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ORIGINAL RESEARCH PAPER

Effects of artificial light on the arrival time, duration of stay, and departure time of nocturnal flying insects

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Abstract
Insects with positive phototaxis fly to artificial light sources at night, stay there for a certain amount of time, and then fly away. Although many studies have been conducted on the arrival time of flying insects at artificial light sources, little is known about the time at which they fly away (departure time), duration of stay, and staying time zone. This information is important to protect phototactic insects from the fatal attraction to light that is known as a serious ecological light pollution. In this study, we aimed to identify the duration of stay and staying time zone for various insect species by marking them with light traps. Among the 63 species belonging to 11 orders observed at the study site, cluster analysis focused on 27 species for which 5 or more data points were obtained, highlighting three predominant stay patterns. Type 1 species arrived approximately 1.3 h and flew away approximately 4.1 h after sunset and stayed for a short period of approximately 2.6 h. Type 2 species arrived at approximately 1.2 h and flew away for approximately 9.6 h, with an 8.4 h stay. Type 3 species arrived later than Types 1 and 2, were attracted for 5.4 h, and flew away approximately 13.5 h with an 8.2 h stay. These results suggest that conservation biological countermeasures against light-attracted flying insects need to consider the stay patterns of insects that remain under outdoor lighting.

Keywords Ecological light pollution · ALAN · Light attraction · Duration of stay · Nocturnal flying insect

Introduction

Many nocturnal insect species exhibit positive phototactic behavior in response to light (Menzel 1979; Williams 1936, 1939). Therefore, many insect species and individuals fly to and remain near artificial light sources at night. The time of insects arriving at artificial light sources has been studied in several groups (Trichoptera: Wright et al. 2013, Hemiptera: Endo 2019; Diptera: Mitchell 1982; Standfast 1965, Lepidoptera: Nowinszky et al. 2007; Williams 1939). In these studies, researchers have attempted to determine the timing of attraction by counting the number of captures per fixed period using light traps. Arrival times are found to vary across species. Lamarre et al. (2015) studied the arrival times of moths from the families Sphingidae and Saturniidae in light traps in French Guiana. They found that Sphingidae species peaked between 19:00 and 20:00, whereas Saturniidae species arrived later at midnight. This indicated a significant difference in arrival times between the two families.

However, the departure time of an insect from an artificial light source has rarely been examined and existing reports are limited. Janzen (1984) observed light trapping in a Costa Rican rainforest. He noted that Sphingidae and Saturniidae moths were stationary near the light source and were unlikely to leave, whereas Sphingidae departed earlier. Hashizume and Hironaka (2019) counted the number of rice grasshoppers *Oxya japonica* (Thunberg) (Orthoptera: Acrididae) flying to the lights of convenience stores every 2 hours. Rice grasshoppers *O. japonica* flew towards the window between 19:00 and 20:00 after sunset, and several individuals began to depart between 6:00 and 8:00 the following morning. The previous studies showed differences in the arrival times of species to artificial lights strongly predict that there are differences in departure times among insect species. If so, the duration of stay across species may also vary and some individuals may continue to stay for longer periods. Moreover, possibly, a temporal variation in staying time zone in artificial light sources at night occurs

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across insect species. However, limited research has been conducted on the duration and staying time zone of insect species under artificial light.

Anthropogenic modification of the light environment, specifically increased artificial light at night (ALAN), has been suggested as a driver of influencing the rapid decline in insects worldwide (Boyes et al. 2021; Grubisic et al. 2018; Owens et al. 2020). Insects that exhibit positive phototaxis are observed to be attracted to artificial light sources and remain exposed for long periods. This may result in various adverse effects (Eisenbeis 2006; Frank 2006; Owens et al. 2020). To effectively implement ecological light pollution countermeasures, examining the duration and staying-time zone of insect species in artificial light after arrival is necessary. The present study aimed to determine the duration of stay and time zone for each nocturnal flying insect by tracking individuals and investigating the arrival and departure times of various taxa of nocturnal flying insects drawn to light traps in the field.

