



Parasitism by multiple strepsipterans accelerates timing of adult parasite emergence

Yuta Nakase¹  | Yuichiro Fukumasu² | Tsubasa Toji³  | Natsumi Ishimoto¹ | Takao Itino^{1,4}

¹Faculty of Science, Shinshu University, Nagano, Japan

²Graduate School of Education, Joetsu University of Education, Joetsu, Japan

³Graduate School of Science, The University of Tokyo, Tokyo, Japan

⁴Department of Biology and Institute of Mountain Science, Shinshu University, Nagano, Japan

Correspondence

Yuta Nakase

Email: yuta.nakase@gmail.com

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Strepsiptera is an order of parasitic insects that exhibit extreme sexual dimorphism: Adult males are free-living, winged insects that spend their lives seeking females to fertilize (Pohl & Beutel, 2005), whereas females are neotenic and completely endoparasitic within their hosts (except for basal parasitoid groups). The female releases free-living first instar larvae via a brood canal opening in the cephalothorax, which then seek a host of their own to parasitize (Kathirithamby, 2018). In Corioxenidae strepsipterans, the first instar larvae parasitize heteropteran nymphs (Kirkpatrick, 1937; Nakase & Kato, 2011). At maturity strepsipteran males and females extrude their cephalothoraxes outside the host body (Figure 1a,b). In *Blissoxenos esakii* (Strepsiptera: Corioxenidae), superparasitism (multiple parasites in a host) is often observed (Miyamoto & Kifune, 1984; Nakase & Kato, 2011), but the space where *B. esakii* can extrude its cephalothorax (the “exit” space) is limited to the membranous area between the dorsal thorax and abdomen of the host *Macropes obnubilus* (Heteroptera: Blissidae) (Figure 1a,b). Because the exit space is limited, at most two *B. esakii* can extrude their cephalothoraxes. Thus, any additional *B. esakii* larvae inside the host body

cannot extrude and eventually die (Nakase & Kato, 2011). *M. obnubilus* is univoltine; nymphs of the new generation emerge in August, and by September most of the previous generation are dead. About half of the new generation become adults in September, but growth varies among individuals, and from September to early summer of the following year the population consists of a mixture of nymphs and adults. First instar larvae of *B. esakii* parasitize *M. obnubilus* nymphs, but they begin to grow inside the body only after *M. obnubilus* has become an adult (Nakase & Kato, 2011). Adult male *B. esakii* typically emerge in May and copulate with female adults, which release first instar larvae in August to parasitize the new generation of *M. obnubilus*.

However, some *B. esakii* reach maturity earlier, in September–December, and the females among them release first instar larvae at that time (November–December). These early-emerging *B. esakii* occur almost exclusively in superparasitized hosts, i.e., those harboring two or more parasites (Figure 2). *Blissoxenos esakii* adults in singly parasitized hosts (i.e., solitary *B. esakii*) occurred only in June–August, that is, a year after the first instar larva parasitized the host (slow emergence).

