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Oviposition behavior in the Australian stick insect *Extatosoma tiaratum*

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Summary. The Australian stick insect *Extatosoma tiaratum* (MacLeay) (Insecta: Phasmida) oviposits by throwing the eggs to a distance of circa 0.80–2.00 m by a strong flick with the abdomen. The initial speed is circa 2.7 m/sec. The rather immobile female just drops her feces, and as these may act as olfactory attractants to predators, the eggs that are flicked away will be safe, lying in a ring around the central deposit of feces.

Different types of oviposition are known to occur in the stick- and leaf-insects (Phasmida)[1], but little is known about the mechanism and biological significance of these. Eggs may be passively dropped, actively flicked away, glued singly or together, stuck into parts of plants, placed singly or together on a substrate. Only a few species are known to flick away their eggs[2–6]. The distance which the egg is thrown varies from 6–8 cm in *Bacillus rossius* (Rossi) to 5–6 m in *Phasma gigas* (Linné)[3,5,6]. In this paper the oviposition in the Australian stick-insect *Extatosoma tiaratum* (MacLeay) is considered.

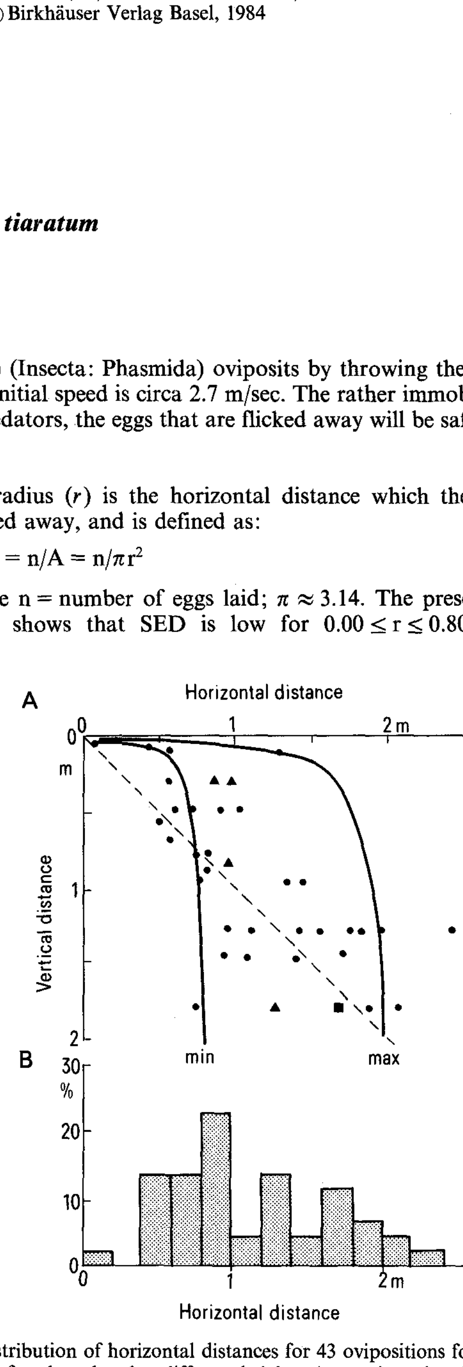
Material and methods. The adult female *E. tiaratum* is a large insect, length and mass of body, 105–130 mm and 10–20 g[7]. The egg is more or less round; height, 3.50–4.50 mm; width, 2.50–3.50 mm; mass, 37–40 mg[8,9]. Females were placed upside-down in their normal resting and ovipositing position on twigs, supplied with leaves of *Quercus robur* Linné. The twigs were arranged at various heights. 5-cm-high obstacles with a 10-cm-distance between them were placed on the ground, giving a ±5 cm range of measurements. The ordinary Newtonian formula for 2-dimensional motion with constant acceleration was used, assuming an inclination angle of 0°.