Materials and methods

We individually tracked insects flying into light traps at Ishikawa Prefectural University Farm. The farm is located in Nonoichi City (36°31'N, 136°36'E), Ishikawa Prefecture, Japan. It is surrounded by rice paddies because it is situated on a plain with active grain production. The hilly terrain extended approximately 3 km east of the farm. Observational surveys were conducted from May to August 2020. Survey data were collected once in May, six times in June, five times in July, and once in August, comprising a total of 13 surveys (Online Resource 1).

The light traps were created as follows. A white cloth (Kanayasu Co., Ltd., No. OX3847-2) was attached to a 2.5 m × 2.5 m metal pipe frame placed vertically as an attracting screen. A metal halide lamp (Iwasaki Electric Co., Ltd., MF400LSH/U) attached to a lamp cover (Iwasaki Electric Co., Ltd., H373S) was used as the artificial light source. The metal halide lamp was fixed at a height of 1.3 m using a scaffold stand to illuminate the center of the attracting screen which was set 5 m away. The light traps were placed on asphalt in an open area of the farm so that the axis connecting the attracting screen and light source was parallel to the north–south axis. In addition to the front and back surfaces of the attracting screen, an area of 5 m in the north and south directions and 1 m in the east and west directions from the attracting screen were set as the observation areas (Online Resource 2).

Observational surveys were conducted before sunset on the first day of each survey up until 10:00 a.m. JST on the following day. The target species were selected based on the following criteria: the expectation of obtaining data from a diverse of taxa; at least 5 mm in body length for marking; and were frequently observed in the preliminary surveys. To minimize bias from the influence of survey date and season, only three individuals of the same species were tracked in a single survey. The metal halide lamps were turned on the day immediately before sunset. When an insect flew into the observation area, the time of arrival was recorded. To identify each individual, the thorax or abdomen was subsequently marked using a water-based pen (Mitsubishi Pencil Co. Ltd., PC-5M8C). Marking was carried out with precision and care, without capturing individuals. Efforts were made to minimize the impact by marking as small an area as possible. No behavioral effects due to marking were observed. We visually checked the observation area every 30 min to determine whether marked individuals remained. If an individual could not be seen within the observation area, the time it left was recorded as its departure time. If an individual reappeared after being recorded as having moved away, it was identified as returned, and the time of reappearance was recorded. The marked insects were photographed using a digital camera. Additional individuals, presumed to belong to the same species, were collected on the same day, subsequently frozen, and identified at the species level using morphological characteristics whenever possible at a later date. To record environmental conditions, we measured the weather conditions, temperature (°C), humidity (%), and wind speed (m/s) every 30 min from sunset at locations unaffected by the metal halide lamp (Online Resource 1). The metal halide lamps were turned off at 8:00 a.m. JST on the next morning and the survey ended at 10:00 a.m. JST. Any insects that remained in the observation area were recorded as non-flying individuals. The departure time of insects that had not yet flown away was recorded at 10:00 a.m. JST for the calculation of the mean duration of stay.

To compensate for seasonal changes in night length, the arrival and departure times were calculated as the time that had elapsed since sunset. We calculated the duration of stay from arrival to departure for each individual observed. For individuals that returned, the times of their first arrival and last departure were used. The duration of stay was calculated by excluding the time between departure and return.

Statistical analysis

Hierarchical cluster analysis was performed on the 27 species of which five or more individuals were observed during the survey. Four variables were used, which are the mean time of arrival and departure from sunset, duration of stay, and percentage of non-flying individuals using Ward's method and Euclidean distance and each variable was standardized. The NbClust package (Charrad et al. 2014) was used to determine the optimal number of clusters. Four variables were tabulated for each cluster to identify the characteristics of stay. Kruskal–Wallis test was used to compare the four variables across clusters, and when significant differences were found, multiple comparisons were made using the Steel–Dwass test.

All the analyses were performed in R (version 4.2.2; R Core Team 2020). The hclust function from the Stata package was used for the hierarchical cluster analysis, and the kruskal.test function from the coin package was used for the Kruskal–Wallis test.

