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SCAVENGING BEHAVIOR IN LEAF-FEEDING CATERPILLARS

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More than 99% of lepidopteran species are phytophagous (Strong et al. 1984, Pierce 1995). However, larvae of some species are carnivorous (Pierce 1995). For instance, some lycaenids feed on immature insects such as ants and aphids (Pierce et al. 2002), and some Hawaiian geometrids prey on active insects (Montgomery 1983). Cannibalism has also frequently been reported in the larvae of phytophagous moths and butterflies (Richardson et al. 2010). Furthermore, Wang and Daane (2014) observed larvae of a tortricid species eating dead larvae of conspecifics under laboratory conditions. These observations suggest that phytophagous lepidopterans may scavenge on dead insects in the wild. Although larvae of several moth groups, such as tineids, feed on dead animals (Stehr 1987), scavenging by phytophagous lepidopterans has rarely been reported under field conditions. In this study, we investigated the scavenging behavior of four species of leaf-feeding moth larvae in a forest in central Japan.

In May 2013, we observed an outbreak of the gypsy moth *Lymantria dispar japonica* (Motschulsky) (Erebidae) in a secondary forest in Hiraoka-kouen, Higashiosaka City, Osaka, central Japan (34°40′N, 135°39′E). The larvae defoliated many tall trees, causing leaf-feeding caterpillars to move to the undergrowth. Thus, there were many caterpillars and their predators on the ground and guardrails in the forest; the mean densities of *L. dispar japonica* and other lepidopteran species were 2.1 and 0.8 larvae /m^2, respectively (Sugiura & Yamazaki 2014). Our observations were carried out along a hiking trail (900 m long, 2 m wide; 160–290 m above sea level) on May 4, 9, 13, and 18, 2013. Over 20,000 caterpillars (2.9 larvae/m^2 × 1,800 m^2 × 4 days) were observed on the ground and guardrails, although the number of larvae of each lepidopteran species was not counted. We recorded the species of lepidopteran larvae that were observed feeding on insect carcasses. The species and instars of scavenging larvae were identified based on morphology, color, and size (Sugi 1987).

Nine larvae of four species, namely, *Phigalia verecundaria* (Leech) (Geometridae), *Lemyra imparilis* (Butler) (Erebidae), *Orthosia limbata* (Butler) (Noctuidae), and *O. paromoea* (Hampson), fed on dead lepidopteran larvae (Table 1; Figs. 1–6). One *O. limbata* larva fed on the carcass of a conspecific (Fig. 4; Table 1), while the other caterpillars scavenged on dead larvae of other species (Figs. 1–3, 5, and 6; Table 1). All scavenging larvae were late instars. Larvae of these four species primarily eat tree leaves (Sugi 1987), suggesting that they are facultative scavengers. Because only 9 of

TABLE 1. Field observations on the scavenging behavior of lepidopteran larvae.

Family	Species	Larval code	Food item (dead insects)
Geometridae	*Phigalia verecundaria* (Leech)	1	A geometrid larva (Fig. 1)
		2	An unidentified larva
Erebidae	*Lemyra imparilis* (Butler)	3	A noctuid larva (Fig. 2)
Noctuidae	*Orthosia limbata* (Butler)	4	An unidentified larva
		5	A noctuid larva (Fig. 3)
		6	A conspecific larva (Fig. 4)
	Orthosia paromoea (Hampson)	7	A *Wilemania nitobei* larva (Fig. 5)
		8	A noctuid larva (Fig. 6)
		9	A noctuid larva

>20,000 caterpillars were observed to feed on dead larvae, the frequency of scavenging behavior was low. However, the scavenging behavior of the most abundant species, *L. dispar japonica*, was not observed at this study site, suggesting that the frequency of scavenging may differ among lepidopteran species.

On the same dates, we frequently observed predacious insects attacking caterpillars on the ground and guardrails in the forest. For example, adult predacious beetles of the species *Calosoma maximowiczi* Morawitz (Carabidae) and *Dendroxena sexcarinata* Motschulsky (Silphidae) preyed on various lepidopteran larvae (c.f. Sugiura & Yamazaki 2007, 2014, Sugiura 2016). Larvae of the ladybird beetle *Aiolocaria hexaspilota* (Hope) (Coccinellidae) and an unidentified hoverfly (Syrphidae) attacked and ate larvae of several lepidopteran species. Scars on the dead larvae on which four lepidopteran species fed showed that the larvae had been split by insects other than lepidopterans prior to scavenging by the lepidopterans (Figs. 2, 3, 6). Thus, predacious insects such as *C. maximowiczi* may have killed the caterpillars that were subsequently consumed by four species of lepidopteran larvae.

