Walbauer and Sternburg 1975). However, I can indicate this sexual dimorphism in deeper color of males existing also in other species of moths. There are no model species for warning color mimicry found in these species, and it suggests that darkening of the male wing color among palatable species to predators can occur by different evolutionary process from Batesian mimicry directly. Rather, given the mimetic relationship with another toxic moth in *N. albofascia*, the present male-only darkening of the wings may be explained as ‘preadaptation’ to sex-limited mimicry of diurnal dark toxic moths with overlapping active time zones. In other words, the evolution of color sexual dimorphism in Lymantriidae may explain the evolution of male-only mimicry and dual mimicry, a specialized form of sex-limited mimicry whose evolutionary process has not been entirely clear.

As I described in Chapter 3, *N. albofascia* may have different mimicry models for males and females: males in *N. albofascia* closely resemble unpalatable *Pidorus atratus* in their color and mottling, and their flight times overlap; females in *N. albofascia* closely resemble unpalatable *Arctia caja* in their color and mottling, and their flight times also overlap. At the same time, *N. disparilis* male, examined in this study for daily activity rhythm and repellent effects, has another moth, *Neochalcosia remota*, with very similar spots; when daily activity rhythm and repellent effects were also measured for *Neochalcosia remota*, both sexes tended to be diurnal (Fig. S4-2) and none of the lizards preyed on them (Table S4-3). Also, *N. disparilis* female resembles *Arctia caja* in its color and mottling and *Arctia caja* in the unpalatable moth (Table S4-3). Therefore, it is possible that a Batesian dual mimicry may also exist between males of *N. disparilis* and *Neochalcosia remota*, females of *N. disparilis* and *A. caja* (Table 4-3). Together with *N. albofascia* mimicry, it is possible to postulate a model in which *N. albofascia* and *N. disparilis* sex-limited mimicry evolved by 'preadaptation' of males to darker wing colors arising from differences in flight time between males and females, with males still resembling diurnal, unpalatable moths with dark wings and females resembling nocturnal, unpalatable moths with lighter wing colors (Fig 4-5). In the six species of Lymantriidae treated in this study, *C. locuples* can be considered to be a species retaining ancestral traits in which there is no difference in wing color between males and females and both males and females are nocturnal; *K. niphonis*, *O. thyellina* and *O. triangularis* are species in which differences have occurred in the flight times of the males and females and the wings of the males are darker; and *N. albofascia* and *N. disparilis* are species in which mimetic relationships with unpalatable moths have evolved, with each sex matching its activity rhythm (Fig. 4-6).

However, the reason of the daily activity rhythm shift between males and females is not known. In the nocturnal moths, it is commonly known that flight time of females are in the early hours in the night due to avoiding the peak activity of birds and insectivorous bats (Acharya 1995). For this reason, female flight times are expected to be less variable, and indeed the peak of activity for all six female lymantriid moths measured in this research is generally in the early evening hours. On the contrary, a shift in mating time occurs between species so as to avoid mis-mating between closely related species often in several moth species (Wilson and Bossert 1963, Hendrikse 1979, Konno *et al.* 1981, Haynes and Birch 1986, Pashley *et al.* 1992, Konno and Tanaka 1996, Monti *et al.* 1997, Sasaerila *et al.* 2000, Samudra *et al.* 2002, Groot *et al.* 2010, Gago *et al.* 2013), with a concomitant shift in male flight time, which is thought to be an example of reinforcement of allochronic reproductive isolation (Kuno 1992, Miyatake 2006). It can be assumed that if such trait substitution occurs between species in which both males and females fly at night, male flight times may shift to twilight-dusk or daytime, resulting in the evolution of a sexual dimorphism in wing color, in which the male wing color is black. Finally, the resemblance between males and diurnal model species having deep colored wing arose independently in females. In the case of dual mimicry, there are two additional possibilities for the evolution of the mimicry on female side. First, resemblance to the nocturnal model species already existed in the homothallic stage and the character has been retained; Second, mimicry arose independently in males after separation of activity time between males and females. The present study was unable to clarify the evolutionary process of mimicry on the part of females; it is assumed that both females *N. albofascia* and *N. disparilis*, and the unpalatable *A. caja*, which has similar spots to them, are nocturnal and often rest during the day with their wings spread on the grass. In doing so, they may have a behavioral similarity in that they are vulnerable to attack by birds and other predators that visually search for prey.

This model of the evolution of sexual dimorphism in wing color cannot explain the evolution of sexual dimorphism in moths with repellent effects on predators. Sexual dimorphism in wing color has also been reported in some species of the family Arctiidae (Kettlewell 1973, Kishida 2011e), which generally have toxic chemical in their bodies, and there may be a difference in the peak activity times of the sexes. Detailed validation experiments on a wider range of cases, including differences in the strength of the venom component between males and females, are needed to examine the evolution of color in these species.

This study points out that differences in activity time between males and females can lead to the evolution of sexual dimorphism in color. Also, the evolutionary relationship between warning color mimicry and sexual dimorphism in color may be indirect through the cryptic color caused by the difference in activity time between the sexes. Finally, the evolutionary process of sexual dimorphism in color and mimicry in moth species, which engage in nighttime activity and pheromone-mediated mating behavior, might be due to different mechanisms from that of diurnal butterflies.

Table 4-1. Results of 3-day feeding trials (eaten, bitten, or unbitten) in which individual male (m) and female (f) moths of *Numenes albofascia*, *Numenes disparilis*, *Kuromondokuga niphonis*, *Orgyia thyellina*, *Orgyia triangularis* and *Cifuna locuples* were given to a total of 36 lizards (SVL, snout to vent length in mm; m, male; f, female). If the moth was eaten, the time from biting to swallowing it was measured in s. If bitten, the time from biting to releasing it was measured based on the recoded movie.

Moths		Lizards		Feeding results					
Species	Sex	SVL (mm)	Sex	1st day	Time in s	2nd day	Time in s	3rd day	Time in s
N. albofascia	m	67	m	eaten	230	eaten	167	eaten	221
N. albofascia	m	68	m	eaten	360	eaten	855	eaten	321
N. albofascia	m	65	f	eaten	131	eaten	120	eaten	97
N. albofascia	f	67	f	eaten	1250	eaten	312	eaten	253
N. albofascia	f	61	f	eaten	412	eaten	226	eaten	187
N. albofascia	f	68	f	eaten	834	eaten	336	eaten	248
N. disparilis	m	58	f	eaten	25	eaten	117	eaten	60
N. disparilis	m	62	f	eaten	31	eaten	50	eaten	56
N. disparilis	m	58	m	eaten	38	eaten	126	eaten	62
N. disparilis	f	65	m	eaten	29	eaten	44	eaten	102
N. disparilis	f	60	m	eaten	27	eaten	58	eaten	50
N. disparilis	f	59	f	eaten	49	eaten	27	eaten	47
K. niphonis	m	55	m	eaten	72	eaten	39	eaten	67
K. niphonis	m	57	m	eaten	19	eaten	48	eaten	29
K. niphonis	m	59	f	eaten	85	eaten	34	eaten	65
K. niphonis	f	54	m	eaten	46	eaten	40	eaten	37
K. niphonis	f	64	m	eaten	38	eaten	45	eaten	75
K. niphonis	f	61	m	eaten	33	eaten	44	eaten	52
O. thyellina	m	58	m	eaten	43	eaten	33	eaten	24
O. thyellina	m	65	m	eaten	40	eaten	69	eaten	19
O. thyellina	m	72	f	eaten	64	eaten	17	eaten	29
O. thyellina	f	62	m	eaten	37	eaten	19	eaten	20
O. thyellina	f	65	m	eaten	35	eaten	50	eaten	58
O. thyellina	f	62	m	eaten	26	eaten	28	eaten	16
O. triangularis	m	68	m	eaten	43	eaten	66	eaten	32
O. triangularis	m	62	m	eaten	40	eaten	57	eaten	44
O. triangularis	m	70	m	eaten	18	eaten	19	eaten	41
O. triangularis	f	63	m	eaten	245	eaten	123	eaten	106
O. triangularis	f	55	f	eaten	102	eaten	271	eaten	313
O. triangularis	f	66	m	eaten	155	eaten	133	eaten	85
C. locuples	m	68	f	eaten	22	eaten	26	eaten	52
C. locuples	m	53	f	eaten	24	eaten	32	eaten	43
C. locuples	m	53	f	eaten	50	eaten	17	eaten	72
C. locuples	f	63	m	eaten	27	eaten	23	eaten	13
C. locuples	f	63	f	eaten	39	eaten	50	eaten	114
C. locuples	f	59	f	eaten	40	eaten	33	eaten	40

Table 4-2. Results of predation experiments in the field during twilight hours. 50 frozen moth males and female each were suspended from a 1-2 m high branch with 0.6 mm nylon fishing line at a distance of 3-6 cm, with each sample approximately 1 m apart. Setting was completed one hour before sunrise (around 4:00) and collection began by the time direct sunlight reached the study site (around 8:00). Following collection, the number of samples lost and those with clear predator damage were counted. a: *Kuromondokuga niphonis*, b: *Orgyia thyellina*.

(a) *Kuromondokuga niphonis*

	date	sex	N	undamged	damaged/lost	Fisher's exact test	Forewing lenth (mm) ±SE	t-test
trial1	17 Apr. 2022	m	50	46	4		16.56±0.20	
		f	50	40	10	P=0.148	16.92±0.23	P=0.230
trial2	18 Apr. 2022	m	50	47	3		16.53±0.22	
		f	50	42	8	P=0.200	16.76±0.22	P=0.454
trial3	23 Apr. 2022	m	50	48	2		16.66±0.18	
		f	50	47	3	P=1.000	16.83±0.20	P=0.538
trial4	24 Apr. 2022	m	50	50	0		16.60±0.15	
		f	50	50	0	P=1.000	16.81±0.20	P=0.402
trial5	25 Apr. 2022	m	50	50	0		16.58±0.16	
		f	50	48	2	P=0.495	16.79±0.23	P=0.464
Total		m	250	241	9		16.59±0.08	
		f	250	228	22	P=0.025	16.82±0.10	P=0.060

(b) *Orgyia thyellina*

	date	sex	N	undamged	damaged/lost	Fisher's exact test	Forewing lenth (mm) ±SE	t-test
trial1	11 Apr. 2022	m	50	46	4		13.43±0.22	
		f	50	41	9	P=0.234	18.43±0.39	P<0.001
trial2	12 Apr. 2022	m	50	50	0		13.75±0.20	
		f	50	44	6	P=0.027	18.44±0.34	P<0.001
trial3	17 Apr. 2022	m	50	45	5		13.84±0.21	
		f	50	42	8	P=0.554	18.40±0.27	P<0.001
trial4	18 Apr. 2022	m	50	50	0		14.13±0.18	
		f	50	50	0	P=1.000	18.31±0.26	P<0.001
trial5	23 Apr. 2022	m	50	49	1		13.68±0.17	
		f	50	47	3	P=0.617	17.80±0.26	P<0.001
Total		m	250	240	10		13.77±0.09	
		f	250	224	26	P=0.009	18.28±0.14	P<0.001

Table 4-3. Lists of occurrences of sexual dimorphism in color, time of male daily activity or copulation, time of female daily activity or egg oviposition, male palatability, female palatability, male possible mimicry model and female possible mimicry model of (a) Lymantriidae and (b) Sarurniidae according to the experiment in this study and references.

(a) Lymantriidae

species	sexual dimorphism in color	male daily activity/ copulation	female daily activity/ egg oviposition	male palatability	female palatability	male possible mimicry model	female possible mimicry model
Numenes albofascia	yes	crepuscular	nocturnal	palatable	palatable	*Pidorus atratus* (Zygenidae)*1	*Arctia caja* (Arctiidae)*1
Numenes disparilis	yes	diurnal	nocturnal	palatable	palatable	*Neochalcosia remota* (Zygenidae)	*Arctia caja* (Arctiidae)
Kuromondokuga niphonis	yes	crepuscular	nocturnal	palatable	palatable		
Orgyia thyellina	yes	crepuscular	nocturnal	palatable	palatable		
Orgyia triangularis	yes	crepuscular	nocturnal	palatable	palatable		
Lymantria dispar	yes	crepuscular*2,4	nocturnalt*3,5				
Lymantria lucescens	weak	crepuscular/ nocturnal*6,7	crepuscular/ nocturnal*6				
Cifuna locuples	no	nocturnal	nocturnal	palatable	palatable		
Ivela auripes	no	diurnal	diurnal	unpalatable	unpalatable		

(b) Sarurniidae

species	sexual dimorphism in color	male daily activity/ copulation	female daily activity/ egg oviposition	male palatability	female palatability	male possible mimicry model	female possible mimicry model
Anisota ssp.	yes	diurnal*8, 9	nocturnal*8, 9				
Callosamia promethea	yes	diurnal *8, 10, 11, 12	nocturnal *8, 10, 12			*Battus philenor* (Papilionidae)*14	
Callosamia securifera	yes	diurnal *8, 11, 13	nocturnal*8, 13			*Battus philenor* (Papilionidae)*14	
Rhodinia fugax	yes	diurnal*15	nocturnal*15				
Saturnia albofasciata	yes	diurnal*8, 16	nocturnal*8, 16				
Saturnia pavonia	yes	diurnal*8, 17	nocturnal*8, 17				
Callosamia angulifera	weak	crepuscular/ nocturnal *8, 11, 12	nocturnal *8, 11, 12				
Antheraea yamamai	no	nocturnal*18	nocturnal*18				
Caligula japonica	no	nocturnal*18	nocturnal*18				
Hyalophora cecropia	no	nocturnal*8, 9	nocturnal*8, 9				
Rothschildia lebeau	no	nocturnal*8, 19	nocturnal*8, 19				
Automeris phrynon	weak	diurnal*8, 20	nocturnal*8, 20	*Automeris io* is toxic at least in larval stage*21	*Automeris io* is toxic at least in larval stage*21		
Eupackardia calleta	no	diurnal*8, 22	nocturnal*8, 22	toxic at least in larval stage*22	toxic at least in larval stage*22	*Battus philenor* (Papilionidae)*14	*Battus philenor* (Papilionidae)*14
Hemileuca spp.	no	diurnal*8, 23	nocturnal*8, 23	*Hemileuca spp.* are toxic at least in larval stage*24	*Hemileuca spp.* are toxic at least in larval stage*24		

References: 1. Chapter 3, 2. Odell and Mastro 1980, 3. Koshio 1996, 4. Koshio 1997, 5. Iwaizumi *et al*. 2010, 6. Nishio 2000, 7. Schaefer 2012, 8. Morton 2017, 9. Tuskes *et al*. 1996, 10. Jeffords *et al*. 1980, 11. Gago *et al*. 2013, 12. Morton 2009, 13. Brown 1972, 14. Walbauer and Sternburg 1975, 15. Mitamura 2003, 16. Tuskes and Collins 1981, 17. Tutt 1902, 18. Mitamura 1995, 19. Agosta 2008, 20. Marquis 1984, 21. Gilmer 1925, 22. Louwagie and Peigler 2016, 23. Tuskes 1984, 24 Pesce and Delgado 1971.