Results

The arrival, departure (Fig. 1), and duration of stay (Fig. 2) of flying insects attracted to light traps differed considerably among the species. An average of 28.6 individuals per night were tracked during 13 surveys, comprising 372 individuals from 63 species in 11 orders (Online Resource 3, Online Resource 4). For 4 out of the 63 species (Chrysopini sp., Elateridae sp., Trichoptera sp., and Icheumonidae sp.), specimens were not collected, and the identification was based on photographs only. Therefore, the species could not be conclusively identified. Most individuals were attracted after sunset, stayed for a certain period, and departed by 10:00 a.m. JST until the end of the observation period. Eleven individuals moved away from the observation area and returned after more than 30 min. This accounted for 3% of the total number of observed individuals (Online Resource 3). Forty-eight individuals did not fly away, accounting for 12% of the total number of individuals recorded (Online Resource 3). The behavior of individuals during their stay in artificial light sources varied according to species. The mole cricket *Gryllotalpa orientalis* Burmeister (Orthoptera: Gryllotalpidae), the assassin bug *Sirthenea flavipes* (Stål) (Hemiptera: Reduviidae), and the small hydrophilid *Hydrochara affinis* (Sharp) (Coleoptera: Hydrophilidae) actively fly and walk around artificial light sources and were attracted to the screens upon arrival. However, after a specific duration, they left the observation area by walking. Several mole crickets *G. orientalis* and the small hydrophilia *H. affinis* were observed hiding in cracks in the asphalt or shallow holes dug into the ground around the observation area after leaving. In many cases, brown marmorated stink bugs *Halyomorpha halys* (Stål) (Hemiptera: Pentatomidae), and other species in the family Pentatomidae of hemipterans were observed to move by walking to the top of the screen, attempted to fly, before landing on the screen again throughout their stay. Meanwhile, many individuals from Coleoptera and Lepidoptera species flew or walked around the artificial light source for 10–30 min after arrival but spent most of the time thereafter stationary on the screen or on the ground. The arrival and departure did not exhibit a distinct pattern at the order level for all 63 species, including those with limited data. In contrast, 27 species with 5 or more individuals exhibited discernible patterns at the family level. The family of the Carabidae (Coleoptera) arrived shortly after sunset and departed 1–2 h later. Hydrophilidae (Coleoptera) also arrived just after sunset and left 5–6 h later. Pentatomidae (Hemiptera) and Scarabaeidae (Coleoptera) arrived shortly after sunset and left approximately 10 h later around sunrise time. Notably, Sphingidae (Lepidoptera), unlike other families, arrived 5–6 h after sunset and departed after sunrise.

A cluster analysis was conducted for 27 of the 63 species observed, where data were available for at least five individuals (Online Resource 3). The optimal number of clusters was three as shown using cluster analysis with Ward's method (Fig. 3). Clusters 1–3 were designated as Types 1–3 in the order of the shortest time between sunset and departure. Type 1 comprises nine species, including the nemobiine crickets *Pteronemobius ohmacii* (Shiraki) (Orthoptera: Trigonidiidae), the assassin bug *S. flavipes*, the refuse beetle *Anisodactylus signatus* (Panzer) (Coleoptera: Carabidae), a carabid beetle *Anoplogenius cyanescens* (Hope) (Coleoptera: Carabidae), the small hydrophilid *H. affinis*, the Hydrophiloid beetles *Berosus punctipennis* Harold (Coleoptera: Hydrophilidae), Asian multicolored lady beetle *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), and the rice crane fly *Tipula aino* Alexander (Diptera: Tipulidae). They arrived approximately 1.3 h and departed approximately 4.1 h after sunset, with an average duration of stay of 2.6 h (Fig. 4a and b). These species are relatively short-lived in nature. Type 2 comprises 13 species, including fruit-piercing stink bugs *Glaucias subpunctatus* Walker (Hemiptera: Pentatomidae), brown marmorated stink bugs *H. halys*, and other Pentatomidae, and Scarabaeidae such as the green chafer *Anomala albopilosa* (Hope) (Coleoptera: Scarabaeidae) and other insects. Those classified as this type had an average arrival time of approximately 1.2 h and a departure time of approximately 9.6 h after sunset (Fig. 4a and b). The mean length of stay was 8.4 h and were identified as twilight-flying species. With five species representing the lepidopteran family Sphingidae, such as the zelkora horn worm *Callambulyx tatarinovii gabyae* Bryk and the vine hawk moth *Theretra oldenlandiae* (Fabricius), insects classified as Type 3 tended to arrive later than those in Types 1 and 2, with an average arrival time of approximately 5.4 h after sunset (Fig. 4a). They departed approximately 13.5 h after sunset (Fig. 4a). The proportion of individuals that did not fly away tended to be higher in Type 3 than those of the other two types (Fig. 4c). This type was a post-dawn flyer, with an average duration of stay of 8.2 h (Fig. 4b). The mean arrival time from sunset was significantly different between Type 3 and the other two types (Fig. 4a; Steel–Dwass test, Type 1 vs. Type 3, $t = 3.04$, $P < 0.001$; Type 2 vs. Type 3, $t = 10.1$, $P < 0.001$). The mean departure time from sunset differed between the types, with significant differences among all types (Fig. 4a; Steel–Dwass test, Type 1 vs. Type