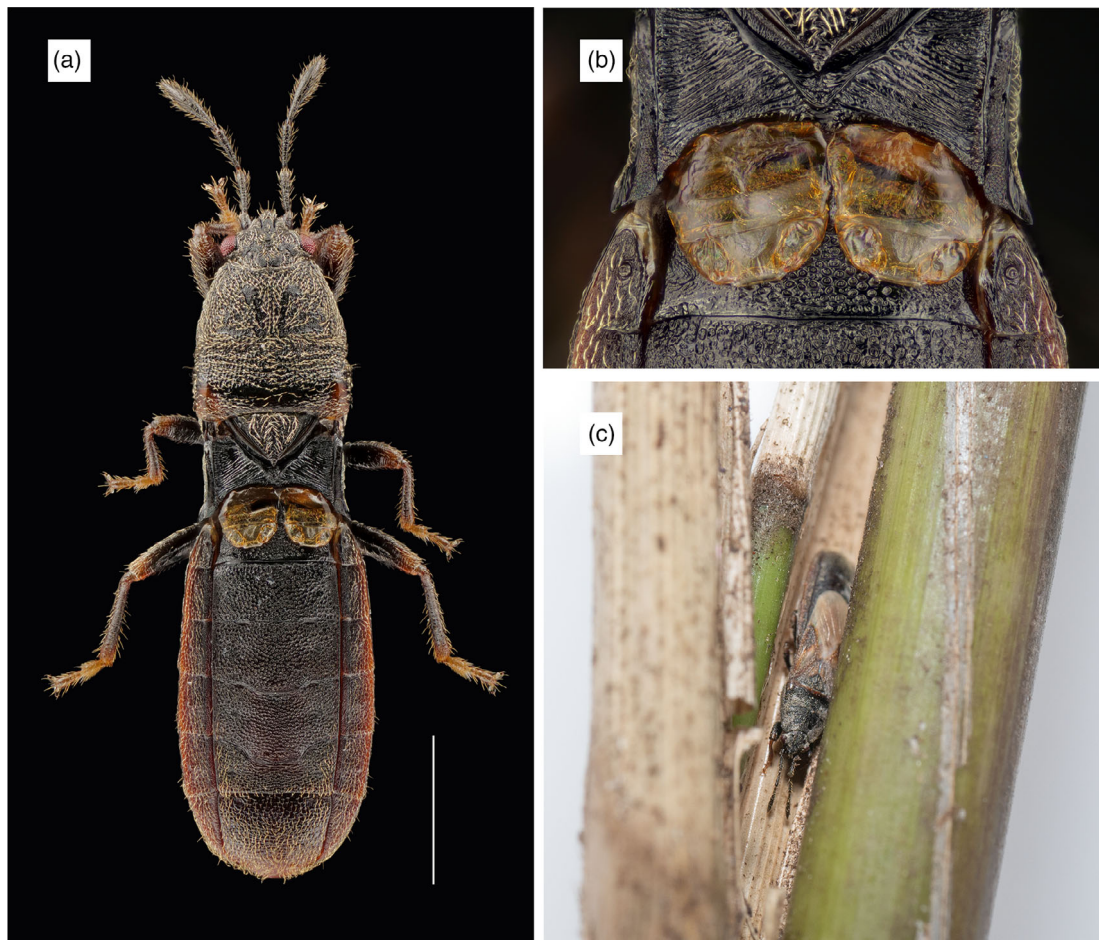


FIGURE 1 Strepsipteran parasite *Blissoxenos esakii* and host bug *Macropes obnubilus*. (a, b) Two male *B. esakii* extrude the cephalothoraxes of their puparia from the membranous area between the thorax and abdomen of *M. obnubilus* (wings removed). Bar = 1 mm. (c) *M. obnubilus* under leaf sheath of dwarf bamboo.

These observations suggest that in superparasitism *B. esakii* individuals grow faster than in solitary parasitism. Superparasitism creates conditions wherein *B. esakii* must compete with one another for access to the limited exit space provided by the host's morphology. As a result, selection might have favored parasites that respond to the presence of conspecifics by shortening the period of larval growth, as this would allow them to complete their life cycle (emergence for males, release of larvae for females) in winter. Thus, superparasitism causes a dramatic change in the life history of this strepsipteran parasite, representing density-dependent phenological plasticity.

In general, superparasitism is the most significant example of density-dependent intraspecific competition among insect parasitoids (Speirs et al., 1991). In insect-parasitic insects, superparasitism often reduces the reproductive efficiency of both the parasite and its host through effects on their survival rate, body size, weight, and growth period (e.g., Potting et al., 1997). Therefore,

to avoid superparasitism, inherently solitary parasitic insects use a variety of strategies, such as avoidance of already parasitized hosts (Harvey et al., 2013). For strepsipteran larvae, which are short-lived and poorly mobile and have no way to exclude other individuals from the same host, avoidance of superparasitism is difficult. Frequent superparasitism was documented in strepsipterans over 100 years ago (Wheeler, 1910). However, when multiple strepsipterans parasitize the same host, the parasites are negatively affected by a decrease in host survival and size (Linsley & MacSwain, 1957; Maeta, 1963).