Results and discussion. When comparing the distance that the eggs were flicked by females placed at different heights (fig. A), a dispersal could be observed, but minimum and maximum limits could be estimated at 0.80 and 2.00 m, respectively. The large length values from low heights show that the females are capable of throwing the eggs long distances from low initial heights. This suggests an inclination angle somewhat larger than 0°, giving a small incline in the initial phase of oviposition. The initial speed was around 2.7 m/s (range: 0.49–7.17 m/s, $\bar{X} \pm SD$: 2.68 ± 1.11 m/s, CV: 42%, n: 43). Since the eggs are thrown away by a strong flick of the abdomen, some of the variations observed (fig. A) could be due to different body-lengths. When comparing the ratio d/bl (d = distance which the egg is thrown away and bl = bodylength) the following results were obtained: 8–15 for *E. tiaratum* (bl = 105–130 mm), 24–36 for *Phyllium bioculatum* (bl = circa 84 mm) and 26–32 for *P. gigas* (bl = circa 190 mm)[3,7]. However, authors reporting distances without describing the experimental conditions must be taken with a pinch of salt, since the egg may well continue to roll along on the ground after landing, and therefore no intepretation can be made of the results.

The surface egg density (SED), previously discussed[1] as the biological reason for flicking away the eggs, states that the immobile female[10] is in the center of a circular area (A), where the radius (r) is the horizontal distance which the eggs are flicked away, and is defined as:

$$SED = n/A = n/\pi r^2 \qquad (1)$$

where n = number of eggs laid; $\pi \approx 3.14$. The present results (fig.) shows that SED is low for $0.00 \leq r \leq 0.80$ and for



A Distribution of horizontal distances for 43 ovipositions for 12 *E. tiaratum* females, placed at different heights. Approximately minimum and maximum limits for the 2-dimensional motion have been indicated, 'min' and 'max' respectively. The dotted line represents the slope of – 1.00. Explanations of symbols used: ●, 1 observation; ▲, 2 observations; ■, observations.

B Percentage distribution of horizontal distances. When summing all primary data from *A* the lower values become overrepresented ($\bar{X} \pm SD$: 1.13 ± 0.51 m, CV: 45%, n: 43). When excluding some of these lower values, a new distribution was found ($\bar{X} \pm SD$: 1.35 ± 0.49 m, CV: 33%, n: 28). Furthermore, it was not stastistically significantly different from the original population (t = 1.866, df: 69, $0.050 < p < 0.025$).

$r \geq 2.00$, and highest for $0.80 \leq r \leq 2.00$ m, and therefore SED should be estimated for the circular ring area, as follows;

$$SED_{cra} = n/\pi \, (r^2_{max} - r^2_{min}) \quad (2)$$

The difference between a complete circular area i.e. $0.00 \leq r \leq 2.00$ m and the cra $0.80 \leq r \leq 2.00$ m is not very large. Assuming $n = 100$ eggs (i.e. a normal egg-production during a 2-week period) the difference is 1.5 eggs/m^2, which is a large numerical difference but a small biological difference during a 2 week period.

The explanation given previously[1], based on the SED theory, only stated that the flicking-away of eggs could have advantages in making it more difficult for a predator to locate the eggs deposited by a more-or-less immobile female. Now further explanations can be given. In *E. tiaratum* (and probably in other Phasmida as well) the feces are just dropped, and not flicked away like the eggs. Furthermore, the 'bad' feeding habits of phasmids often results in the dropping of large fragments of leaves on to the ground below[10]. It is very likely that these somewhat moist residues can act as olfactory attractants to predators. Therefore the eggs lying in a circular ring outside the centre of feces and food-plant residues, will be safe from predators locating these residues, especially since SED_{cra} is extremely low. Furthermore, the adult female living high up in the canopy will also be safe from this type of predation. The extremely low value of SED_{cra} in centre of the cra is shown in figure B.