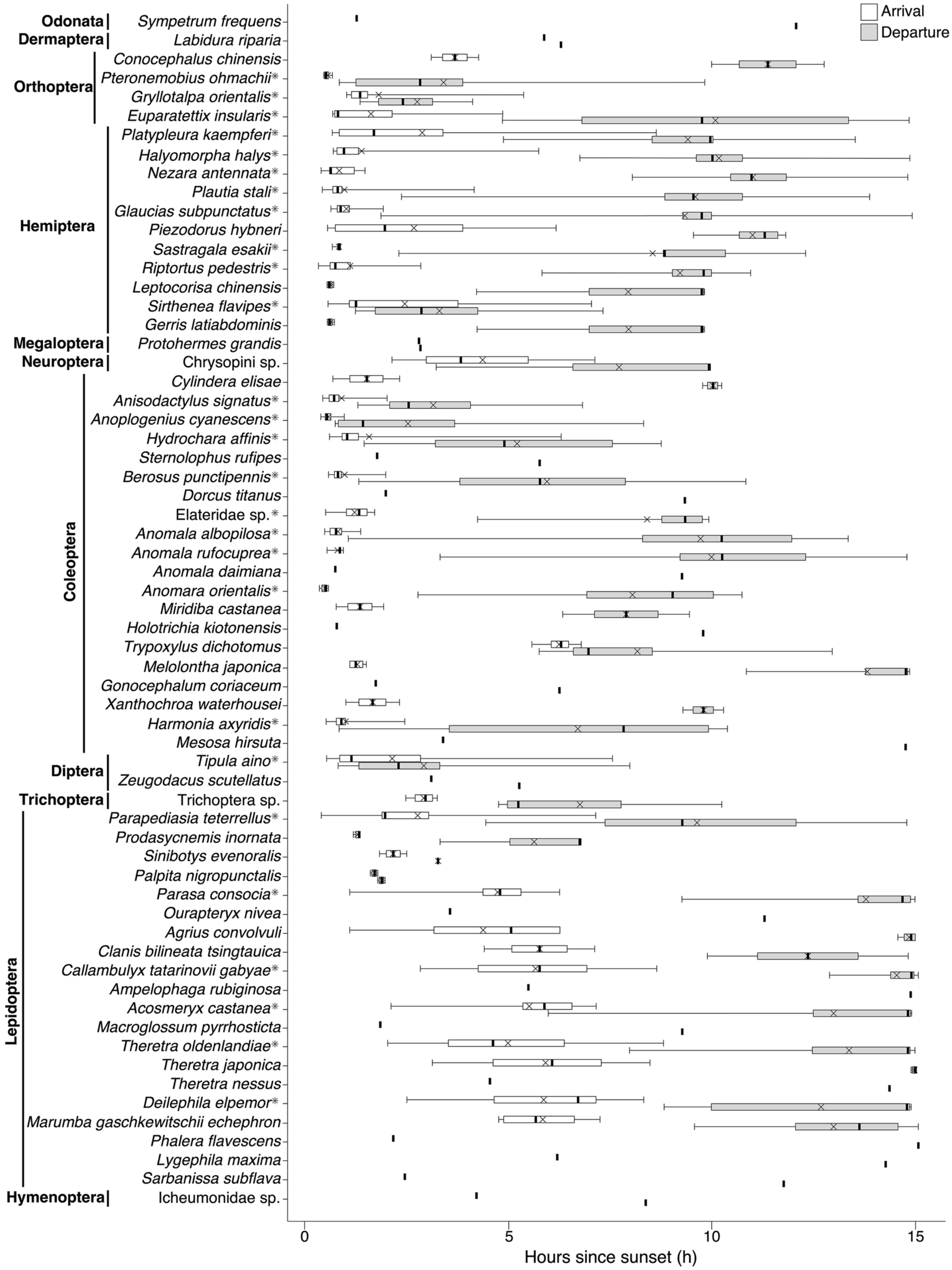

Fig. 1 Arrival and departure times for 63 insect species for the light trap. Arrival and departure times are expressed as the time elapsed from sunset time on the survey day. The left, center (bold), and right lines in each box indicate the first, second (median), and third quartiles, respectively. Crosses in the boxes indicate mean values. The left and right ends of the whiskers indicate minimum and maximum values. Species for which only one individual was observed do not have a box and their data are indicated by a single bold line. Species name marked with an asterisk indicate that they were used in a cluster analysis