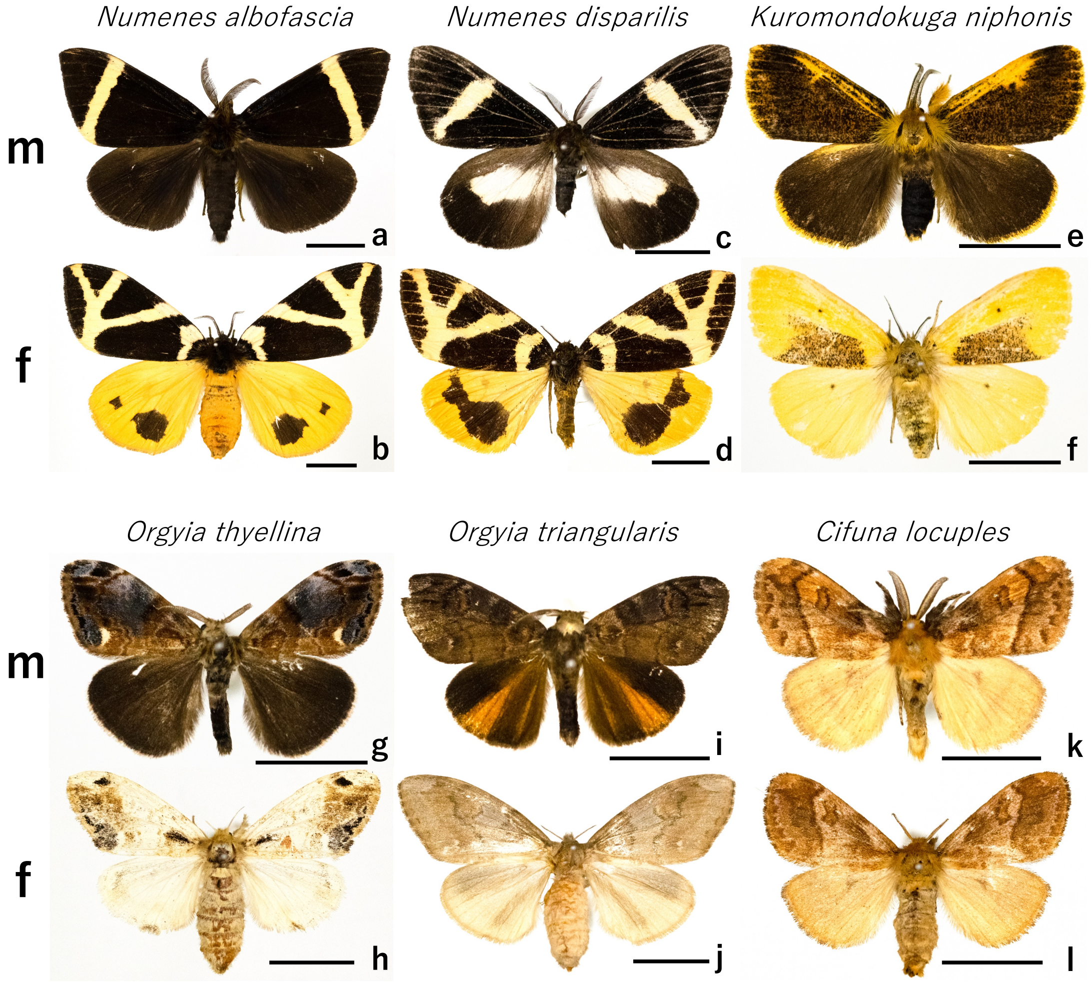


Figure 4-1. Materials of the experiments. *Numenes albofascia* (a: male, b: female), *Numenes disparilis* (c: male, d: female), *Kuromondokuga niphonis* (e: male, f: female), *Orgyia thyellina* (g: male, h: female), *Orgyia triangularis* (i: male, j: female) have remarkable difference in wing color between the sexes. On the contrary, *Cifuna locuples* (k: male, l: female) does not have a great difference in wing color between the sexes. Scale bars: 10 mm.

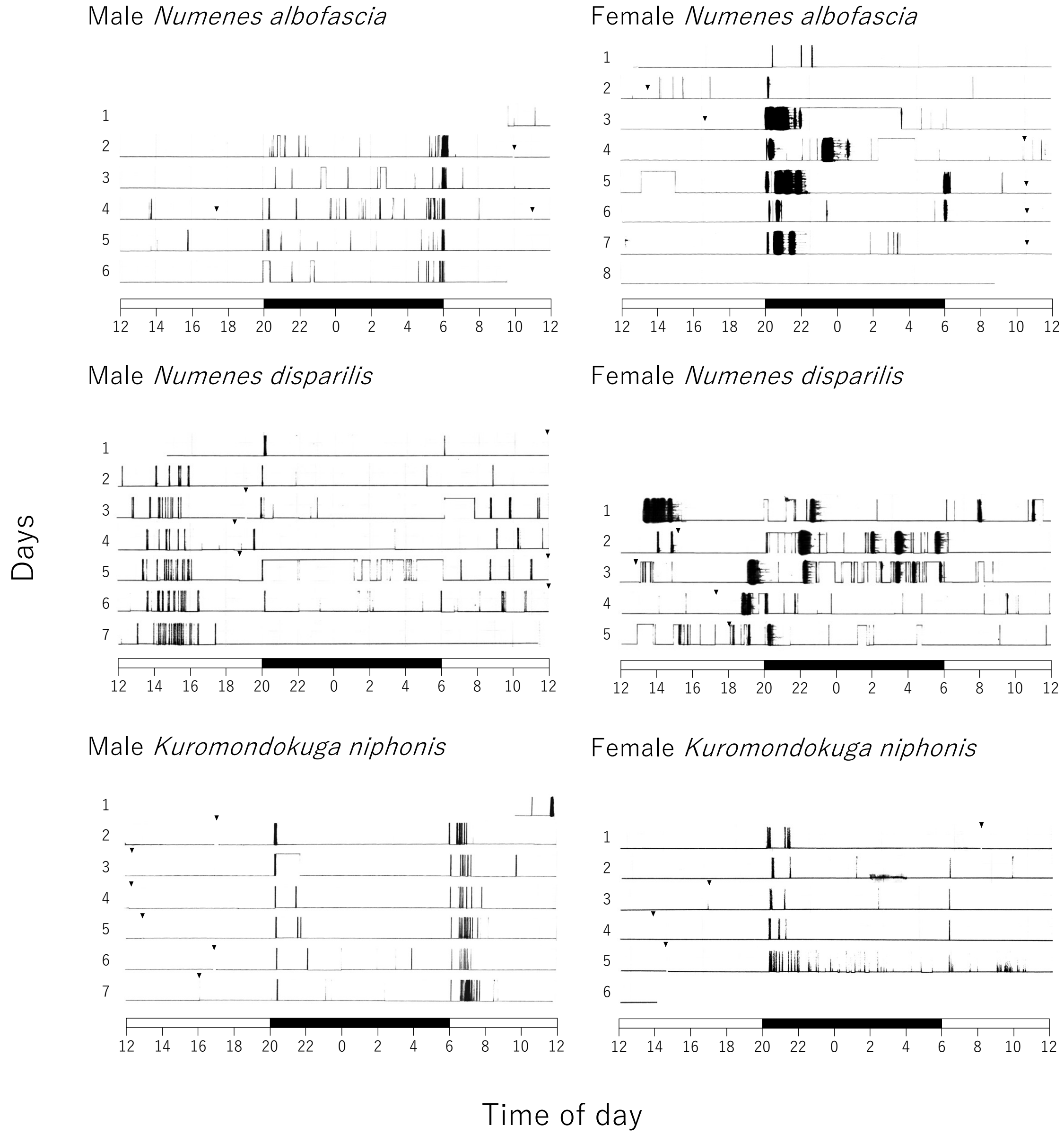
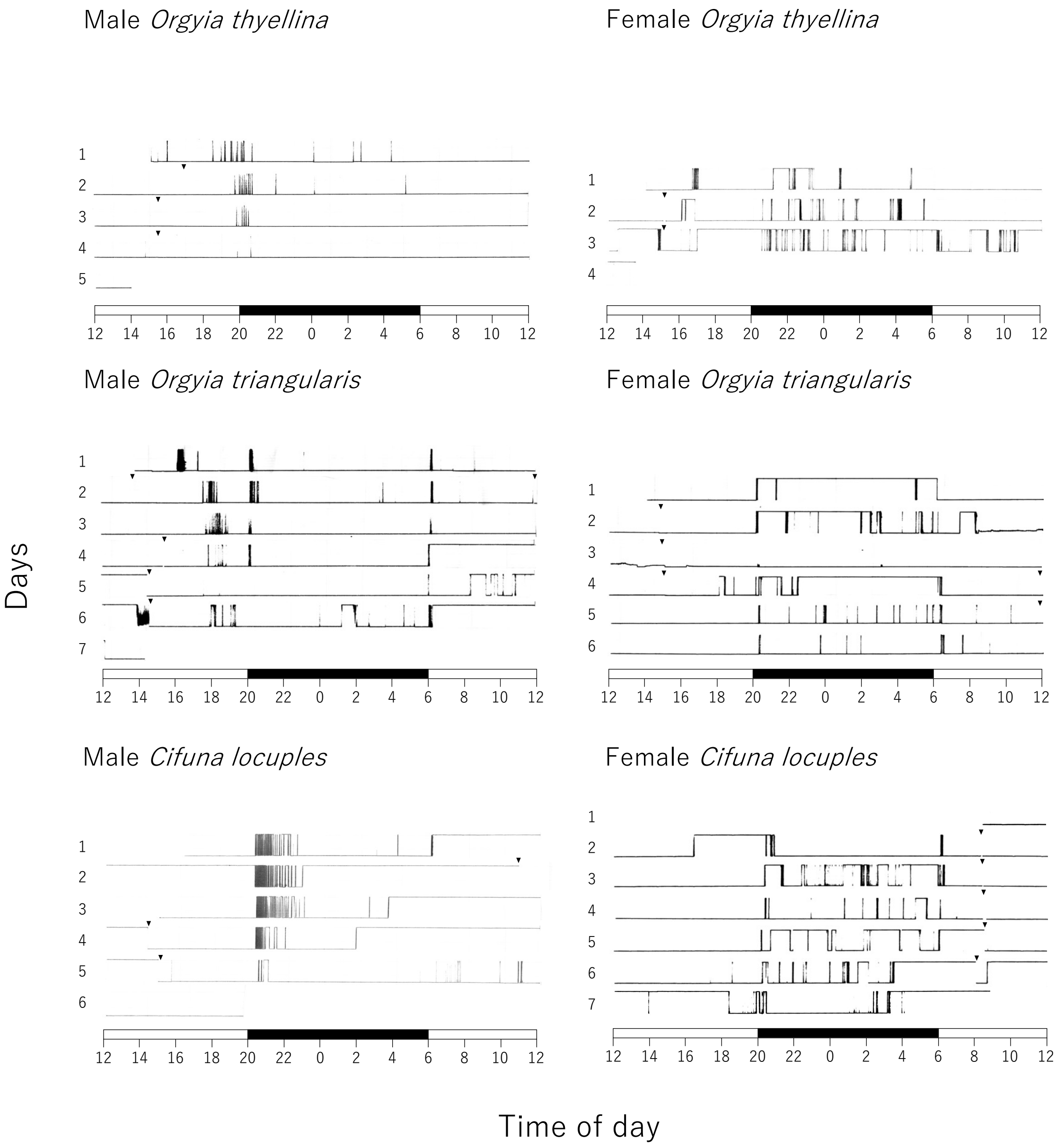


Figure 4-2. Actograms of male *Numenes albofascia*, female *N. albofascia*, male *Numenes disparilis*, female *Numenes disparilis*, male *Kuromondokuga niphonis*, female *Kuromondokuga niphonis*, male *Orgyia thyellina*, female *Orgyia thyellina*, male *Orgyia triangularis*, female *Orgyia triangularis*, male *Cifuna locuples*, female *Cifuna locuples* obtained in the laboratory. All interceptions of a fine beam through the rearing glass vessel are recorded on a chart sent at 10 mm/h of the pen recorder. The recording condition was at 25±1°C with a 14-h light (6:00–20:00) and 10-h dark (20:00–6:00) cycle. Each arrow head shows the time when water is added to the filter paper on the bottom of the vessel. The data in *Numenes albofascia* are reproduced in Fig. 3-3.



Male *Orgyia thyellina*

Female *Orgyia thyellina*

Male *Orgyia triangularis*

Female *Orgyia triangularis*

Male *Cifuna locuples*

Female *Cifuna locuples*

Figure 4-2. Continued.

(a) *Numenes albofascia*

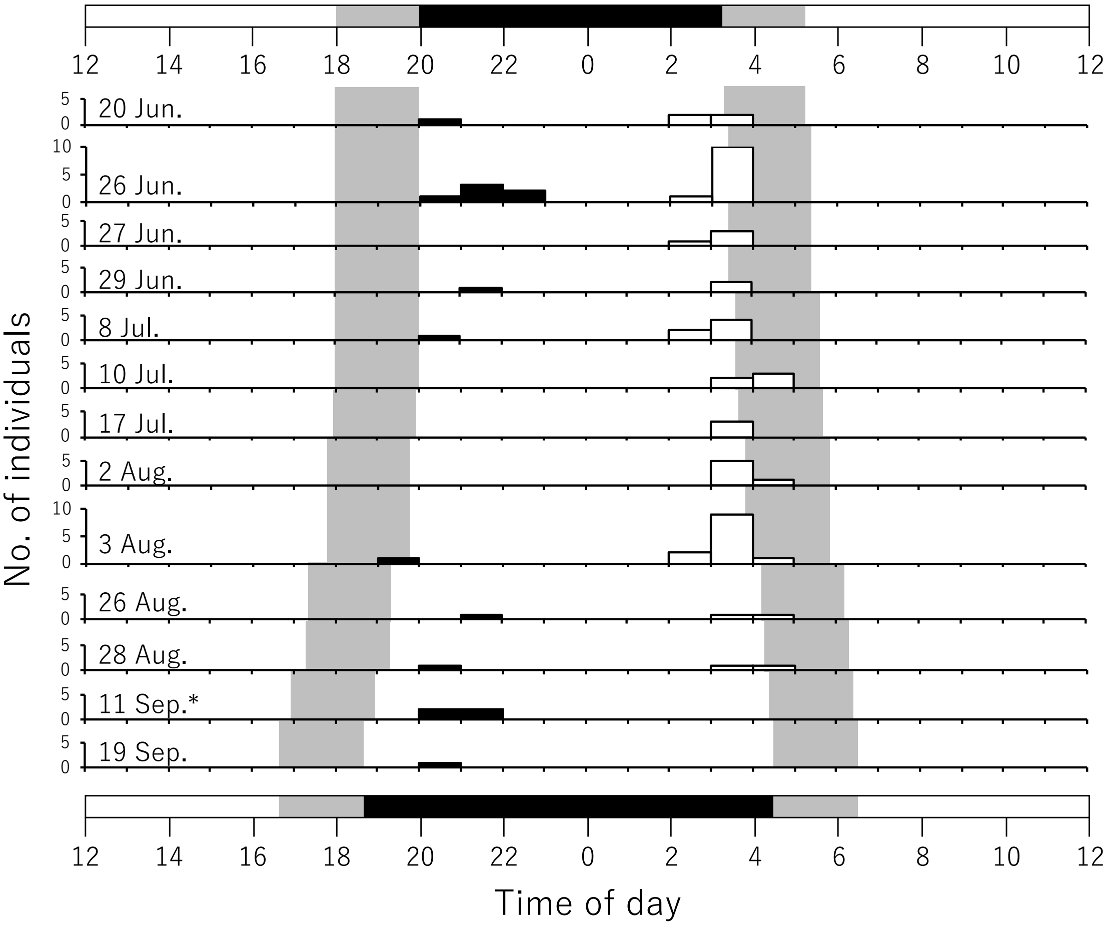
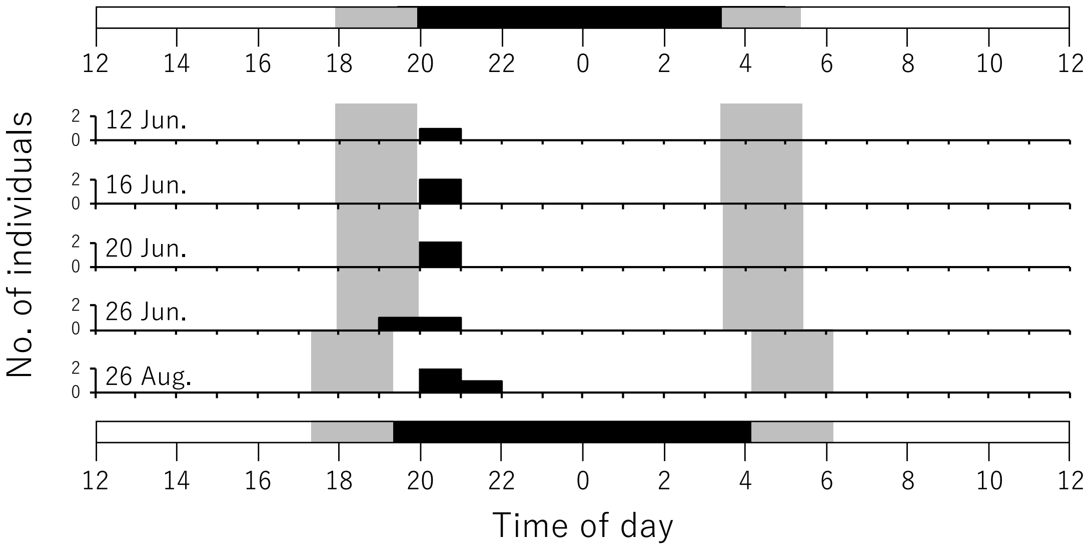
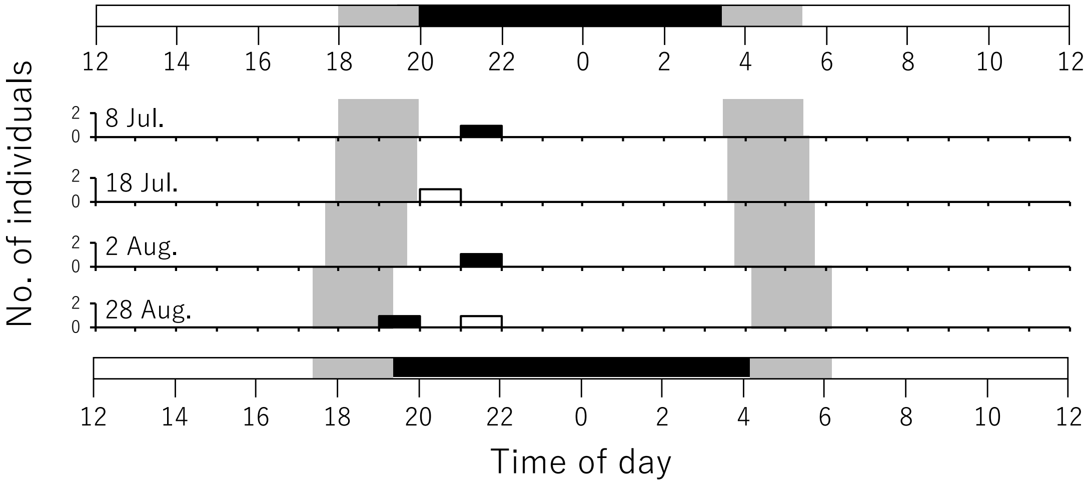


Figure 4-3. (a) Number of males (open bars) and females (closed bars) of *Numenes albofascia* collected by the overnight light traps at Okutama, western Tokyo, on 13 nights during late June to mid-September (*until the midnight because of heavy rain). A crepuscular period is shown with gray by defining it as 120 min centered around the time of sunset and sunrise. (b) *Kuromondokuga niphonis* at Okutama on 5 nights. (c) *Orgyia thyellina* at Okutama on 4 nights. (d) *Cifuna locuples* at Matsumoto, Nagano, central Japan on 4 nights. (e) Results of mating experiments in the laboratory. Closed bars indicates the number of pairs initiating copulation per hour. The data in *Numenes albofascia* are reproduced in Fig. 3-4.