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A mild winter delays supercooling point elevation in freeze tolerant *Chymomyza amoena* larvae (Diptera: Drosophilidae)

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Summary. Supercooling point elevation to -3.2 ± 1.3°C among 17 freeze tolerant *Chymomyza amoena* larvae was delayed until January, 1983 in the mild winter of 1982–83 and occurred despite particulate matter in the gut. The larval population in mid-Michigan is polymorphic for both freeze tolerant and freeze sensitive larvae. One substrate, *Malus coronaria* fruits, appears to be a neutral niche supporting both phenotypes in the population.

Insects have 2 basic mechanisms for overwintering survival: they may become tolerant to freezing or they may remain freeze intolerant and rely on supercooling to maintain body fluids in the liquid state. Freeze tolerant (FT) insects may actually elevate the supercooling point (SCP) in winter to hasten freezing[2–8]. Insects which remain freeze sensitive (FS) need to reduce the chance of innoculative freezing and so may lower the SCP or adopt means to mask or eliminate nucleators[9–16]. These insects remain susceptible to innoculative freezing induced by food in the gut[10, 14–16], so usually evacuate the gut prior to entering diapause[10]. Insects which are freeze tolerant are able to survive freezing despite particulate matter in the gut[8, 9, 16]. One species was found to show a shifting polymorphism between FT and 50% FS types in a severe winter but in mild ones many larvae remain FS[11, 17].

Chymomyza in the family Drosophilidae overwinter as larvae[18–22]. *C. costata* larvae diapause and evacuate the gut, as expected[20]. *C. amoena* larvae appear to be among the dipteran species that have no obligate diapause[21, 23].

C. amoena is the first drosophilid overwintering in the larval stage to be studied in the natural environment. In mid-Michigan this species has now been found to breed successively in endemic crabapples, *Malus coronaria*, in spring, apples in summer, and pears, apples, ornamental crabapples, black walnuts and endemic crabapples in autumn. The latter 4 are overwintering niches. It also manifests polymorphism for freeze tolerant and freeze sensitive types.

A feeding polymorphism seemed indicated[3]. Larvae in frass (insect excreta) or around the apple seed were found to be potentially FT, those in apple flesh were FS and were eliminated by November while SCPs among the FT group elevated to -4°C. Numbers were low. Larvae found in walnuts *(Juglans nigra)* in January continued to be FS with an average SCP of -14°C[22].

The ability to sample larvae from a variety of substrates from spring through winter of 1982–83 has provided more data on larval cold hardiness. Additional contrasts with *C. costata* and other species emerge. Among 17 FT larvae SCPs elevated to -3.2 ± 1.3°C in all substrates and despite the presence of food in the gut. This was delayed until January, 1983 during the mild 1982–83 winter[24]. However, the population is polymorphic for both FT and FS larvae. *Malus coronaria* fruits appear to act as a neutral niche for both phenotypes which can manifest differential survival in other substrates as apples and walnuts. The probable genetic mechanism underlying the polymorphism remains unknown.

Materials and methods. Larvae were sampled from endemic crabapples, *Malus coronaria;* apples; ornamental crabapples and black walnut husks, *Juglans nigra.* In late May the potential cold hardiness characteristics of larvae 3 mm, 3.5 mm and 4 mm in *M. coronaria* fruits were determined to compare 2nd and 3rd instar larvae. By late June females oviposit in apples. Later in summer this niche is shared with *Drosophila melanogaster* and *D. simulans* larvae as are ornamental crabapples[25, 26]. *C. amoena* can readily be distinguished from other drosophilids or pest larvae as *Rhagoletis pomonella.*

In May, 27 softened overwintered *M. coronaria* fruits and in June, 21 small green apples were collected, inspected for *C. amoena* eggs, kept at 22°C and 3 each were dissected for larvae several weeks later. All other cold hardiness determinations were ideally made on larvae taken from substrates either the same day substrates were collected (September, Oc-