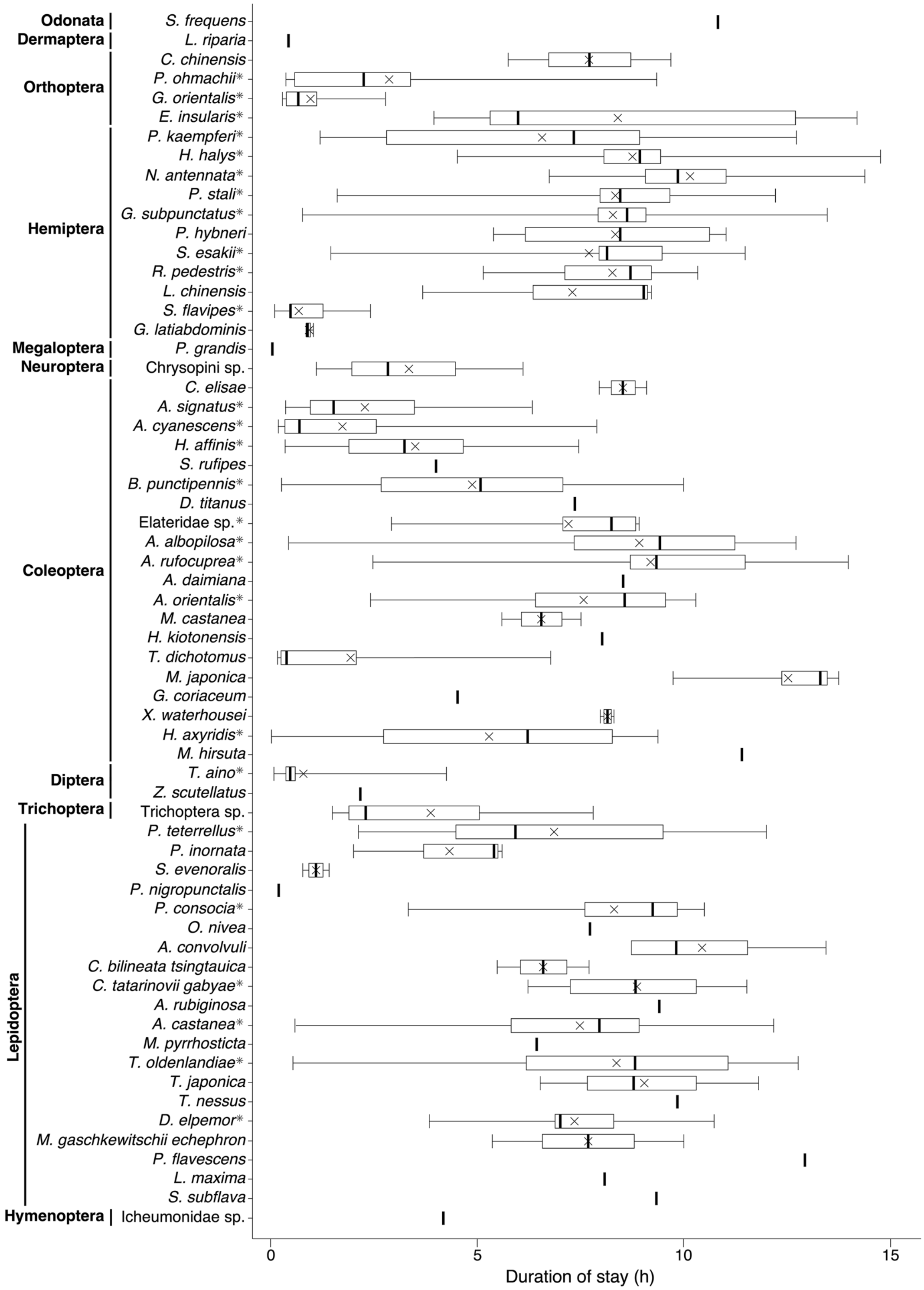

Fig. 2 Duration of stay around the light trap for 63 insect species. The duration of stay was calculated from the time of arrival and departure. The left, center (bold), and right lines in each box indicate the first, second (median), and third quartiles, respectively. Crosses in the boxes indicate the mean values. The left and right ends of the whiskers indicate the minimum and maximum values. Species for which only one individual was observed do not have a box and their data are indicated by a single bold line. Species name marked with an asterisk indicate that they were used in a cluster analysis