Scavenging behavior has rarely been documented in leaf-feeding lepidopterans. At this study site, such unusual scavenging behavior may have been driven by the recent gypsy moth outbreak, which reduced food sources for many leaf-feeding larvae and increased predator numbers, which in turn increased numbers of dead caterpillars. We did not observe any lepidopteran larvae feeding on dead caterpillars at the study site in

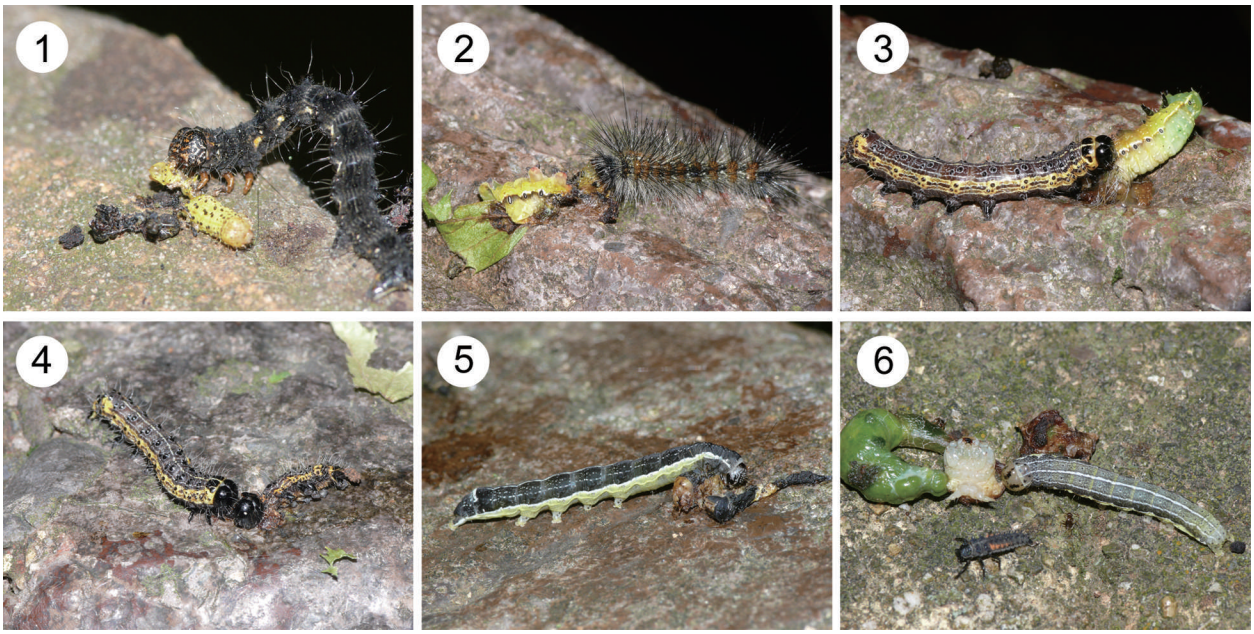

FIG.1–6. Scavenging behavior in four species of leaf-feeding caterpillars. **1.** A *Phigalia verecundaria* larva feeding on a dead geometrid larva. **2.** A *Lemyra imparilis* larva feeding on a dead noctuid larva. **3.** An *Orthosia limbata* larva feeding on a dead noctuid larva. **4.** An *O. limbata* larva feeding on a dead conspecific larva. **5.** An *O. paromoea* larva feeding on a dead *Wilemania nitobei* larva (Geometridae). **6.** An *O. paromoea* feeding on a dead noctuid larva.

May 2014–2016, years during which there were no outbreaks of gypsy moth.

What is the adaptive significance of scavenging behavior in leaf-feeding lepidopterans? Scavenging behavior may increase longevity and growth rate because of the high levels of protein in dead insects (e.g., Richardson et al. 2010; Polis 1981). However, it may also increase the risk of infection with disease (e.g., Rudolf & Antonovics 2007). Further experiments are needed to clarify the benefits and costs of scavenging behavior.

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