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Ivela auripes BUTLER¹⁾ in Hokkaido: Behavior and Morphology
of Females; Host Egg Defense Mechanism against
Parasitism by *Trichogramma* sp. nov.²⁾

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Synopsis *Ivela auripes* (BUTLER) (Lepidoptera: Lymantriidae) is highly stenophagous on *Cornus controversa* HEMSL. (Cornaceae) and univoltine, overwintering as eggs laid in single-layer, geometrically shaped masses on the trunks of host trees. Egg mortality analysis showed 30.5% egg parasitism (8.9 progeny/host; 92% parasitism of egg masses) by *Trichogramma* sp. nov. which was nearly thelyotokous (4.6% males). Parasitized eggs were not evenly distributed throughout the egg mass (81% were perimeter eggs). Similarly, uppermost perimeter eggs were more frequently parasitized than those lowermost in the egg masses.

A gray dust material (precise origin unclear) covers the exposed surface of the egg mass and the dust appeared as a barrier to *Trichogramma* oviposition in non-perimeter eggs. The source of the dust and morphological adaptations to facilitate dust acquisition and storage was explored.

Ivela auripes females, but not males, both normally diurnal, were observed to fly at night and were attracted to street lights.

The stenophagous yellow-legged tussock moth, *Ivela auripes* (BUTLER), occurs in Japan, Korea, and China, and it reportedly feeds on leaves of *Cornus controversa* HEMSL., *Cornus brachypoda* C. A. MEY., *Styrax japonica* SIEB. et ZUCC., and *Styrax obassia* SIEB. et ZUCC. (INOUE, 1956). It is univoltine with eggs overwintering on the trunks of host trees. Eggs hatch about mid-May in Hokkaido and larvae ascend the trees and feed on leaves of *Cornus controversa* in Hokkaido. During the mid-1970's, the moth populations increased to the point that individual host trees scattered through the deciduous forests were defoliated annually. By late June to mid-July, the diurnally active adults appeared and both sexes flew about the canopy fluttering around individual *Cornus* trees. Oviposition occurred on the smooth bark of host trees where the geometrically shaped, single layer egg masses are covered with a gray dust material.

Information on *I. auripes* is generally scattered. Brief bibliographies can be found in SHIRAKI (1952) and FOREST RESEARCH INSTITUTE (Seoul) (1969) while

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4) Relocation to Seoul, Republic of Korea, occurred in 1981.

INOUE (1956) provides a taxonomic bibliography. Parasites of *I. auripes* are listed in YASUMATSU and WATANABE (1965) but no egg parasites are recorded.

As *I. auripes* often occurs sympatrically with the gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae), a study was made to determine if any egg parasites were common to both these related species.

Observations on the morphological structure of the female genitalia as it applies to the source of the gray dust material covering egg masses, the preoviposition behavior of females, and the nocturnal flight of females are included herein but information presented concentrates mainly on parasitism in the overwintering eggs by a well synchronized *Trichogramma* sp. nov.⁵⁾ (Hymenoptera: Trichogrammatidae) (hereafter referred to simply as *Trichogramma*).

Methods

Preliminary examination of old *I. auripes* egg masses, which remain attached to host trees for several seasons, showed evidence of the emergence of a small egg parasite. To clarify the mortality factors which occurred during the egg stage, 3 *C. controversa* trees were felled in a forest on the lower slopes of Mt. Teine, Sapporo, during March 1979. Felled trees were cut into 1 m lengths and returned to the laboratory where the numbers of new and old egg masses were counted. All new egg masses were removed and the eggs counted and isolated in vials. The individual egg masses were processed by submersion in commercial bleach (Bright brand, Lion Oil & Fat Co., Ltd, Tokyo)⁶⁾, which contained a negative ion surface activating agent, diluted 1:9 parts water. Allowed to stand in this solution for 8–12 hours at room temperature, the eggs separated, cleared, and the chorion partly dissolved which left the contents (unhatched larvae or parasite aggregations) floating free in solution. *Trichogramma* parasites were still in their larval stage and masses of larvae from individual eggs adhered together. One or 2 parasite aggregations from each sample were removed and dissected to determine the number of parasites per host egg.