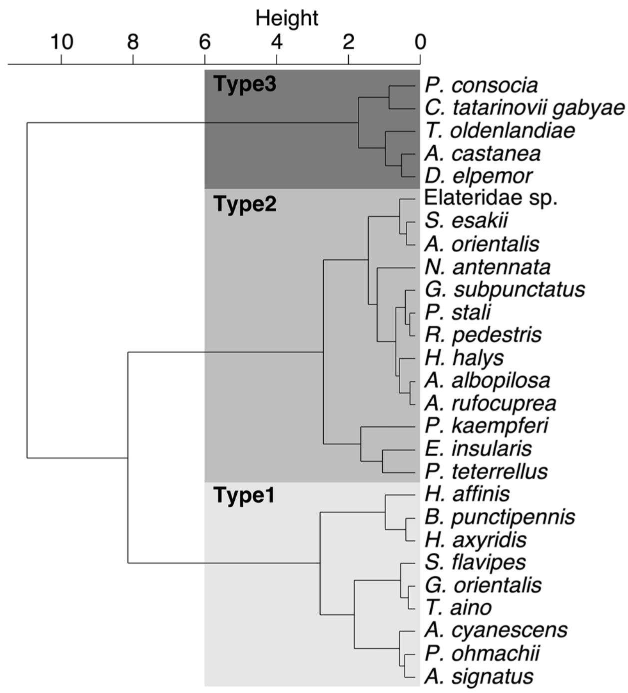

Fig. 3 Stay pattern of 27 insect species by cluster analysis. The average time from sunset to arrival and departure, the average duration of stay, and the percentage of individuals that did not fly away were used to perform a Ward's method cluster analysis. Three clusters were determined to be appropriate using the Nbclust package. The three clusters were designated Type 1 to Type 3 in descending order of mean elapsed time from sunset to departure, that is, the earlier the departure time. The height on the x-axis indicates similarities in the absolute values of the Euclidean distance among the variables