To examine whether *B. esakii* in superparasitized hosts in fact grow faster than solitary *B. esakii*, we collected *M. obnubilus*, the host of *B. esakii*, in Yamanashi Prefecture, Honshu, Japan, from June to December 2019 and recorded the seasonal occurrence patterns of both *B. esakii* and its host *M. obnubilus* (Appendix S1: Section S1). From June to August, *M. obnubilus* adults consisted mostly of individuals of the previous

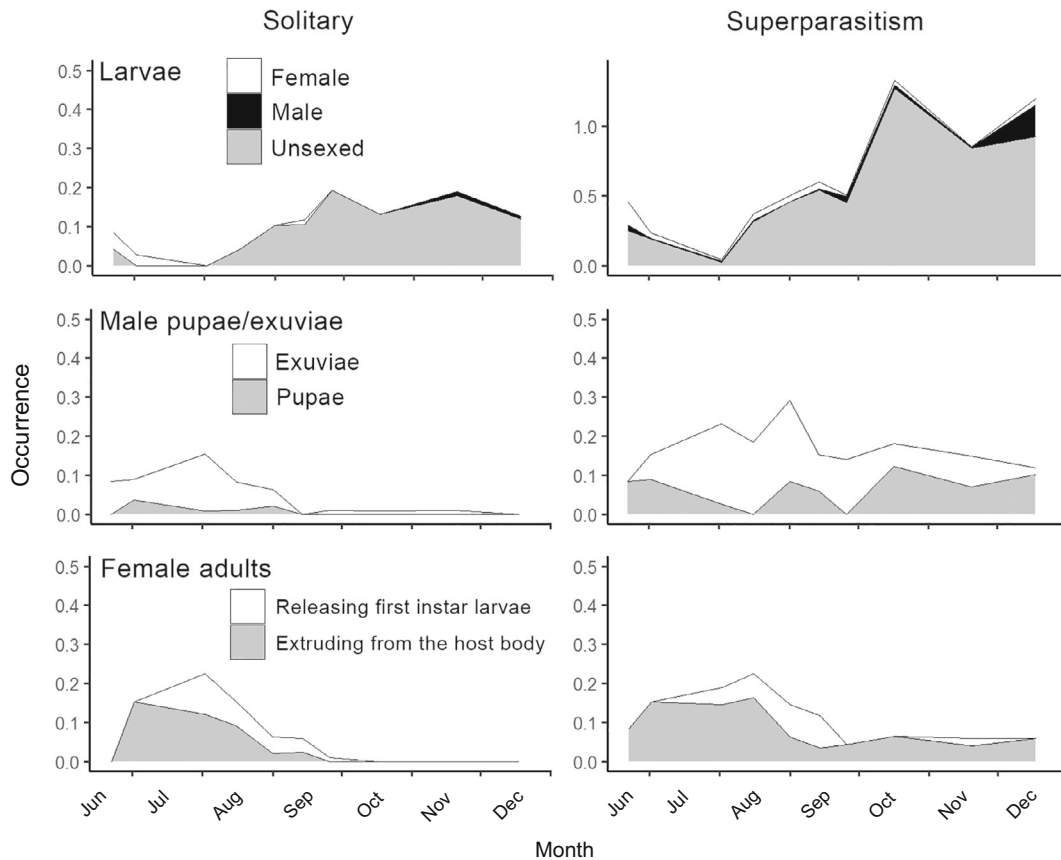


FIGURE 2 Occurrence (number of parasites at each stage: total number of adult hosts) of strepsipteran parasite *Blissoxenos esakii* in their host bug *Macropes obnubilus* in each month of survey. Solitary (left column) data are those obtained from hosts parasitized by a single parasite, whereas the superparasitism (right column) data are those obtained from hosts parasitized by two or more parasites. Very few male or female adults were found in autumn and winter (September–December) in the solitary group, whereas both were abundant during those seasons in the superparasitism group. This result implies that solitary groups remain larvae in autumn and winter, whereas when there are multiple larvae in a host, they continue to develop and emerge as adults during autumn and winter.

generation, but most of this generation died in September. Nymphs of the new generation of *M. obnubilus* emerged in August, and about half of them became adults in September. From September until December, the proportion of adults was always about 50% (details in Appendix S1: Table S1).

From June to August, *B. esakii* adults, including females releasing first instar larvae, were observed in both superparasitized and singly parasitized hosts. *Blissoxenos esakii* adults were abundant only in superparasitized hosts (Figure 2). The ratio of larvae to adults was significantly different between solitary parasitism and superparasitism from 26 September to 18 December (i.e., *M. obnubilus*'s new generation) (superparasitism, larvae 435, adults 89, 17.0%; solitary parasitism, larvae 68, adults 4, 5.56%; Pearson's chi-squared test, $\chi^2 = 6.279$, $df = 1$, $p = 0.0122$) (Figure 2). In November, some adult *B. esakii* females in superparasitized hosts released first instar larvae. During the entire study period, a total of 915

M. obnubilus adults were collected. Among these, 464 (50.7%) were parasitized by a total of 1051 *B. esakii*. Of the parasitized *M. obnubilus*, 204 were singly parasitized and 260 were superparasitized (Appendix S1: Figure S1A). Among the *B. esakii*, 847 (80.6%) were in hosts parasitized by two or more strepsipterans, and 605 (57.6%) were in hosts parasitized by three or more strepsipterans (Appendix S1: Figure S1B). No more than two *B. esakii* had their cephalothoraxes extruding from the host even when the host was superparasitized with three or more larvae (Appendix S1: Figure S1C).