Ten old egg masses were removed from each 1 m length and examined under a dissecting microscope. Inasmuch as emerging caterpillars normally leave a crescent-shaped emergence hole, successful host larval hatch was determined by counting the number of eggs with characteristic crescents. Likewise, unhatched eggs and eggs with small circular holes indicative of parasite emergence were counted. These data permitted an estimation of overall generational egg mortality and ap-

5) Identified as an undescribed species by Carl E. GOODPASTURE, subsequently confirmed by Akey C. F. HUNG and PANG Xiongfei (visiting scientist from South China Agric. College, Guangzhou, PRC), all at USDA, Insect Identification and Beneficial Insects Introduction Laboratory, Beltsville, Maryland 20705, U.S.A.

6) Mention of a proprietary product does not constitute endorsement by the U.S. Dept. Agriculture.

parent overwintering survival. During examination of these egg masses, the positions within the egg masses of parasite killed eggs were recorded.

Periodic collections of egg masses were made April through June to determine parasite development and emergence.

Observations were made on *I. auripes* during the flight periods 1978–79 and on one occasion females were collected at street lamps, frozen, and subsequently examined morphologically. Dust, covering the egg masses, was collected from females and egg masses for microscopic examination.

On several occasions, recovered parasite females were provided with dehaired eggs of *L. dispar* to determine acceptability of this potential host.

Observations on the attempted oviposition by *I. auripes* on *Styrax obassia* were made at the Hokkaido University, Botanical Gardens, in Sapporo. Leaves of *S. obassia* were presented to small numbers of caged *I. auripes* larvae.

Results and Discussions

Female Anatomy, Ovipositional Behavior, and Host Utilization

Examination of frozen females revealed the source of the gray dust material which covered the egg masses. Located in the tip of the abdomen were paired sac-like structures or “dust sacs” with large external openings just laterad of the gonopore (Fig. 1). A dry dust-like gray material was present in these paired sacs. Examination of teneral adult females showed these same sacs to be empty and partially deflated. The gray dusty material was thus acquired during the preovipositional period. On July 15, 1979, several females of *I. auripes* were observed positioned on trunks of *C. controversa* and they exhibited an unusual side-to-side motion of the body. This motion did not resemble typical ‘calling behavior’ of *L. dispar*. Since these females readily took flight when disturbed, careful approach and close observation showed these females were not ovipositing but were rubbing (hereafter called “rasping”) the tree surface with their genitalia.

Integrating the field observations and the apparent function of the female’s external genital structures, led to the supposition that during the preovipositional period, females rasped the tree surface to obtain the gray dust which was later used to cover the egg masses. The morphological structure apparently responsible for scraping the surface is the “rasper” (Fig. 1, B4) with many stiff protrusions, and any dislodged particles were perhaps collected by numerous recurvate setae surrounding the entire external genitalia. By some unknown mechanism, the gray dust accumulated in the dust sacs through the large openings (Fig. 1, B3) for storage until the act of oviposition. During egg laying, eggs were obviously first glued to the tree surface and then the dust was extruded or blown onto the newly laid eggs. The dust adhered to the eggs and formed a protective covering over the entire mass.

The dust within the dust sacs of dissected gravid females was completely dry and powdery. Initially, the dust would float on a water miniscus and would not