(b) *Kuromondokuga niphonis*



(c) *Orgyia thyellina*



(d) *Cifuna locuples*

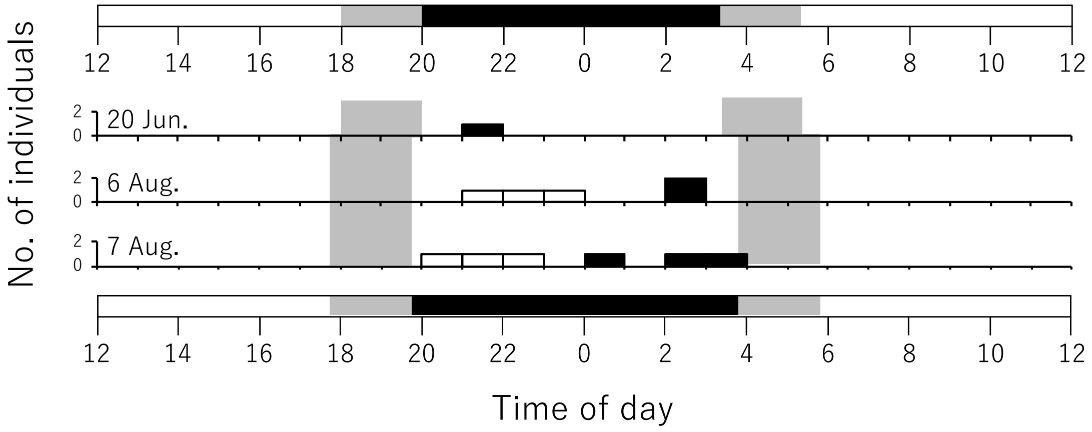


Figure 4-3. Continued (1).

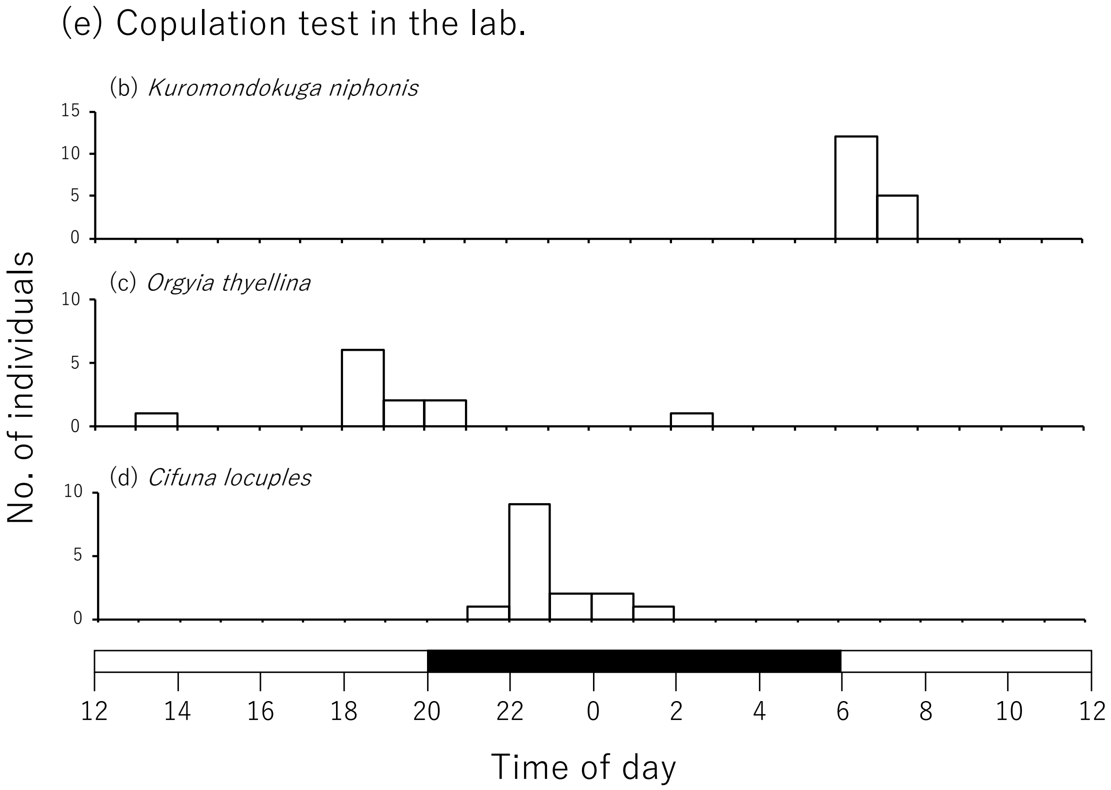
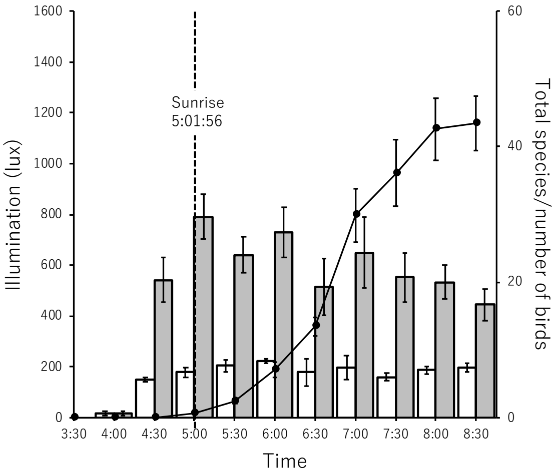


Figure 4-3. Continued (2).

(c) 4/23



(d) 4/25

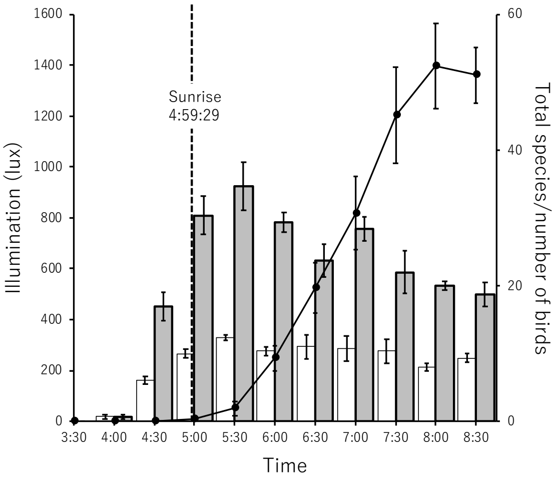
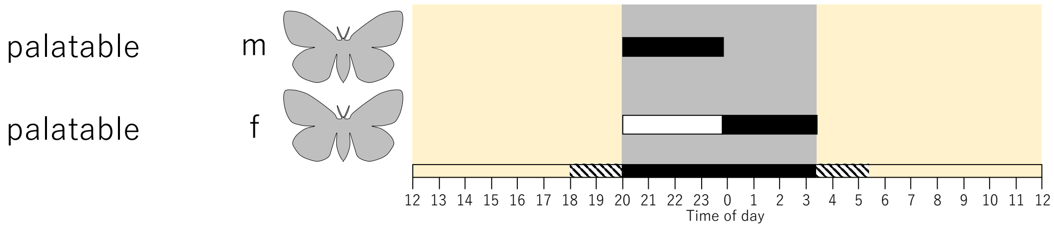
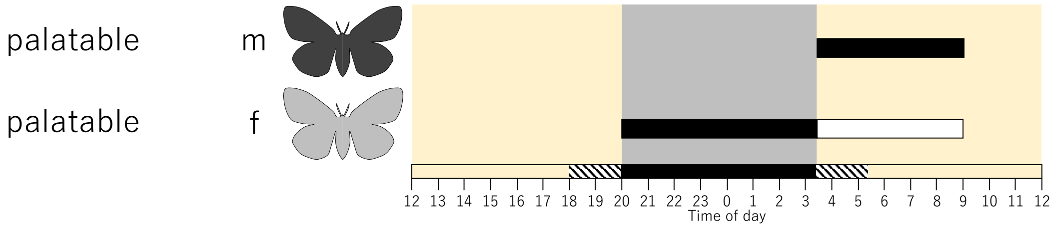


Figure 4-4. (a, b) Male *Kuromondokuga niphonis* hanging from a tree during twilight hours. a: male, b: female. (c,d) The environmental conditions of the feeding experiment in the field are shown in the graph. The abscissa represents the time trend and the ordinate represents the illuminance (lux). Bars represent the total number of bird species (white) and total number of bird individuals (grey) estimated from the call recordings. Error bars represent SE. a: 23 April 2022 in Karuizawa, Nagano, central Japan, b: 25 April 2022 in Karuizawa.

(a) Without sexual dimorphism



(b) Sexual dimorphism with male dark color



(c) Possible sex-limited mimicry with male dark color as 'preadaptation'

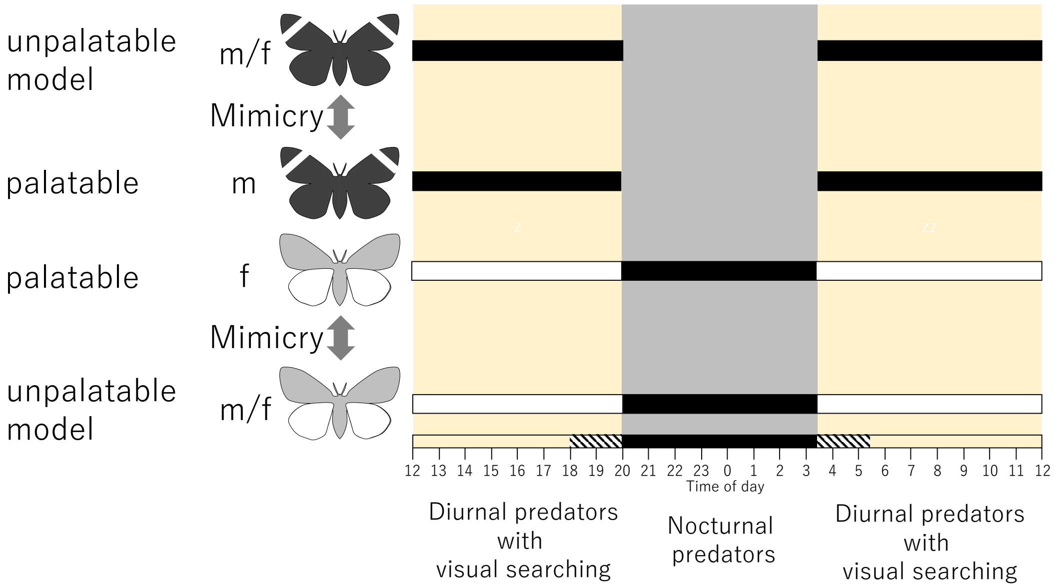


Figure 4-5. Schematic diagram of the evolution of sexual dimorphism in Lymantriidae with dark colored male wings. Black bars: time of flight, white bars: calling (female stopping and releasing sex pheromones) (a) In species where both sexes are active at night, sex-specific predation pressure is less likely and sexual dimorphism in wing color does not evolve. (b) Visual predation pressure is exerted specifically on males in species where the sexes have a shift in activity time, with females active at night and males at twilight-dusk or during the daytime. As a result, cryptic dark color evolves only in males. (c) Part of a sexually dimorphic species, where mimicry can evolve in males against diurnal, dark colored, unpalatable moths, and in females against nocturnal, light colored, unpalatable moths.

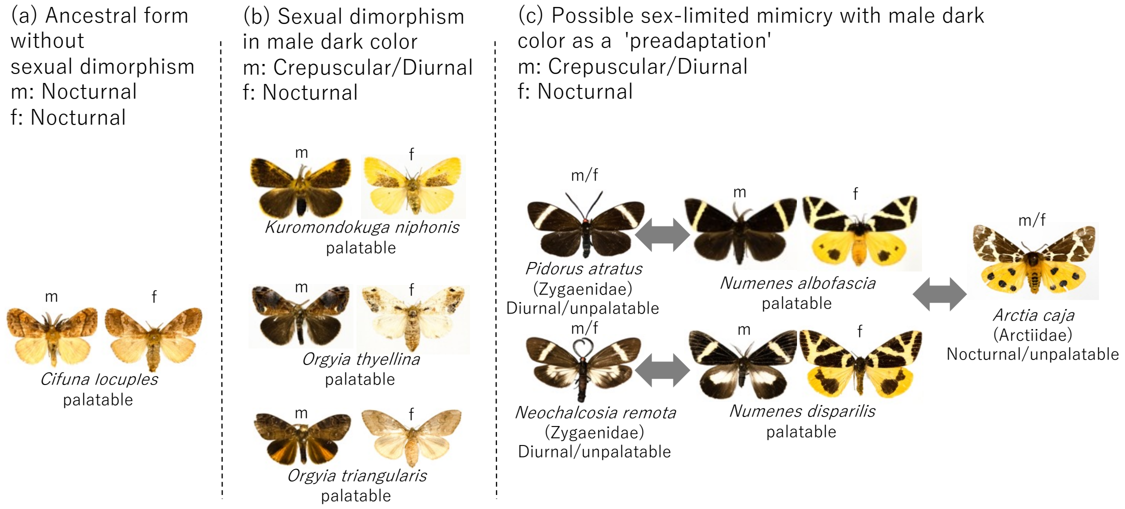


Figure 4-6. Diagram of the stages of evolution of sexual dimorphism and sex-limited mimicry in the lymantriid moth species treated in this study. (a) *Cifuna locuples* was the species that retained the ancestral trait. There is no difference in wing color between males and females, and both sexes are nocturnal. (b) *Kuromondokuga niphonis*, *Orgyia thyellina* and *Orgyia triangularis* showed differences in the activity times of the sexes, with males flying at twilight-dusk or during the day and females at night. As a result, male wings were darkened and sexual dimorphism in wing color had evolved.
(c) *Numenes albofascia* and *Numenes disparilis* possibly mimic of *Pidorus atratus* and *Neochalcosia remota*, respectively, which are dark winged colored unpalatable moths with matching activity times. Both species of females may also be mimicking *Arctia caja*, which is a moth with light colored wings with matching activity times. This could be an evolution of sex-limited mimicry, with the dark wing color of the male described above being 'preadaptation'.

Table S4-1. List of insectivorous bird species recorded during field experiments in Karuizawa, Nagano prefecture, Japan. called: species recorded by recording their calls during the experiments; observed: species whose calls were not recorded but which were seen during the experiments.