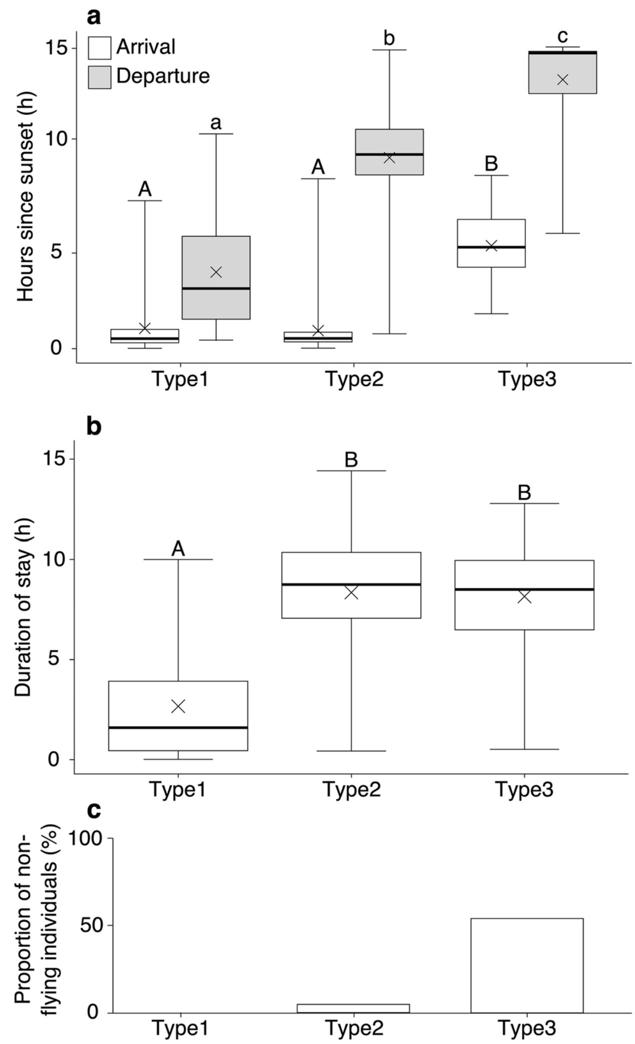

Fig. 4 The arrival and departure times (**a**), duration of stay (**b**), and percentages of individuals that did not fly away (**c**) for each type. Comparison of each of the four factors for each of the three types classified by cluster analysis showed significant differences among the types. In **a** and **b**, the top, middle, and bottom lines in each box indicate the third, second (median), and first quartiles, respectively. Crosses in the boxes indicate the mean values. The top and bottom edges of the whiskers indicate the maximum and minimum values. Differences in the letters at the top of the whiskers (A, B, C, and **a**, **b**, **c**) indicate significant differences based on the Steel–Dwass test ($P < 0.001$)

2, $t = 10.8$, $P < 0.001$; Type 1 vs. Type 3, $t = 9.89$, $P < 0.001$; Type 2 vs. Type 3, $t = 7.70$, $P < 0.001$). Significant differences in the duration of stay between Type 1 and the other two types were observed (Fig. 4b; Steel–Dwass test, Type 1 vs. Type 2, $t = 10.9$, $P < 0.001$; Type 1 vs. Type 3, $t = 8.26$, $P < 0.001$).

Discussion

In this study, we identified three types of stay patterns for nocturnal flying insects around the light traps based on the cluster analysis results from 27 species. Type 1 species arrived after sunset, stayed for a few minutes to a few hours, and departed before twilight. Type 2 species arrived at dusk, remained until twilight, and departed around sunrise. Type 3 species arrived later than the other types, approximately midnight, and departed in the morning after sunrise. The remaining 36 species, for which fewer than five individuals were observed in this study, tended to belong to one of the three types. In the present survey, observation of individuals concluded at 10:00 a.m. JST on the morning following the survey day, and approximately 53% of all individuals classified as Type 3 did not depart until 10:00 a.m. JST. Thus, Type 3 species may include at least two subtypes, one that does not depart before 10 a.m. JST but is expected to fly away in the morning or afternoon, and another that does not depart until the next night. Therefore, the insect taxa examined could be subdivided further into several types. Not only the number of types, but also the stay pattern of each type are not definitive. For example, phototactic behavior of insects is greatly influenced by environmental factors (e.g., light intensity, spectral composition, polarization, exposure time of light, weather, and season) and physiological factors (e.g., sex, age, mating status, and adaptation to darkness) (Kim et al. 2019). The stay patterns of insect under artificial light sources may vary depending on various factors, as well as their phototactic behavior. More observations are needed on the stay patterns of many species under a variety of conditions.