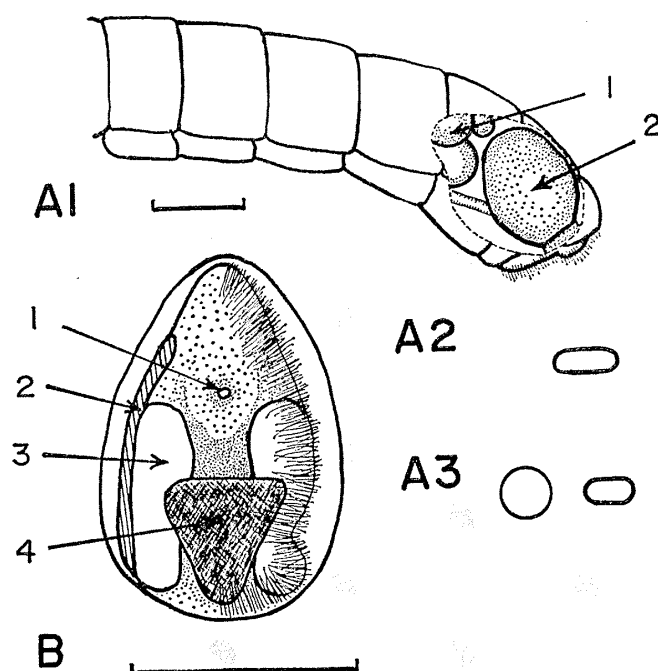


Fig. 1. Female *Ivela auripes* abdominal anatomy. Lateral view of abdomen (A1) with cutaway section in posterior segments showing matured ova (1) and one of the paired internal "dust sacs" (2). Outline of dust sac opening (A2) and mature ova (A3) at same scale as abdomen (A1). Ventral view of external genitalia (B), illustrating gonopore (1), lateral rim of ovipositor lobe removed (2), opening of dust sac (3), and "rasper" (4). Setae illustrated only on right half of figure (B). Both scales indicate 2 mm.

wet readily. Following shaking of the vial, the dust would mix with water but would eventually settle to the bottom on standing. Microscopically, the dust appeared as irregular shaped, crystal-like, abrasive particles, transparent to visible light, and up to 24 microns in size, but most were considerably smaller. The precise origin of the dust is unclear. It is hypothesized that it is inorganic dust which adheres to the trees or originates as products of cryptogamic flora, i.e. lichens, which occur on the host tree trunks.

Although the recorded host tree, *Styrax obassia* only grows naturally in the extreme southern areas of Hokkaido (not in the Sapporo area), Tosio KUMATA, Entomol. Institute, Hokkaido University, kindly brought it to my attention that in the Botanical Gardens of Hokkaido University no oviposition or larval feeding by *I. auripes* occurred on one tree of *S. obassia* although adjacent *C. controversa* trees were noticeably damaged by feeding larvae. Although *S. obassia* could be mistaken for *Cornus* due to gross similarities, it appears that the record of *S. obassia* as a host plant (INOUE, 1956) is questionable. In attempts to force *I. auripes* larvae to feed on *S. obassia* leaves, all larvae died without feeding. Either *Styrax* spp. are acceptable in other geographical areas or are unacceptable host trees; in either case, further clarification is needed. In Sapporo, the *S. obassia* was un-