Species	Family	23 Apr. 2022	25 Apr. 2022
Phasianus colchicus	Phasianidae	called	called
Streptopelia orientalis	Columbidae	called	called
Cuculus canorus	Cuculidae	called	
Milvus migrans	Accipitridae	called	called
Buteo buteo	Accipitridae	obsereved	
Strix uralensis	Strigidae	called	called
Dendrocopos kizuki	Picidae	called	called
Dendrocopos major	Picidae	called	called
Picus awokera	Picidae	called	called
Pericrocotus divaricatus	Campephagidae	called	called
Lanius bucephalus	Laniidae		called
Garrulus glandarius	Corvidae		called
Corvus corone	Corvidae		called
Corvus macrorhynchos	Corvidae	called	called
Poecile montanus	Paridae		observed
Poecile varius	Paridae	called	called
Periparus ater	Paridae	called	called
Parus minor	Paridae	called	called
Hirundo rustica	Hirundinidae		observed
Hypsipetes amaurotis	Pycnonotidae	called	called
Cettia diphone	Cettiidae	called	called
Zosterops japonicus	Zosteropidae		called
Sitta europaea	Sittidae	observed	observed
Agropsar philippensis	Sturnidae		called
Turdus cardis	Muscicapidae		called
Turdus pallidus	Muscicapidae	observed	
Tarsiger cyanurus	Muscicapidae	called	
Ficedula narcissina	Muscicapidae	called	
Cyanoptila cyanomelana	Muscicapidae	called	called
Motacilla cinerea	Motacillidae		observed
Motacilla alba	Motacillidae	called	
Chloris sinica	Fringillidae		called
Eophona personata	Fringillidae	called	called
Emberiza cioides	Emberizidae	called	called
Garrulax canorus	Timaliidae, invasive species	called	called

Table S4-2. Results of 5-day feeding trials (eaten, bitten, or unbitten) in which individual male (m) and female (f) moths of *Ivela auripes* were given to a total of 6 lizards (SVL, snout to vent length in mm; m, male; f, female). This data was taken from a joint experiment with Makoto Tsubuki.

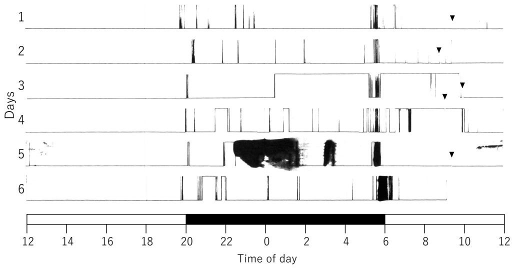
Moths		Lizards		Feeding results				
Species	Sex	SVL (mm)	Sex	1st day	2nd day	3rd day	4th day	5th day
I. auripes	m	64	m	bitten	bitten	unbitten	unbitten	unbitten
I. auripes	m	60	m	bitten	unbitten	unbitten	bitten	unbitten
I. auripes	m	54	f	bitten	regurgitated	unbitten	unbitten	bitten
I. auripes	f	61	m	bitten	bitten	unbitten	unbitten	unbitten
I. auripes	f	60	m	bitten	bitten	unbitten	unbitten	unbitten
I. auripes	f	66	m	bitten	unbitten	unbitten	unbitten	unbitten

Table S4-3. Results of 3-day feeding trials (eaten, bitten, or unbitten) in which individual male (m) and female (f) moths of *Neochalcosia remota* and *Arctia caja* were given to a total of 6 lizards (SVL, snout to vent length in mm; m, male; f, female). If the moth was eaten, the time from biting to swallowing it was measured in s. If bitten, the time from biting to releasing it was measured based on the recoded movie. The data for *Arctia caja* are restated as described in Chapter 3.

Moths		Lizards		Feeding results					
Species	Sex	SVL (mm)	Sex	1st day	Time in s	2nd day	Time in s	3rd day	Time in s
N. remota	m	57	f	bitten	7	unbitten		unbitten	
N. remota	m	65	m	bitten	2	unbitten		unbitten	
N. remota	m	66	m	unbitten		unbitten		unbitten	
N. remota	f	61	m	unbitten		unbitten		unbitten	
N. remota	f	59	m	bitten	32	unbitten		unbitten	
N. remota	f	65	f	bitten	20	unbitten		unbitten	
A. caja	m	61	m	unbitten		unbitten		unbitten	
A. caja	m	63	f	bitten	231	unbitten		unbitten	
A. caja	m	58	m	unbitten		unbitten		unbitten	

Male *Numenes albofascia*

#1



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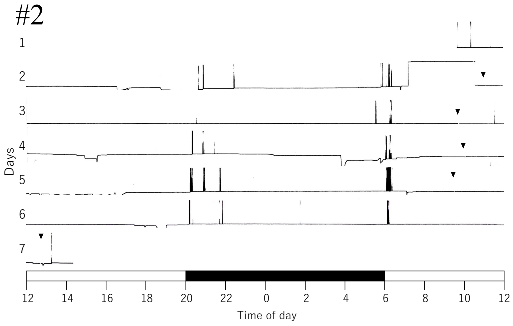

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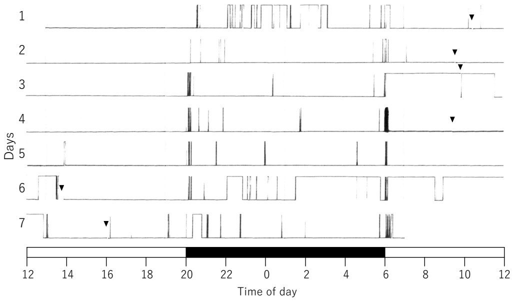

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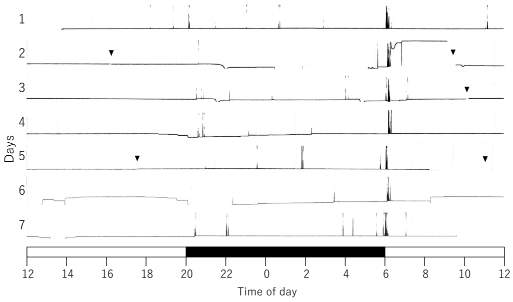

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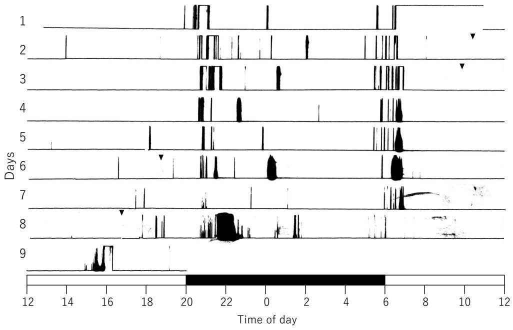

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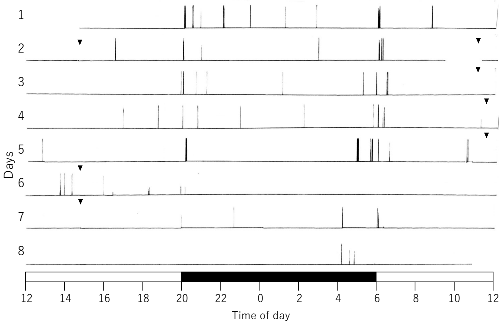

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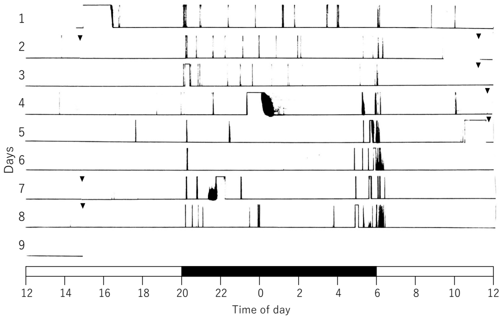

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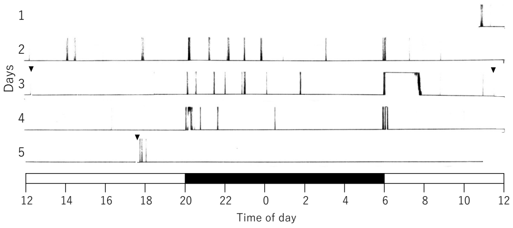

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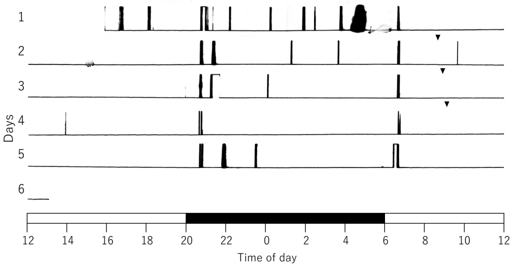
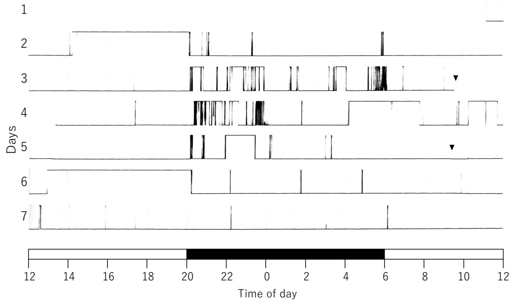


Female *Numenes albofascia*

#1



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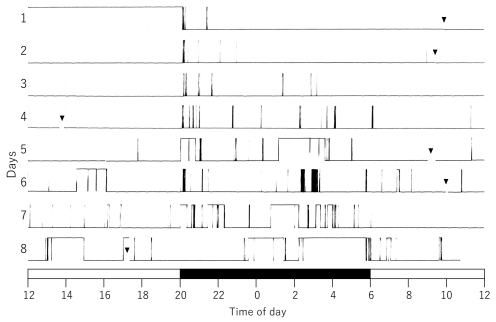

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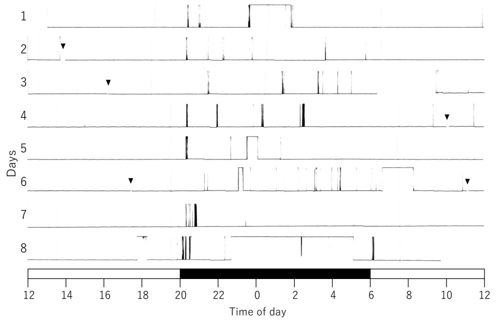

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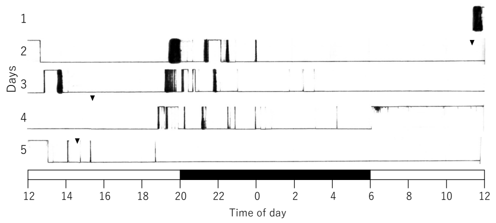
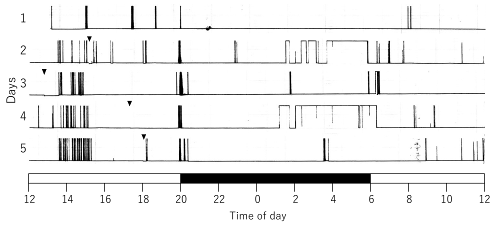


Male *Numenes disparilis*

#1



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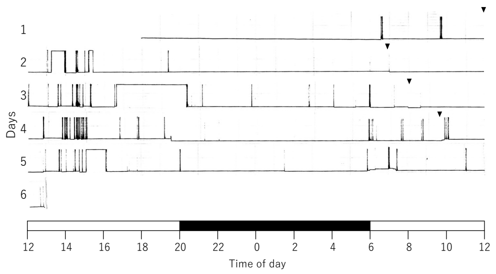

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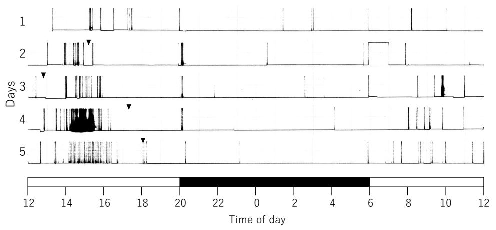

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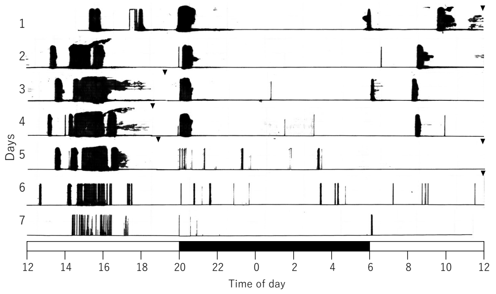

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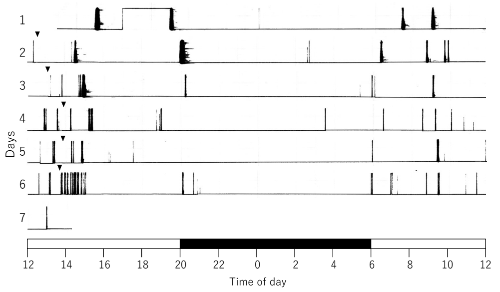

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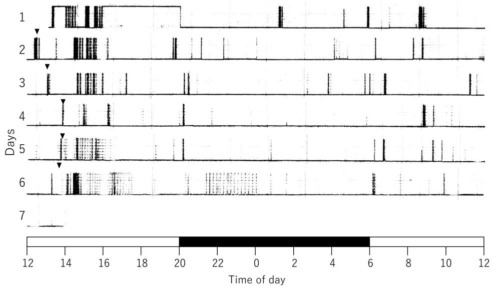

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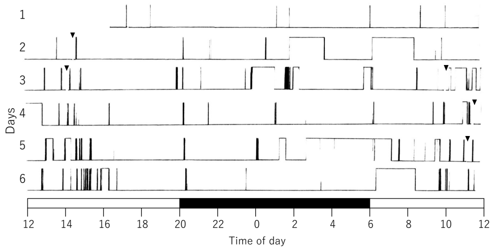

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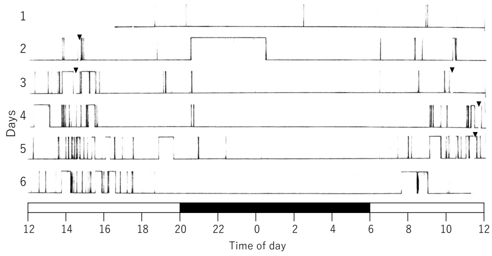

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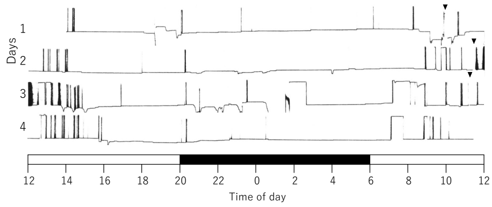

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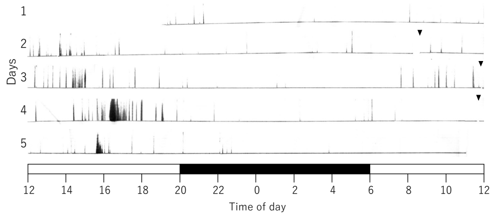

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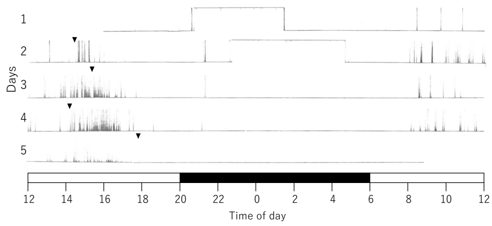

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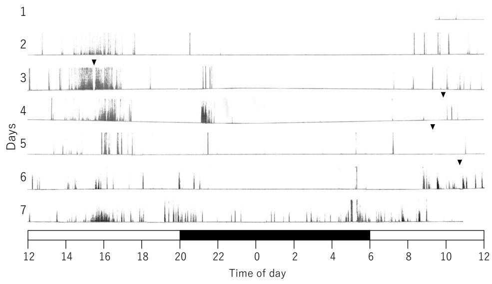
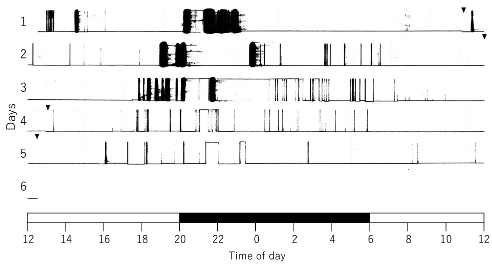


Female *Numenes disparilis*

#1



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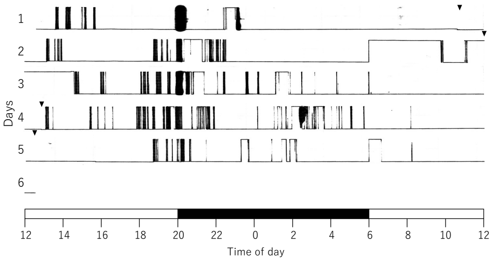