Our results lead to the question of what are the biological factors that lead to three types of stay patterns. Although multiple types occurred within the same order, such as Orthoptera, Hemiptera, Coleoptera, and Lepidoptera, multiple types were not observed in the same family. The results of the cluster analysis of the 27 species do not fully explain stay patterns-based solely on phylogenetic factors. In addition to phylogenetic factors, the results could be attributed to the fact that differences in activity time under natural conditions shape the stay patterns. However, this explanation does not align with the findings of previous studies. For example, the subspecies *A. albopilosa sakishimana* Nomura of the green chafer *A. albopilosa* only feeds from dusk to dawn under natural light conditions in laboratory experiments (Arakaki et al. 2004). Soybean beetles *A. rufocuprea* (Motschulsky) are more active in their feeding behavior at night than during the day (Setokuchi et al. 1984). These two species, which are known to increase nocturnal activity, were stationary under artificial light sources in our observations. No related behaviors, such as feeding or host-seeking behavior, were observed. Similarly, the vine hawk moth *T. oldenlandiae*, which has been reported to visit flowers at night (Miyake and Yahara 1998) and is thought to be nocturnally active under natural conditions, remained predominantly stationary in our observations.

Specific behaviors reported under artificial light may explain the types of stay patterns. Eisenbeis (2006) named the “fixation or captivity effect” as the inability of insects to escape from the vicinity of a lamp and exhibit a variety of behaviors. These include endless circling around the lamp, leaving the lamp to find shelter from a darker place, or resting on the ground or plants. In the present study, all of these behaviors were observed and other different behavioral tendencies were also recorded depending on the type of stay. Type 1 insects were observed to hide behind objects, whereas Type 3 insects were observed to rest on a cloth or the ground for a long time under light illumination. Based on these observations, the three stay patterns may be associated to behaviors reported as fixation or captivity effects. Further investigations on behaviors during the stay are necessary to understand the mechanisms that generate multiple types.

The negative impacts of ALAN on insects have been focused on “fatal attraction” (Owens and Lewis 2020; Rodríguez et al. 2014), and several studies have been conducted (Altermatt and Ebert 2016; Kaunath and Eccard 2022). Fatal attraction refers to the negative effects resulting from positive phototactic behavior, which entails being attracted to an artificial light source. Moreover, the negative effects caused by staying after attraction are considered (Owens and Lewis 2020). These effects are diverse and include increased predation risk (Collins and Watson 1983; Yoon et al. 2010), roadkill encounters (Hessel 1976; Ohba and Takagi 2005), trauma from collisions (Eisenbeis 2006; Hausmann 1992), accelerated desiccation (Hausmann 1992; Ohba and Takagi 2005), and suppression of feeding behavior (van Langevelde et al. 2017), mating behavior (van Geffen et al. 2015), oviposition behavior (Sambaraju and Phillips 2008), flight behavior (Yoon et al. 2012), locomotion, cleaning and searching activities (Shi et al. 2017), and dispersal (Degen et al. 2016). Circadian rhythm resets and drowning are also of concern (Frank 2006). This study identified an average duration of stay of over 6.4 h for the 63 observed species. Type 2 species, which accounted for 39% of the total, had an average stay time of 8.4 h, indicating that the average individual spent approximately 89% of their total time between sunset and sunrise under artificial light. This strongly suggests that insects staying under artificial light at night, which represents ecological light pollution, have a substantial adverse impact. To address these effects, further research and conservation management are required to mitigate their consequences effectively. In the future, understanding the behavioral mechanisms of duration of stay and departure of insects from artificial light will offer crucial insights for resolving the issue of insects lingering under artificial light.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s13355-024-00864-x.

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Author contributions MK and MH conceived the idea, designed the study, performed the experiments, analyzed the data, and wrote and reviewed the manuscript.

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Data availability The datasets are available from the corresponding author on reasonable request.

Declarations

Conflict of interest No potential conflict of interest was reported by the authors.

Ethical approval Not applicable.

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