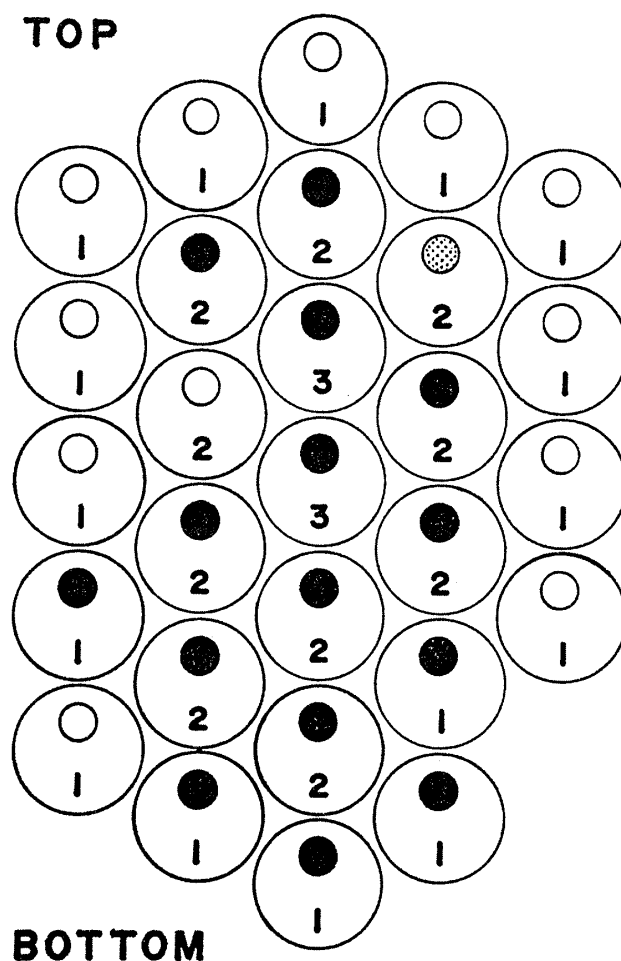


Fig. 2. Diagrammatic representation of an actual *Ivela auripes* egg mass illustrating characteristic geometric shape, actual *Trichogramma* parasitized eggs, and the ranking scheme (RR number 1, 2, etc. substituted for I, II, etc. used in text) designating eggs within a mass. Open circles denote parasite emergence, closed circles successful host emergence, and stippled circles indicate mortality from unspecified causes.

acceptable as a host for *I. auripes*.

Egg Mass Size and Distribution

Egg masses averaged 54.6 eggs per mass (SD=26.15, N=173, Max. 127) and were arranged in geometrical shapes made up of from 3 to 8 columns of closely packed eggs. Figure 2 diagrams one actual egg mass with 5 egg columns.

Within tree stratification showed that the greatest number of egg masses were positioned between 1 and 3 m on the tree trunks (Fig. 3). The intergenerational disparity between 'old' and 'new' egg masses suggests a loss of some old egg masses from the trees as a result of mechanical abrasion during settling by accumulated snow which may reach 2 m in depth by late winter.

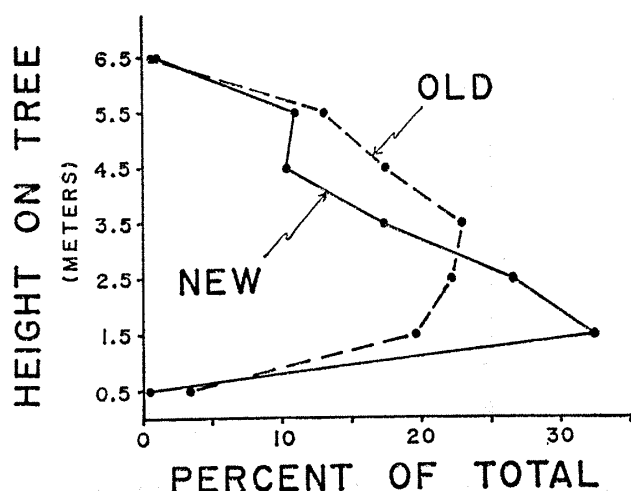


Fig. 3. Mean height above ground of *Ivela auripes* egg masses of previous generation (Old or egg masses with empty or dead eggs) and current generation (New or egg masses with live embryonated hosts or parasite larvae) on *Cornus controversa* trunks at Teine, Sapporo, Hokkaido, Japan. Data from 3 trees ($\bar{x}$ = 12.0 cm diameter breast high, ca. 21 years of age) felled in March 1979 when 1.1 m snow cover remained. Data at 6.5 m from 1 tree only. Old N=1619, New N=172.

Egg Parasitism

Two egg parasite species were recovered. *Trichogramma* was common and in some egg masses caused significant mortality. *Trichogramma* developed gregariously with 8.86 larvae/host egg (SD=1.36, N=300, Max. 13). Over 66% of all parasitized eggs contained 8 or 9 larvae of *Trichogramma* and progeny were nearly unisexual with 4.6% males among emerging adults. Emergence of adults first occurred in mid-July closely synchronized with the beginning of the host's ovipositional period. All evidence indicated that *Trichogramma* was univoltine. Overwintering occurred as larvae within the host eggs.

Trichogramma accounted for 30.5% egg parasitism overall while 92.5% of the 173 current season's egg masses contained *Trichogramma*. Overwintering egg mortality was generally less than 13% (Fig. 4). Parasitism did not vary appreciably from ca. 30% mean parasitism, regardless of height on the tree (Fig. 4). This lack of any height preference indicated that the parasite was equally efficient at host utilization at all heights on the trees.