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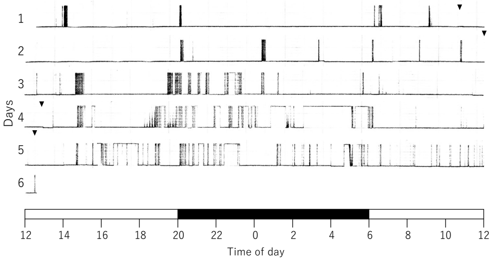

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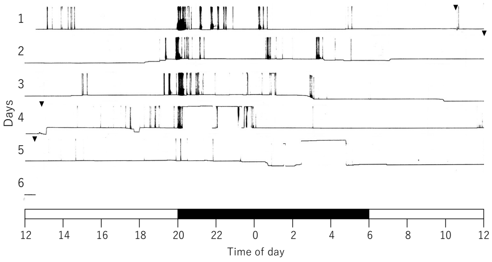

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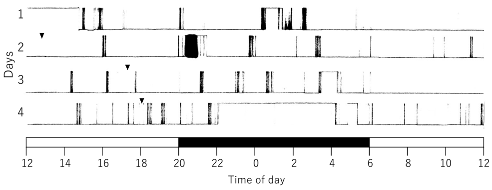

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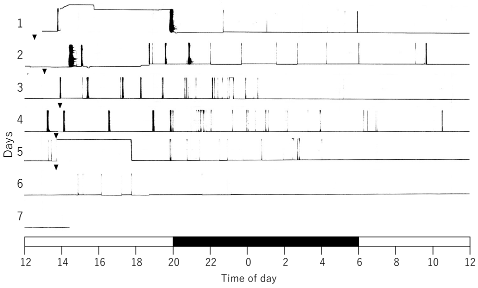

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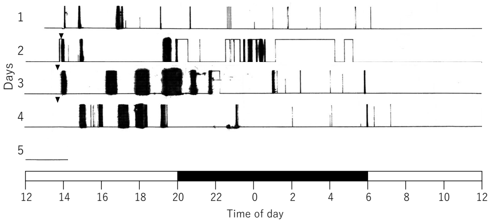

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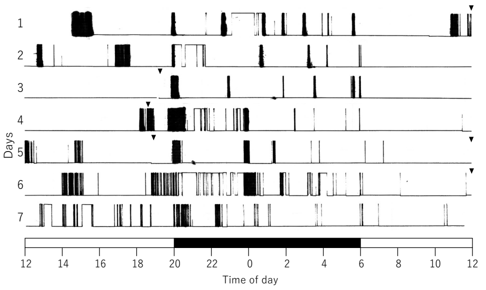

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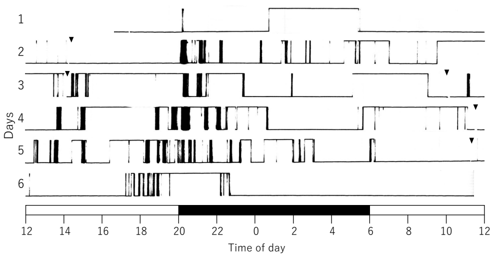

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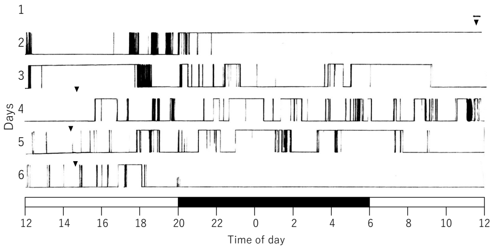

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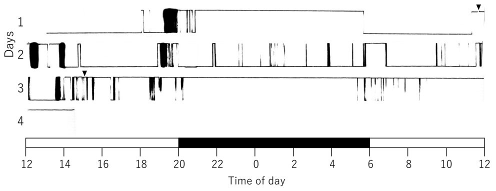

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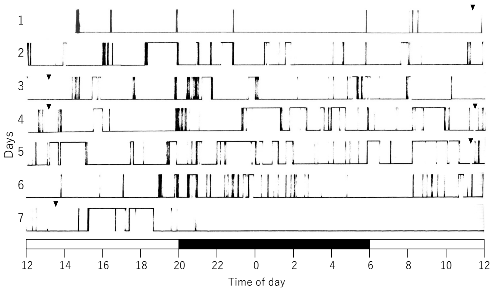

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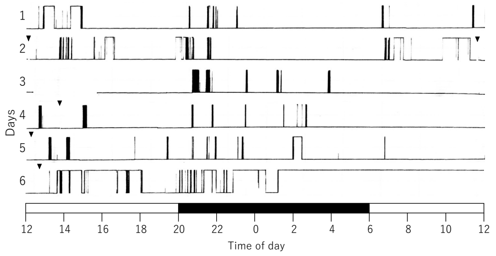
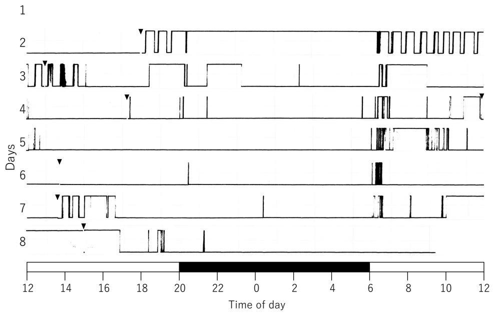


Male *Kuromondokuga niphonis*

#1



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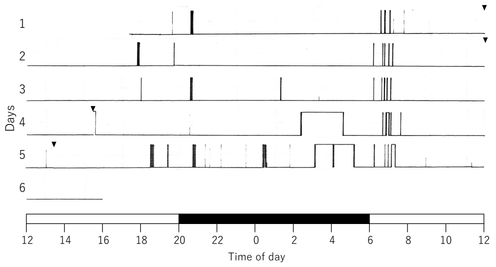

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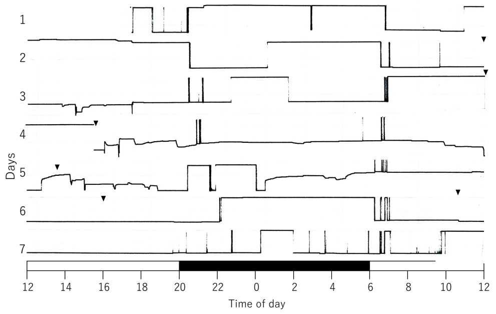

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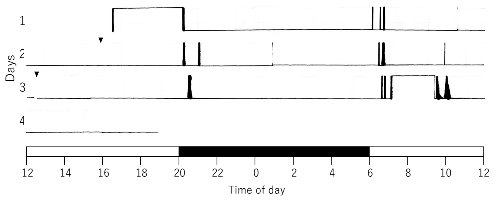

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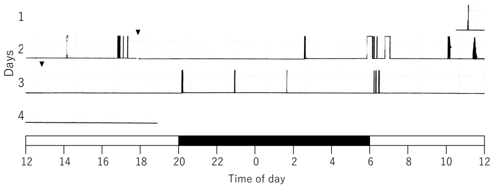

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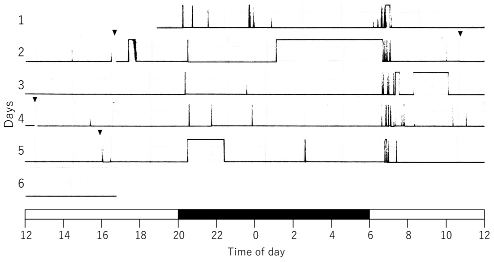
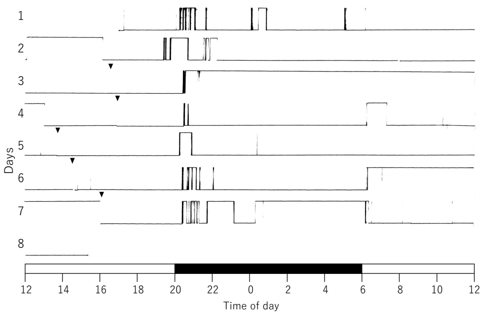


Female *Kuromondokuga niphonis*

#1



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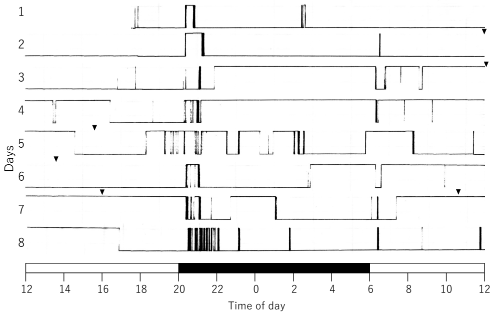

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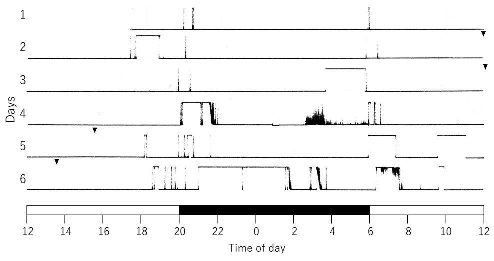

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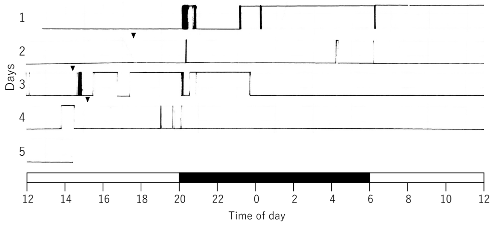

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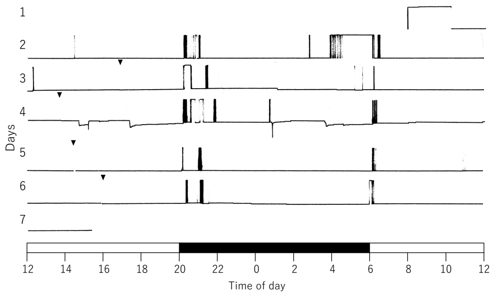

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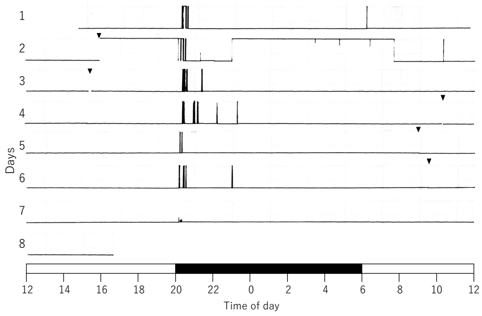

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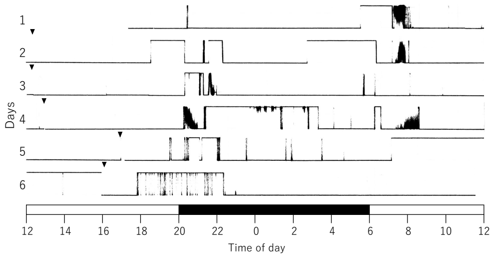

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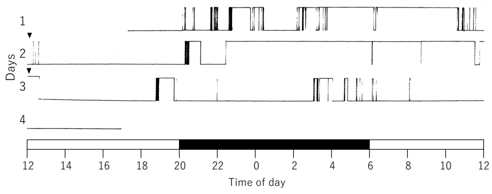

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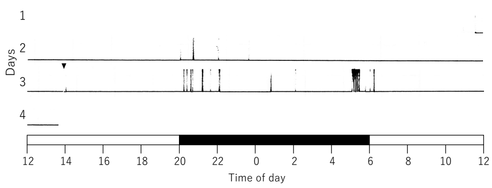
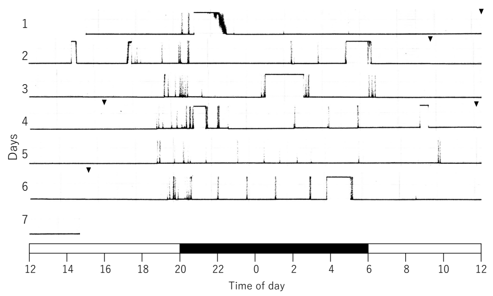


Male *Orgyia thyellina*

#1



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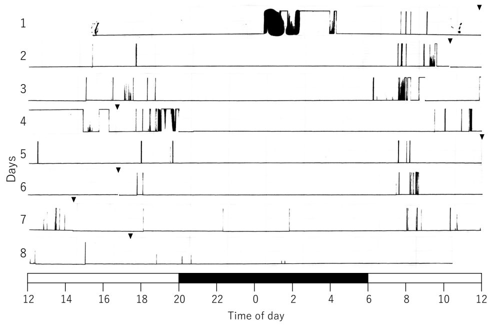

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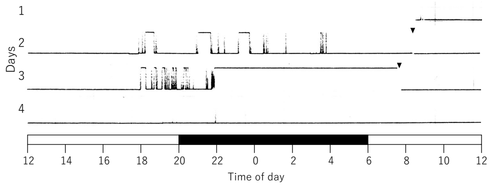

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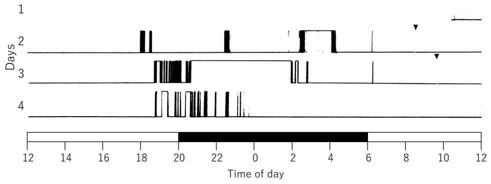

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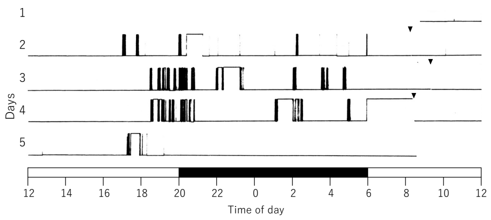

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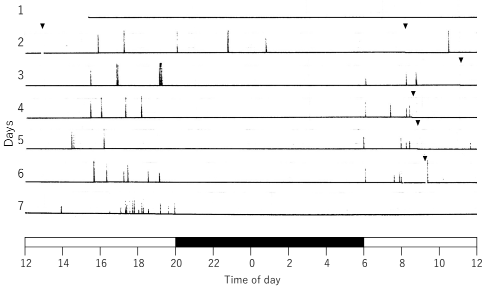

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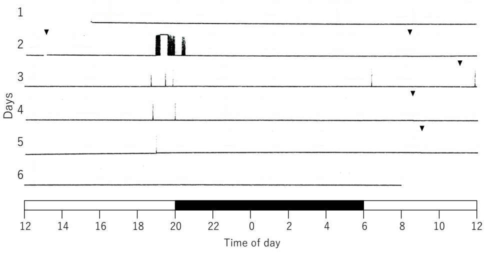

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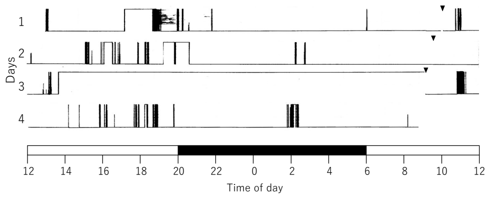

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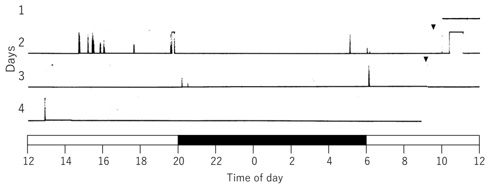
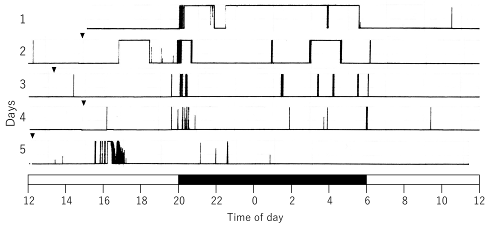


Female *Orgyia thyellina*

#1



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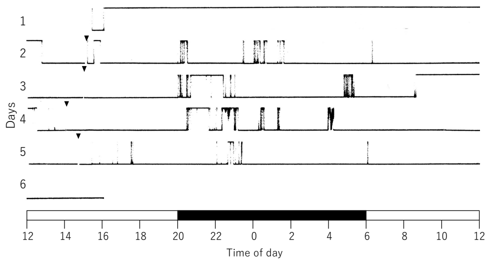

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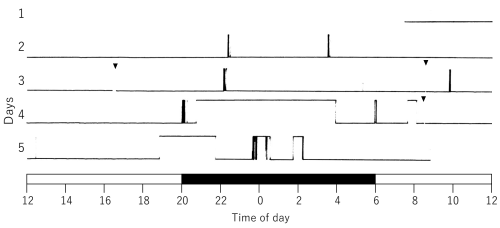

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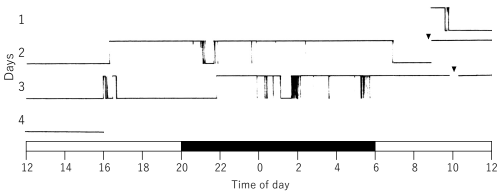