If an individual is to complete its life cycle, it must win the interlarval competition for the limited exit space in a single host. Therefore, it must grow faster than other individuals in the same host to claim an extrusion place. *M. obnubilus* nymphs are always available for parasitizing by strepsipteran larvae. Except for a short period in early summer, about half of the sampled *M. obnubilus* individuals were nymphs (Appendix S1: Table S1; Nakase &

Kato, 2011); thus, when fast-growing *B. esakii* females become adults and release first instar larvae, host nymphs of the same generation are available for parasitism. This allows *B. esakii* to parasitize *M. obnubilus* without having to synchronize its own life history with that of the host. *M. obnubilus* maintains the nymph-to-adult proportion by the previous generation individuals being adults and the new generation being larvae in the summer and half of the new generation growing to adult in the winter.

In winter, when first instar *B. esakii* larvae are released from females, the *M. obnubilus* population still includes nymphs; thus, the larvae can find *M. obnubilus* nymphs to parasitize, but their success rate may be lower because some *M. obnubilus* have already become adults, leaving fewer nymphs available for *B. esakii* to parasitize. Despite this disadvantage of faster growth of *B. esakii* in superparasitized hosts, over 80% of *B. esakii* were in superparasitized hosts as described earlier; thus, for *B. esakii*, superparasitism is not a rare, unfortunate event but is experienced by many individuals. Therefore, the fitness of *B. esakii* individuals having an adaptive strategy for superparasitism (= faster growth) would be significantly improved.

Generally, hosts of solitary strepsipteran females, including those of *B. esakii*, may have a longer life span than unparasitized hosts (e.g., Beani et al., 2021; Kathirithamby, 1978). However, hosts superparasitized by *B. esakii* may die before completing half of their usual lifespan. Although we did not investigate the winter population of the *M. obnubilus* bugs, Nakase and Kato (2011) did and reported that the percentage of superparasitized hosts decreased after February. Their finding suggests that the growth acceleration of *B. esakii* in superparasitized hosts leads to the early death of the host.

Insect growth rates and phenology can usually be explained by photoperiod and temperature (e.g., reviewed in Forrest, 2016). However, we showed that phenological differences among *B. esakii* individuals of the same population experiencing the same environmental conditions, including photoperiod and temperature, exhibited different growth rates and phenology depending on the parasite density per host. Life histories evolve in response to the environment they experience (Stearns, 1992). For example, the size and timing of metamorphosis in amphibians shift with flexibility depending on the predation rate in the habitat (Rowe & Ludwig, 1991). The faster growth of *B. esakii* is also the plasticity of life history for responding to the environment, but is rather extreme, showing changes across life history, such as changing voltinism, which halves generation time. Even if the generation time of *B. esakii* is halved, the host remains univoltine, so the target of parasitism is not the

next generation of the host but the same generation of the host that is currently being parasitized. Furthermore, because *B. esakii* parasitizes *M. obnubilus* nymphs but only starts growing after *M. obnubilus* becomes an adult (Nakase & Kato, 2011), all *B. esakii* larvae in the same host should start growing at the same time. Curiously, the growth stages of *B. esakii* individuals in superparasitized hosts varied from small larvae to adults within the same host in our observation. It has been proposed that all strepsipterans in a single superparasitized host may often be siblings (Vannini et al., 2008). Thus, competitive interactions among *B. esakii* individuals within the same host may have more complex interactions than expected, perhaps related to inclusive fitness.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Nakase et al., 2022) are available in Figshare: <https://doi.org/10.6084/m9.figshare.20055143>.

ORCID

Yuta Nakase  <https://orcid.org/0000-0001-5925-4564>

Tsubasa Toji  <https://orcid.org/0000-0003-4899-3390>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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