This undescribed species of *Trichogramma* was taxonomically different from *Trichogramma ivelae* PANG et CHEN, which attacks *Ivela ochropoda* EVESRMANN and other species in China (PANG & CHEN, 1974). Apparently both *Trichogramma* species occupy similar niches by attacking congeneric host species in different geographical areas.

Exposure of female *Trichogramma* to eggs of *L. dispar* showed that females were certainly interested in these unnatural host eggs but no successful stinging and progeny development occurred.

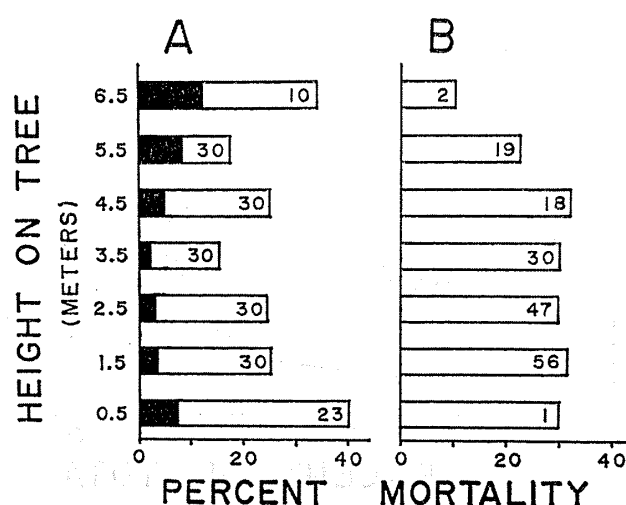


Fig. 4. Mean mortality in eggs of *Ivela auripes* at Teine, Sapporo, Hokkaido, Japan, based on previous generation(s) (A) or overwintered generation as of March 1979 (B). Shaded area indicates unknown mortality within the egg while open bar denotes apparent parasitism based on emergence holes in (A) or on presence of gregarious larvae of *Trichogramma* sp. in (B), following extraction from eggs with bleach solution. Number of masses included in mean is indicated at the end of each bar.

One single specimen of *Telenomus* sp.⁷⁾ (Hymenoptera: Scelionidae) was recovered from *I. auripes* eggs.

Intramass Distribution of Parasites

Preliminary observations indicated that parasitized eggs were not distributed evenly throughout the egg mass. Eggs positioned at the top (perimeter row) of each column (see Fig. 2 as one actual example) were more likely parasitized than those eggs at the bottom (63.3% vs. 32.2% parasitism, $X^2=88.7^{**}$, $P\ll 0.001$) based on the analysis of 141 egg masses from previous generations which had contained parasites.

Further analysis of these selected egg masses was a record of the position of each parasitized egg within the mass. Since the eggs were packed in closely appressed columns, numbering from 3 to 8 columns (mean=5.4), the shape of each mass determined the number of eggs exposed on the perimeter, one row removed from the perimeter, 2 rows, etc., was dependent on the total number of eggs in that egg mass and on the number of columns composing that mass.

Using models within the range of egg mass size (3 to 8 columns, 10 to 80 total eggs), the expected number of eggs in row rank (RR) I, II, III, and IV (perimeter row, adjacent to perimeter row, etc., respectively) was determined as the mean of each number in RR for each possible number of packed rows at intervals of 10, up to 80. These calculations produced an expected percent of the total eggs to fall

7) Identified by Kazuaki KAMIJO, Hokkaido Forest Experiment Station, Bibai, Hokkaido, Japan.

Table 1. Intramass distribution and comparison of expected and actual percent egg parasitism by *Trichogramma* sp. in *Ivela auripes* egg masses.

Row Rank (RR)	Av. Expected Percent ^a	Actual Distribution of Parasitized Eggs		Expected Number ^b
		Number	% of Total	
I (Perimeter)	46	1520	81.1	862
II	31	243	13.0	581
III	16	104	5.5	300
IV	7	7	0.4	131
Total		1874		(1874)

a. Based on sphere packing model. Average is derived from calculations of the results of from three to eight simulated columns totaling from 10 to 80 spheres at each 10 sphere interval and corrected to the nearest whole percentage point. b. Based on average expected percent of spheres in row rank category. Chi squared testing ($X^2=944^{**}$, $P \ll 0.001$) supports the rejection of the H_0 that parasitized eggs were distributed evenly throughout the row rank categories, although there is very uneven distribution of packed spheres (Column 2).