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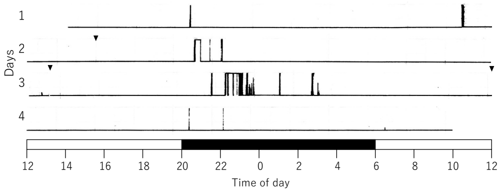

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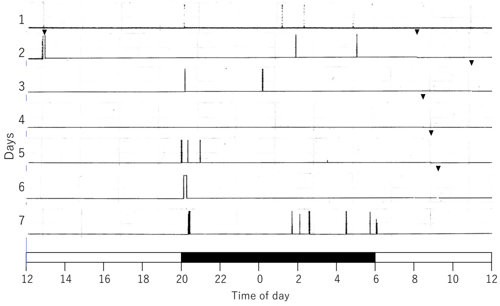
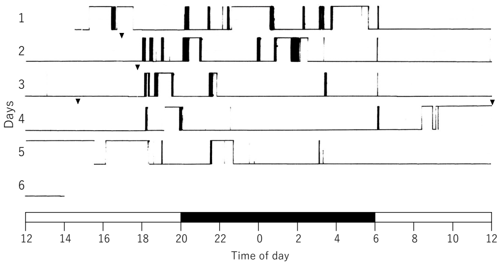


Male *Orgyia triangularis*

#1



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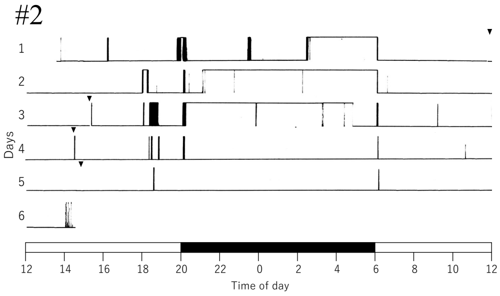

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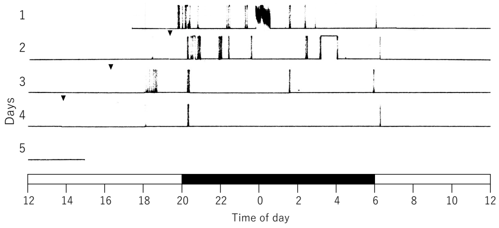

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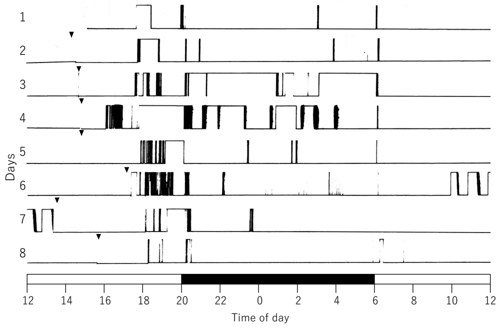

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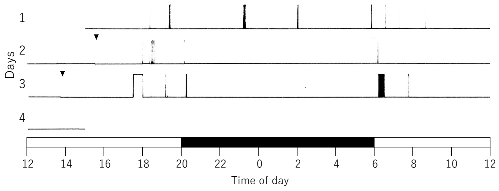

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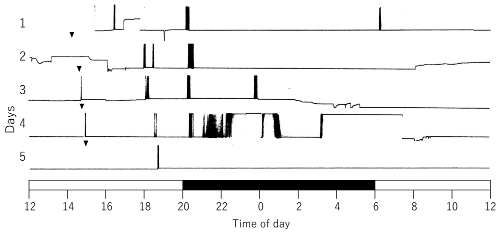

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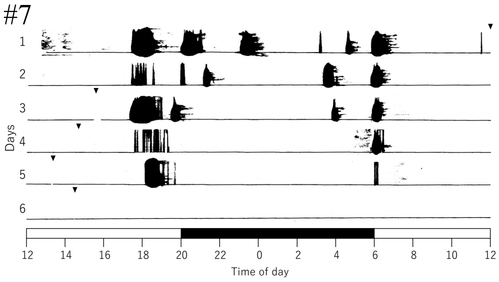

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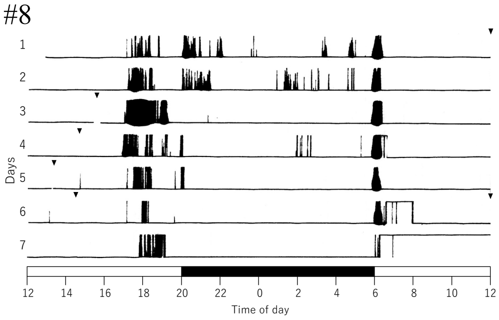

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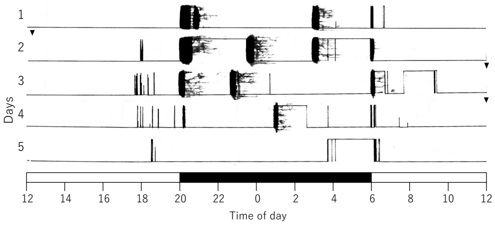
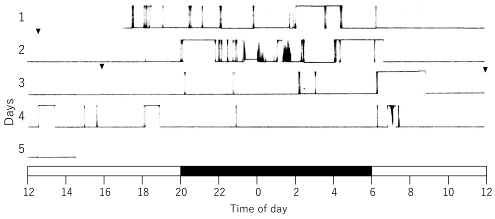
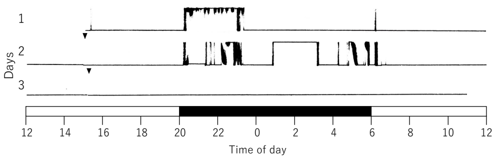


Female *Orgyia triangularis*

#1





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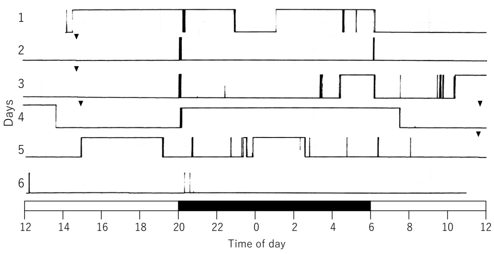

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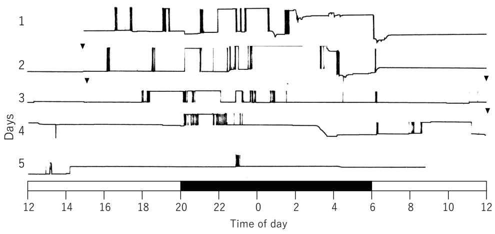

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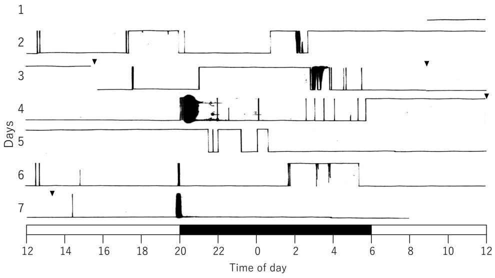

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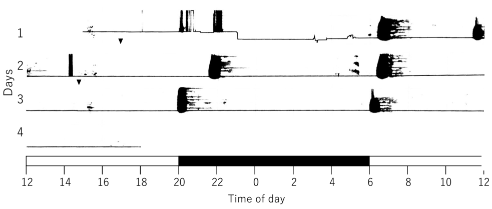

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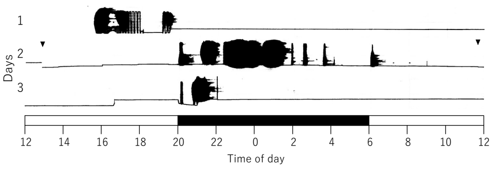
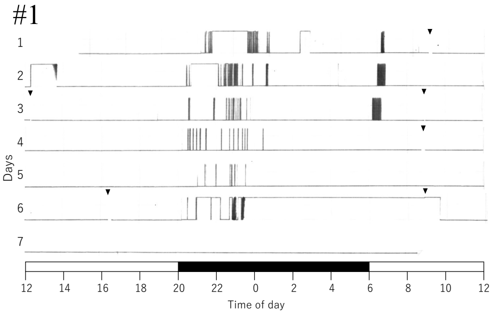
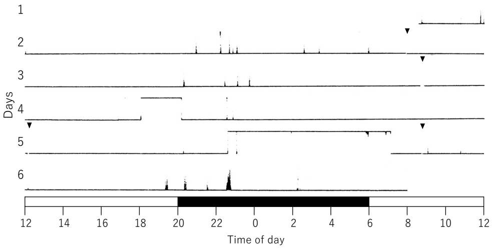


Male *Cifuna locuples*

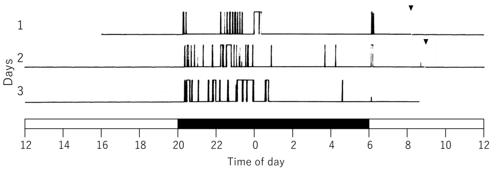
#1



#2



#3



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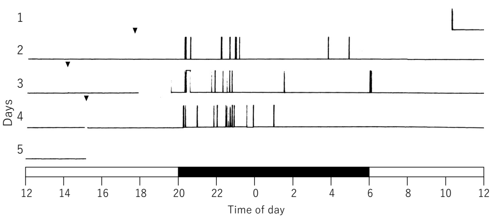
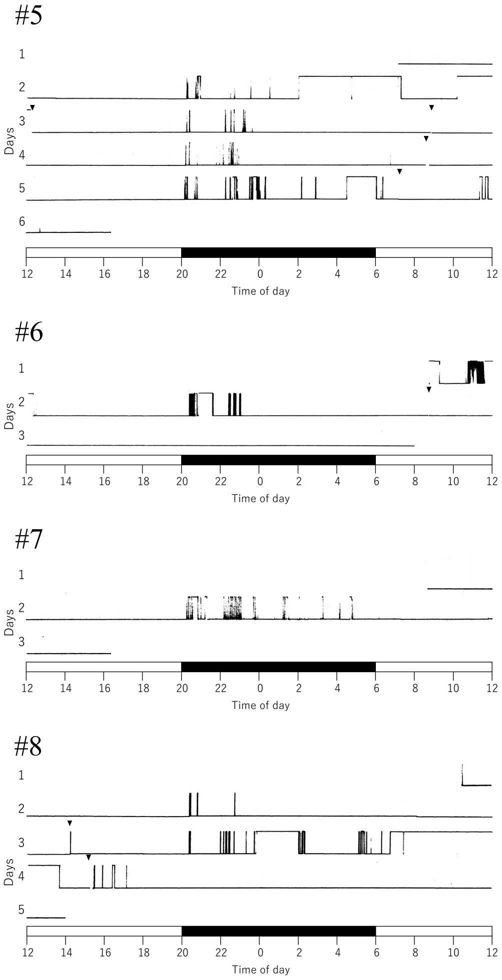
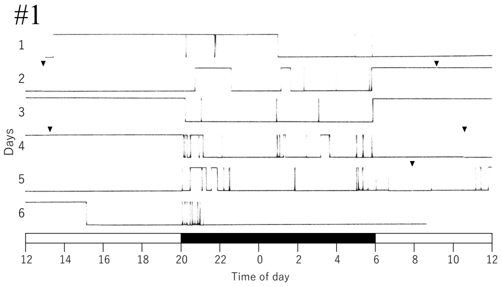




Female *Cifuna locuples*



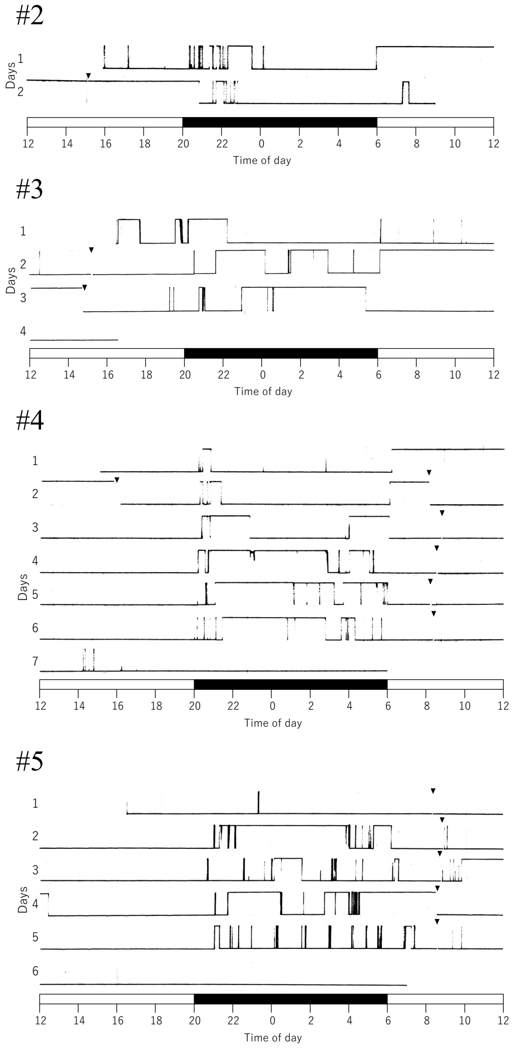
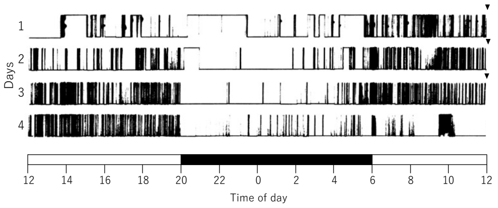


Figure S4-1. Additional actograms to Fig. 2 of 9 male *Numenes albofascia*; 4 female *Numenes albofascia*; 12 Male *Numenes disparilis*; 13 Female *Numenes disparilis*; 6 Male *Kuromondokuga niphonis*; 9 Female *Kuromondokuga niphonis*; 9 Male *Orgyia thyellina*; 6 Female *Orgyia thyellina*; 9 Male *Orgyia triangularis*; 7 Female *Orgyia triangularis*; 8 Male *Cifuna locuples*; 5 Female *Cifuna locuples*. All interceptions of a fine beam through the rearing glass vessel are recorded on a chart sent at 10 mm/h of the pen recorder. The recording condition was at 25±1°C with a 14-h light (6:00-20:00) and 10-h dark (20:00-6:00) cycle. Each arrow head shows the time when water is added to the filter paper on the bottom of the vessel.

Male *Ivela auripes*

#1



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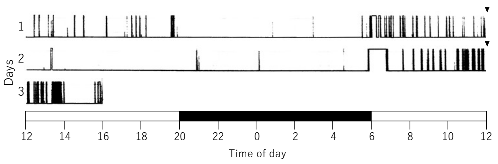

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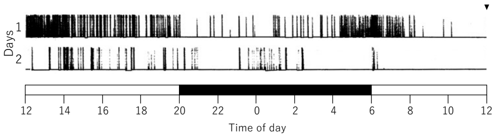

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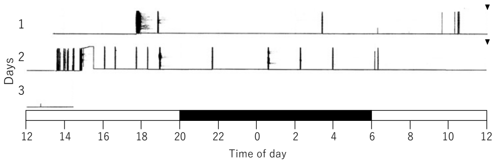

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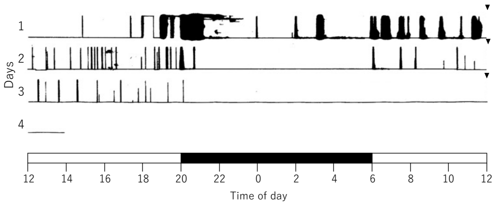

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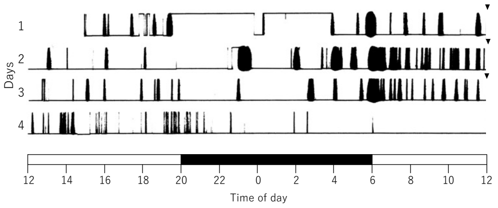

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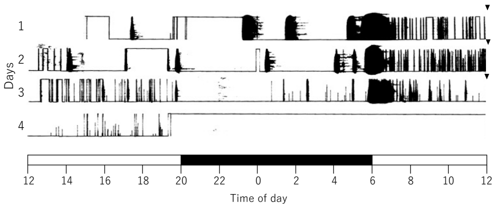

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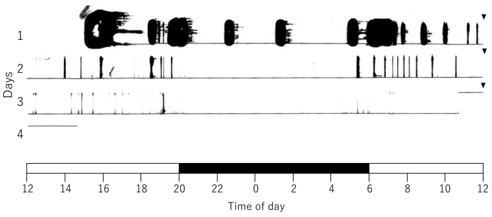
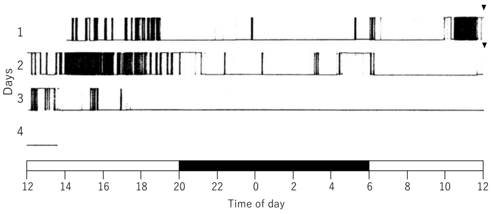


Female *Ivela auripes*

#1



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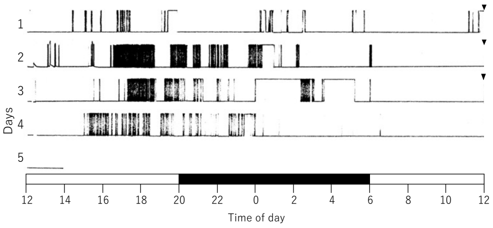

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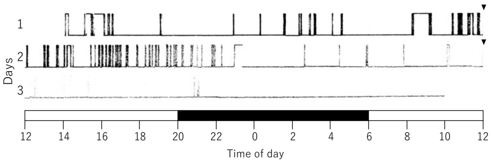
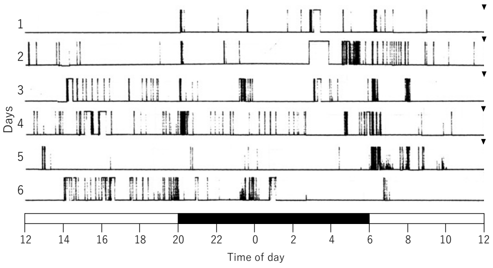


#4



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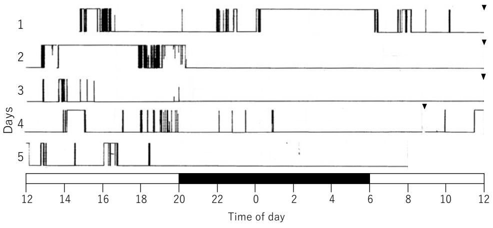
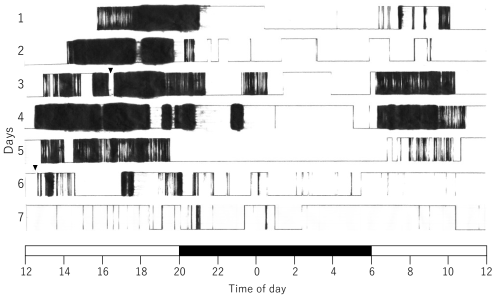


Male *Neochalcosia remota*

#1



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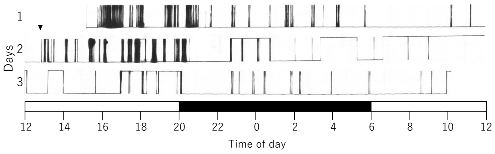

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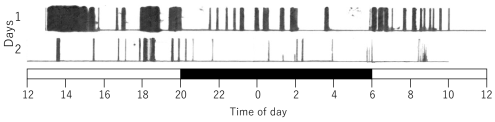

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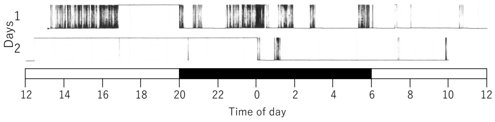
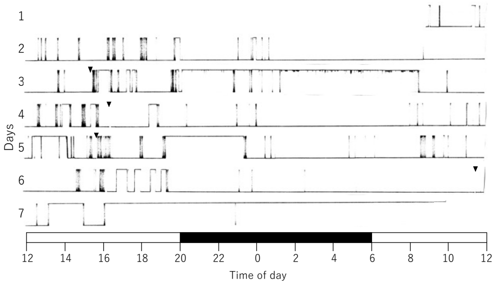
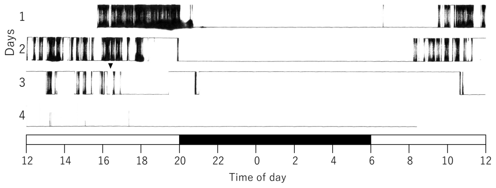


#5

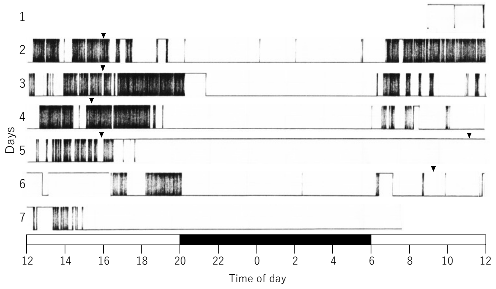


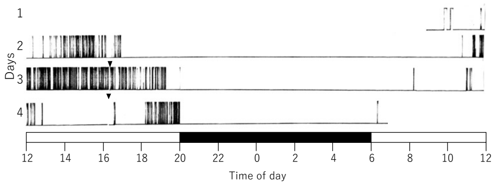
Female *Neochalcosia remota*

#1

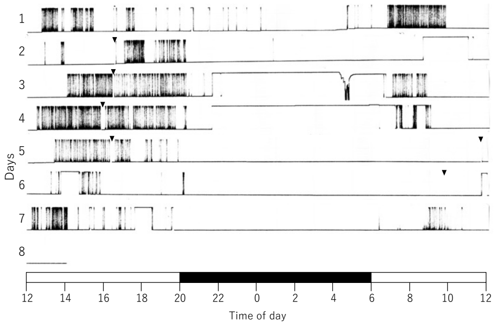


#2





#4



#5

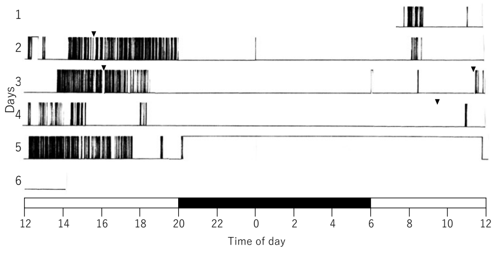


Figure S4-2. Actograms of 8 male *Ivela auripes*; 5 female *Ivela auripes*; 5 male *Neochalcosia remota*; 5 female *Neochalcosia remota*. All interceptions of a fine beam through the rearing glass vessel are recorded on a chart sent at 10 mm/h of the pen recorder. The recording condition was at 25±1°C with a 14-h light (6:00-20:00) and 10-h dark (20:00-6:00) cycle. Each arrow head shows the time when water is added to the filter paper on the bottom of the vessel.

5. General discussion

5-1. Warning color mimicry between different developmental stages

In this study, two mimetic relationships specific to moths are experimentally verified, and the evolutionary process of mimicry is further discussed.

Mimicry at different developmental stages, larvae and pupae, is reported for the first time, not only in Lepidoptera but also in insects as a whole. The rounded form, yellow surface color and black longitudinal stripes are similar not only in the two insects discussed in this study, larva *P. sinica* and pupa *I. auripes*, but also in other insects. For example, the larva of *Elcysma westwoodii* (Zygaenidae) is a toxic example showing similar morphological features (Nishida 1994, Jinbo 2005) and could serve as a model species for mimicry. On the other hand, *Aporia crataegi* (Pieridae) (Shirozu 1965), the *Naxa seriaria* (Geometridae) (Nakamura 2004), *Cystidia stratonice* (Geometridae) (Nakamura 2004) and *Amata germana* (Arctiidae) (Okagaki 1956) are the examples of similar features on their pupae, but their repellent effect on predators has not been confirmed. These larvae and pupae, which are very similar in size and color, appear at about the same time in May and June and have in common the characteristic that they are all seen during the day in highly conspicuous places such as tree tops and man-made walls. This season is just before the young birds leave the nest and is known to be a time when warning color mimicry can be very effective (Mappes *et al*. 2014). It is possible that the Batesian and Müllerian mimicry complex between species belonging to different families of Lepidoptera and at different developmental stages may have been constituted by convergent evolution. In the future, it will be necessary to conduct the same kind of examination of these species as in the present study in order to grasp the overall picture of the 'yellow and black stripe' mimicry complex. The similarity of the spots in the ultraviolet light range, which predators such as lizards and birds can recognize (Chen *et al*. 1984, Chen and Goldsmith 1986, Fleishman *et al*. 1993, Pérez i de Lanuza and Font 2014), should also be verified for this mimetic system, and the similarity from the predator's point of view should be confirmed more carefully.

5-2. Warning color mimicry with sexual dimorphism

In Chapter 3, I experimentally tested a new example of sex-limited dual mimicry, in which males and females of *N. albofascia* form Bates-type mimicry to *P. atratus* and *A. caja* respectively.

Among the four types of sex-limited mimicry (I. Unimodal mimicry, II. Female-limited mimicry, III. Male-limited mimicry, IV. Dual mimicry), unimodal mimicry (type I) and female-limited mimicry (type II) have been well studied (Ruxton *et al.* 2018). In 1865, Alfred Wallace recorded seven examples of female-limited mimicry firstly in diurnal papilionid butterfly in South Asia, besides eight examples of unimodal mimicry in the same group (Wallace 1865). Since then, the female-limited mimicry has been an excellent source of theoretical research, particularly in the cases of diurnal butterflies (Darwin 1871, Fisher 1958, Kotler 1980, Allen 2011, Ruxton *et al.* 2018).

One of the main questions of the debate has been why sex-limited mimicry in diurnal butterflies occurred limitedly to female, in other words, why there were almost only type I and II found (Mallet and Joron 1999, Ohsaki 2005, Kunte 2008). There have been four reasons indicated so far. First, flight abilities of heavy females carrying eggs are restricted and the females are more vulnerable to predation (Wallace 1865, Chai and Srygley 1990, Srygley and Chai 1990, Marden and Chai 1991, Ohsaki 1995, Ohsaki 2005, Kunte 2008, Kunte 2009b). Second, females carrying eggs are more valuable for predators as food resources than males (Wallace 1865, Chai and Srygley 1990, Srygley and Chai 1990, Marden and Chai 1991, Ohsaki 1995, Ohsaki 2005, Kunte 2008, Kunte 2009b). These two explanations emphasize the high predation pressure by predators on females. Third, males with different colors from ancestral (original) traits have disadvantages in combat between males (Silberglied 1984, Lederhouse and Scriber 1996). Finally, males with different color from ancestral (original) traits have disadvantages in mate choice by females (Belt 1874, Turner 1978, Kunte 2009b). The latter two explanations emphasize the selection pressure on males within a species. Recent studies indicated that several models can be supported in the evolution of the sexual dimorphism in color within a single taxon (Oliver and Monteiro 2010), or selection pressures can vary among different species groups (Burns 1998, Ord and Stuart-Fox 2006, Kunte 2008).

However, only a few examples are recorded with insects and spiders so far for male-limited mimicry (type III) and dual mimicry (type IV). Eight cases of male-limited mimicry (Table 5-1), *Coleosoma* spp. (Theridiidae; Reiskind and Levi 1967), *Anatea formicaria* (Theridiidae; Reiskind and Levi 1967), *Mynes katharina* (Nymphalidae; Vane-Wright 1974), *Chrysobothris humilis* (Buprestidae; Hespenheide 1975), *Callosamia promethea* (Saturniidae; Walbauer and Sternburg 1975, Sternburg *et al.* 1977, Jeffords *et al.* 1979, Jeffords *et al.* 1980, Waldbauer and Sternburg 1987), *Callosamia securifera* (Saturniidae; Walbauer and Sternburg 1975), *Mynes anemone*

(Nymphalidae Vane-Wright 1976), syrphid hoverflies (Gilbert 2005), and eight cases of dual mimicry (Table 5-2), *Chirodamus* spp. (Pompilidae; Evans 1968) , *Austrochares* spp. (Pompilidae; Evans 1969), *Mycalesis drusillodes* (Nymphalidae; Vane-Wright 1971, Vane-Wright 1974), *Eristalis arbustorum* (Syrphidae; Heal 1981), *Propetes schmidti* (Cicadellidae; Takiya *et al.* 1999）, *Papilio erostratus* (Papilionidae; Kunte, 2008, Kunte 2009a,), *Elymnias hypermnestra* (Nymphalidae; Wei *et al.* 2017; Panettieri *et al.* 2018; Ruttenberg *et al.* 2021） and *Delias lemoulti* (Pieridae: Morinaka *et al.* 2018) have been reported. Among them, four cases in male-limited mimicry (*M. katharina*, *C. promethea* and *C. securifera, M. anemone*) and four cases in dual mimicry (*M. drusillodes*, *P. erostratus*, *E. hypermnestra*, *D. lemoulti*) were about species of Lepidoptera. However, these studies defined the similarity between suspected model and mimic species by the human visionary identification, and experimental verifications were not conducted except for two cases below. A series of studies by Sternburg, Waldbauer and Jeffords was the only field experimental study of male-limited mimicry (type III). They showed male *C. promethea* and poisonous butterfly *Battus philenor* (Papilionidae) may have a relationship of Batesian mimicry (Walbauer and Sternburg 1975, Sternburg *et al.* 1977, Jeffords *et al.* 1979, Jeffords *et al.* 1980, Waldbauer and Sternburg 1987). Other studies about *E. hypermnestra* revealed that the evolution of dual mimicry (type IV) in this butterfly occurred independently in several areas in South and Southeast Asia, from chemical analyzes of pigment manifestation (Panettieri *et al.* 2018) and of systematic geography (Ruttenberg *et al.* 2021). Still, the function and the evolutionary process of the relationship between warning color mimicry and sexual dimorphism in color in type III and IV remain unclear.

This study is the first experimental investigation of the possibility of dual mimicry (type IV) in terms of morphological and behavioral similarity, using ultraviolet photographs and diurnal activity measurements. On the other hand, learning experiments by predators will be the subject of future work. Because of the small populations of mimic species in the complex, the methods of previous studies such as estimation from population dynamics in the field by long-term capture surveys or observation of predation pressure by beak marks (Benson 1972, Edmunds 1974, Uesugi 2000, Ohsaki 1995, Tsurui-Sato *et al.* 2019) could not be used in this study. To investigate further detailed relationships between species in the mimicry complex, it is necessary to develop a new research method suitable for the complex including memorize experiments of the repellent effect to the predators (Brower 1958, Sexton 1960, Edmonds 1974, Uesugi 1996, Pinheiro 2003, Wüster *et al.* 2004) or examining the similarity of wing color and spot pattern with phylogenic (Yen et al. 2005a) and mathematical analysis (Otaki 2009, Nijhout 2017).

In Chapter 4, I experimentally show that the evolution of sexual dimorphism in color, in which males are dark and females are light, which is common in the moths in Lymantriidae, is due to differences of daily activity rhythm between males and females, which exert visual predation pressure on the males.

Sexual dimorphism of wing color in Lepidoptera has traditionally been studied mainly in diurnal butterflies, as in the study of mimicry, of which there are many examples. Based on the pictures of The Standard of Butterflies in Japan (Shirozu 2006) and The Standard of Moths in Japan (Kishida 2011a, 2011b, Hirowatari *et al*. 2013), my visual count of Japanese lepidopteran species with distinct sexual dimorphism of wing color shows that approximately 28.0% of butterfly species have sexual dimorphism (Table 5-3). All five families of butterflies from Japan have more than 10% of sexual dimorphism in color among them. In contrast, the relatively large sized moth families (Callidulidae, Drepanidae, Epicopeiidae, Uraniidae, Geometridae, Lasiocampidae, Eupterotidae,Bombycidae, Saturniidae, Brahmaeidae, Sphingidae, Notodontidae, Lymantriidae, Arctiidae, Aganaidae, Micronoctuidae, Nolidae, Noctuidae, Hepialidae, Limacodidae, Zygaenidae, Sesiidae, Cossidae) have only 1.1% of sexual dimorphism in wing color (Table 5-1). Only two families, Hepialidae (55.6%) and Lymantriidae (18.9%), have a proportion of sexual dimorphism in color that exceeds 10%. It is also important to note that the evolutionary pathway of sexual dimorphism assumed for butterflies does not apply to sexual dimorphism in Lymantriidae. Well-known reasons for the evolution of sexual dimorphism in butterflies include the development of flamboyant color in the males by sexual selection and the mimicry of toxic species only in the females, which have relatively low flight ability (Ohsaki 1995, Kunte 2008, 2009b, Tsurui-Sato et al. 2019, van der Bijl *et al*. 2020). Sexual dimorphism in Hepialidae has also been suggested to be related to gamete choice, with flamboyant color in males (Turner 1976, Mallet 1984, Andersson 1998, Rydell 1998). In contrast, in Lymantriidae, the males are rather more subdued and there are numerous species in which the females do not appear to mimic anything. Conventional evolutionary models have failed to explain the sexual dimorphism of moth species, which engage in mating via sex pheromones rather than vision and are active at night, and the origin of dual mimicry, particularly the significance of male mimicry, necessitating speculation on a new evolutionary process. In this sense, the evolution of sexual dimorphism driven by high predation pressure on the males in this study is significant because it presents and demonstrates a new evolutionary model of color sexual dimorphism in Lepidoptera.