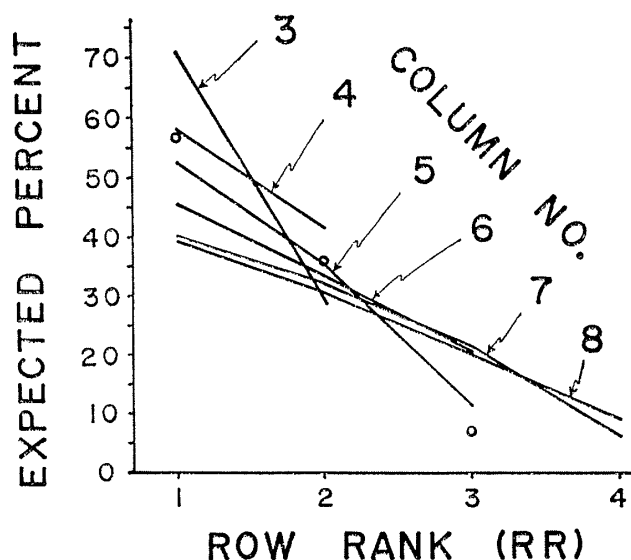


Fig. 5. Expected percentage of packed spheres simulating eggs of *Ivela auripes* among Row Rank (RR) based on the number of columns making up the entire egg mass. Data for *I. auripes* egg mass illustrated in Fig. 2 is plotted (open circles) for illustration.

within each RR, as plotted in Fig. 5. As an example, in one 3-column egg mass, 72% of all eggs were in RR I (=perimeter) with all remaining eggs centrally located in RR II. Similarly, up to 8-column egg masses were partitioned into RR categories.

Parasitized eggs in the 141 masses tended to concentrate around the perimeter since 81.1% of 1874 parasitized eggs were positioned in RR I (leaving 18.9% of internally located eggs parasitized), but based on the model only ca. 46% of eggs

were RR I eggs (Table 1). *Trichogramma* parasitized those eggs on the perimeter (RR I) much more frequently ($X^2=944^{**}$, $P\ll 0.001$) than internally positioned eggs (RR II and up). Figure 2 also shows the intramass distribution of parasitized eggs in one exemplary egg mass in which 56% (11 of 16) of the RR I eggs were parasitized, while 10% (1 of 10) and 0% parasitization occurred in RR II and RR III respectively.

Flight Behavior

During the flight period of the diurnally active *I. auripes*, large numbers of adults were observed flying about street lights just south of Asahikawa, Hokkaido. At about 2200 hrs. 10 July 1978, numerous *I. auripes* swarmed about the street-lights and 138 were netted. Examination revealed that every individual was a female. Therefore, contrary to a statement by INOUE (1956), at least females will fly about lights at night. It was unclear how far these females had flown to reach the lights. Female nocturnal flight may represent an important means of population dispersal. Differential attraction to the lights by the 2 sexes was apparent by the conspicuous absence of males at these lights.

Conclusions

Evidence presented illustrates that *Trichogramma* selects for oviposition, eggs positioned on the perimeter of an egg mass. Such a distribution was believed related to the absence, or diminished quantity, of gray dust. Individual eggs in intact masses were well concealed in a line of sight perpendicular to the tree trunk surface. Visible eggs were those on the perimeter of the egg mass (RR I) where the deposition of gray dust covered the top surface but left the sides of these same eggs exposed as viewed from an oblique angle. From the intramass distribution of parasitized eggs, there appeared to be an ovipositional deterrent quality to the gray dust adhered to the nonperipheral eggs. Perhaps the parasites were physically unable to recognize host eggs below the dust layer or unable to insert their ovipositors through the abrasive dust. The composition of this dust remains unknown but it not only camouflaged the eggs (presumably as a deterrent to predators) but in some way protected eggs from ovipositing *Trichogramma*. In spite of the protection the dust may have given to some underlying host eggs, *Trichogramma* was a well adapted egg parasite of *Ivela auripes* in Hokkaido.

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