There are three main points that this study will next target. The first is to ascertain whether this evolutionary model can be applied to moths with black male wing sexual dimorphism outside the family Lymantriidae. *Rhodinia fugax* in Saturniidae or *Dimorphicosmia variegata* in Erebidae are good examples of such moths. The second is the type of sexual dimorphism in which only the male wings are transparent such as *Perina nuda* in Lymanriidae or *Pyrosis idiota* in Lasiocampidae, both of which are expected to be diurnal, as the males are difficult to collect by night light (Kishida 2011c, 2011d). Lepidopteran scales are known to have the ability to absorb bat ultrasound, but it is assumed that this function can degenerate if activity takes place during the day (Neil *et al*. 2020). Therefore, daily activity rhythm differences between males and females may be related to differences in wing morphology, and experimental verification is needed to measure their daily activity rhythm and to confirm whether they are repellent to predators. The third is to construct an evolutionary model in which males and females differ in color while having repellent effects on predators. The model presented by this study assumes predation pressure on males, so if moths have a repellent effect, a further evolutionary model needs to be envisaged. Many species in Arctiidae are thought to contain toxic components in their bodies (Rothchild *et al*. 1979). In the family habiting in Japan, *Lemyra imparilis* and *Lithosia quadra*, are good examples of such a model, and in addition, there are many examples of the family Zygaenidae, known for chemical defense by cyanide (Yen *et al*. 2005b), with a similar sexual dimorphism with dark males and light females, from the southern islands of Japan to South-East Asia (Endo and Kishida 1999), represented by *Milleria formosana*. Experimental verification of the differences in venom strength between males and females will be necessary.

5-3. Exploring further peculiar mimicry in moths.

Chapter 2 of this study examined a peculiar form of mimicry in moths: the possibility of interspecific mimetic relationships at different developmental stages, larvae and pupae. Another example of such a unique mimetic relationship at different developmental stages is the occurrence of intraspecific mimicry in moths, known as a form of automimicry (Lees and Zilli 2019). *Zerenopsis lepida*, African moth of Geometridae, has very similar orange and black color and mottling of larvae and adults within the same species, and the adults share the toxins from the cycad hostplants eaten by the larvae (Staude and Curle 1997, Staude and Sihvonen 2014). Other examples of larval and adult color and mottling being similar within a species, as well as sharing toxic components within the body, are *Abraxas grossulariata* in Geometridae, *Utetheisa ornatrix* and *Utetheisa pulchella* in Arctiidae (Sourakov 2016). At present, this pattern of intraspecific Müllerian mimicry has only been described in a small number of reports and its evolutionary process is not clear. Investigation of further examples and clarification of their evolution will be a future challenge.

Another example of peculiar mimicry in moths is mimicry to the wandering spider, which is often observed in smaller moths. This peculiar case of Batesian mimicry differs from the common warning color mimicry structure described so far, which is to appeal to predators searching for the prey visually with a repellent effect, in that it mimics the predator, the wandering spider itself, a rare example that has rarely been observed in other animals and there has been little experimental verification of this (Zaret 1977, Perrone 1981, Stevens 2005). Rota and Wagner (2006) showed experimentally that a small moth of the genus *Brenthia* with spider-like patterns on their wings actually has a high predation avoidance capacity against jumping spiders, and that the moth can even be visually misidentified as jumping spiders by the jumping spiders themselves. Wang *et al*. (2017) also showed that the mimicry of moths of the genus *Brenthia* is effected by a combination of two factors: the jumping spider-like spots on the wings and their choppy movements. These two studies have greatly advanced our previously unclear understanding of 'predator mimicry' through small moths. Hill *et al*. (2019) and Hill (2022) are reviews that report several insects with these wandering spider-like patterns, but the majority of the examples listed there are small moths. Whether the spider-like pattern on the wings of moths other than *Brenthia* spp. has a mimetic effect has not been tested at all, and further reports of mimetic cases and their experimental verification are needed.

In addition to visual mimicry as a means of defense against visual predators, recent years have seen the discovery of acoustic mimicry by moths. In moth species, many of which are nocturnal, many species have ears that can detect bat echolocation aurally (Regier *et al*. 2013). They can also pronounce against bat echolocation with their click organs or other means to disturb their sonar (Fullard *et al*. 1994, Corcoran *et al*. 2009, Kawahara and Barber 2015) or startle the bats (Bates and Fenton 1990). Beside these, acoustic aposematism is known to exist in the family Arcitiidae to communicate the unpalatability of moths to bats (Hristov and Conner 2004), and even acoustic mimicry is also known. Corcolan and Hristov (2014) indicate an example of acoustic

Batesian mimicry that the palatable moth *Eubaphe unicolor* (Geometridae) pronounce a click sound that is extremely similar to that of the unpalatable arctiid moths that live sympatrically. Barber and Conner (2007) also showed in predation experiments with bats that there is an acoustic Batesian mimicry relationship between the unpalatable moth *Cycnia tenera* (Arctiidae) and the palatable moth *Euchaetes egle* (Arctiidae). In addition, they succeeded in showing experimentally that acoustic Müllerian mimicry also functions between *Cycnia tenera* and the unpalatable *Syntomeida epilais* (Arctiidae). Barber *et al*. (2022), after a decade of research in tropical South America, Africa and Asia, found that many taxa of large-bodied moths, relatively more species with ears, have species that produce anti-bat sounds, and that much of their adaptive significance is acoustic aposematism and acoustic mimicry. The existence of multiple mimicry rings among moth species across these taxa was confirmed, and the authors emphasize its significance as "ultrasonically signaling moths comprise one of the largest mimicry complexes on earth"(Barbar *et al*. 2022). O'Reilly *et al*. (2019) showed that there is an acoustic Müllerian mimicry even among the small-bodied moths, relatively less species with ears. Moths in the genus *Yponomeutina,* which are unpalatable for predators but do not have ears, pronounce click sounds which are quite similar to that of arctiid moths. The mimicry of lepidopterans has been studied mainly in relation to diurnal butterflies and visual predators, but the mimicry between nocturnal moths and nocturnal predators such as bats that capture prey acoustically has only just begun and is expected to make great progress in the future.

For the major ecological theme of 'mimicry', which has been building up since Darwin, studying the peculiar case of the new material of moths opens up the possibility of examining it from a completely new angle, which could be beneficial for a deeper exploration of the phenomenon of mimicry.

Table 5-1. List of male-limited mimicry cases reported so far

Species	Family	Order	Model of male	Mimic pattern of male	Evaluation of mimicry	References
Coleosoma spp.	Theridiidae	Araneae	"Ants"	Batesian	Human vision	1
Anatea formicaria	Theridiidae	Araneae	*Chelaner croceiventre* (Formicidae)	Batesian	Human vision	1
Mynes katharina	Nymphalidae	Lepidoptera	*Tellervo* spp. (Nymphalidae), *Symbrenthia hippalus* (Nymphalidae)	Unknown	Human vision	2
Chrysobothris humilis	Buprestidae	Coleoptera	*Clytrinae* spp. (Chrysomelidae)	Batesian	Human vision	3
Callosamia promethea	Saturniidae	Lepidoptera	*Battus philenor* (Papilionidae)	Batesian	Predation experiments	4, 5, 6, 7, 8
Callosamia securifera	Saturniidae	Lepidoptera	*Battus philenor* (Papilionidae)	Batesian	Human vision	4
Mynes anemone	Nymphalidae	Lepidoptera	*Tellervo* spp. (Nymphalidae)	Unknown	Human vision	9
Syrphidae spp.	Syrphidae	Diptera	"Bumblebees" (Apidae)	Batesian	Human vision	10

1. Reiskind and Levi 1967, 2. Vane-Wright 1974, 3. Hespenheide 1975, 4. Walbauer and Sternburg 1975, 5. Sternburg *et al*. 1977, 6. Jeffords *et al*. 1979, 7. Jeffords *et al.* 1980, 8. Waldbauer and Sternburg 1987, 9. Vane-Wright 1976, 10. Gilbert 2005

Table 5-2 List of dual mimicry cases reported so far

Species	Family	Order	Model of male	Mimic pattern of male	Model of female	Mimic pattern of female	Evaluation of mimicry	References
Chirodamus spp.	Pompilidae	Hymenoptera	*Mischocyttarus alfkenii* (Vespidae) and related species	Batesian	*Apoica thoracica* (Vespidae) and related species	Müllerian	Human vision	1
Austrochares spp.	Pompilidae	Hymenoptera	*Polybia parvula* (Vespidae) and related species	Batesian	*Dicranoplius satanus* (Pompilidae) and related species	Müllerian	Human vision	2
Mycalesis drusillodes	Nymphalidae	Lepidoptera	*Tellervo* spp. (Nymphalidae) and related species	Batesian	*Taenaris* spp. (Nymphalidae) and related species	Batesian	Human vision	3, 4
Eristalis arbustotum	Syrphidae	Diptera	"Wasps an other yellow and black Hymenoptera"	Batesian	"Small dark bees (mainly mining bees)"	Batesian	Human vision	5
Propetes schmidti	Cicadellidae	Heteroptera	*Polvbia rejecta* (Vespidae) and other paper wasps	Batesian	*Myschocyttarus ypiranguensis* (Vespidae) and other paper wasps	Batesian	Human vision	6
Papilio erostratus	Papilionidae	Lepidoptera	*Battus polydamas* (Papilionidae)	Batesian	*Parides photinus* (Papilionidae)	Batesian	No description	7, 8
Elymnias hypermnestra	Nymphalidae	Lepidoptera	*Euploea* spp. (Nymphalidae)	Batesian	*Danaus* spp. (Nymphalidae)	Batesian	Human vision	9, 10, 11
Delias lemoulti	Pieridae	Lepidoptera	*Delias splendeida* (Pieridae), *Delias eileenae* (Pieridae)	Müllerian	*Delias timorensis* (Pieridae)	Müllerian	Human vision	12

1. Evans 1968, 2. Evans 1969, 3. Vane-Wright 1971, 4. Vane-Wright 1974, 5. Heal 1981, 6. Takiya *et al*. 1999, 7. Kunte 2008, 8. Kunte 2009, 9. Wei *et al*. 2017, 10. Panettieri *et al*. 2018, 11. Ruttenberg *et al*. 2021, 12. Morinaka *et al*. 2018

Table 5-3. Visual counts of the frequency of color extremes and sexual dimorphism in large Japanese Lepidoptera. Subjects covered were (a) All species of Japanese butteries, (b) Species from the relatively large sized moth families (Callidulidae, Drepanidae, Epicopeiidae, Uraniidae, Geometridae, Lasiocampidae, Eupterotidae, Bombycidae, Saturniidae, Brahmaeidae, Sphingidae, Notodontidae, Lymantriidae, Arctiidae, Aganaidae, Micronoctuidae, Nolidae, Noctuidae, Hepialidae, Limacodidae, Zygaenidae, Sesiidae, Cossidae).

(a) Butterflies

Family	Species with markable sexual dimorphism in color	Number of species in the family	ratio (%)
Papilionidae	3	24	12.5
Pieridae	19	29	65.5
Lycaenidae	40	80	50.0
Nymphalidae	11	105	10.5
Hesperidae	4	37	10.8
Summary	77	275	28.0

Table 5-3. Continued.

(b) Moths

Family	Species with markable sexual dimorphism in color	Number of species in the family	ratio (%)
Callidulidae	0	2	0.0
Drepanidae	0	71	0.0
Epicopeiidae	0	3	0.0
Uraniidae	0	25	0.0
Geometridae	4	866	0.5
Lasiocampidae	1	25	4.0
Eupterotidae	0	1	0.0
Bombycidae	0	7	0.0
Saturniidae	1	13	7.7
Brahmaeidae	0	1	0.0
Sphingidae	0	76	0.0
Notodontidae	0	122	0.0
Lymantriidae	10	53	18.9
Arctiidae	4	116	3.4
Aganaidae	0	6	0.0
Micronoctuidae	0	6	0.0
Nolidae	0	110	0.0
Noctuidae	3	1242	0.2
Hepialidae	5	9	55.6
Limacodidae	1	38	2.6
Zygaenidae	1	29	3.4
Sesiidae	1	43	2.3
Cossidae	0	7	0.0
Summary	31	2871	1.1

6. Acknowledgments

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8. Appendices

8-1. Publications

Yazaki, H., Kishimura, M., Tsubuki, M. and Hayashi, F. (2019) Müllerian mimicry between cohabiting final-instar larval *Pryeria sinica* Moore, 1877 (Lepidoptera: Zygaenidae) and pupal *Ivela auripes* (Butler, 1877) (Lepidoptera: Lymantriidae). Pan-Pacific Entomologist, 95: 83-91.

8-2. Title and summary in Japanese

学位論文要旨（博士（理学））

蛾類における特異な警告色擬態：
異なる発育段階での擬態および雌雄で異なるモデルへの擬態（英文）

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　視覚で餌を探す鳥類や爬虫類などの捕食者から身を守るため、有毒な昆虫などが目立つ色彩（警告色）を発達させることがある。この警告色を介した擬態には、ベイツ型擬態（無毒種が有毒種に似る）とミュラー型擬態（有毒種どうしが似る）の２つが存在する。鱗翅目における警告色擬態の研究は、これまで昼行性の蝶類を対象として盛んに行われてきた。本研究では、一般的に夜行性と考えられている蛾類において、系統の異なる種の幼虫と蛹の間に警告色擬態が生じている例と、同種の雌雄間でそれぞれ別のモデル種に擬態している例を見いだし、それらの擬態の成立要因および進化過程についての実証的研究を行なった。

　まず、発育段階の異なる間での警告色擬態として、ミノウスバ（マダラガ科）の幼虫とキアシドクガ（ドクガ科）の蛹の関係を調べた。これらの幼虫と蛹は、同所的、同季節に見られ、体型は楕円状、黄緑色の体表に黒すじ模様が目立つ。両者とも昼間に地上の目立つ場所で見られ、捕食者に対する露出性が高い。ニホンカナヘビによる捕食実験および野外でのシジュウカラの捕食行動の観察において、どちらも捕食者に対して忌避性を示した。これらは、系統的に離れた種の異なる発育段階間でのミュラー型擬態の初めての発見例と考えられる。

次に、雌雄で異なるモデルへの擬態の可能性について、翅色彩の顕著な性的二型を示すシロオビドクガ（ドクガ科）の成虫の形態比較と行動調査を行った。そのオスはホタルガ（マダラガ科）に、メスはヒトリガ（ヒトリガ科）に、それぞれ体の大きさおよび色彩が酷似する。それぞれの組み合わせの分布と成虫の出現時期も重複している。一方、ホタルガは昼行性、ヒトリガは夜行性であるが、シロオビドクガのオスは早朝（薄明時）に飛翔し、メスは夜行性であった。ヒガシニホントカゲを用いた捕食実験では、シロオビドクガは全て捕食され、モデル種は全て忌避されたため、雌雄で異なるモデルへの擬態は、どちらもベイツ型擬態とみなされた。これは雌雄別モデル擬態という極めて稀な擬態についての初めての検証となる。さらに、雌雄で日周活動が変化し、その結果としてそれぞれのモデル種への擬態が起こるという進化の前適応と考えられる段階を見いだすことができた。ドクガ科では、オスの翅が暗色、メスの翅が明色となる色彩に性的二型を示す種が存在する。そこで、オスの翅が暗色の種と暗色でない（性的二型がない）種の活動の日周性を比較した結果、オスの翅が暗色の種ではオスのみが薄明薄暮あるいは日中に飛翔し、その時間帯にメスがコーリングを行って（フェロモンを放出して）交配することが明らかとなった。ヒガシニホントカゲを用いた捕食実験では、全種がトカゲに捕食された。また、野外に蛾を吊るして捕食率をみると、薄明下（鳥類の捕食活動が高くなる）では暗色のオスの方が捕食されにくく、オスの暗色の翅は薄暗い環境で隠蔽効果を発揮することが確認された。上述のシロオビドクガの雌雄別モデル擬態では、祖先種の雌雄の日周活動がずれ、薄明薄暮下で目立たないオスの色彩（暗色）がまず起こり、このオスの翅の暗色化が前適応となって、次に、昼行性の有毒種のモデル（暗色な翅に目立つ模様をもつ）との間に擬態が起こるのではないかと推測された。